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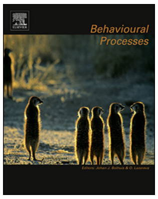

Perception of predation risk by African giant pouched rats (*Cricetomys* sp. nov) is higher in forest-edge microhabitats

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ABSTRACT

How rodents perceive predation risk may alter their seed foraging behaviour and therefore potentially influence the recruitment of tree species. In this study we used two methods to investigate the effect of predation risk on habitat use by the African giant pouched rat (*Cricetomys* sp. nov) in Ngel Nyaki forest reserve, Nigeria. The first method was ‘giving up density’ (GUD), an index of perceived risk of predation at an artificial food patch, and the second was the ‘spool-and-line’ approach, whereby unravelling spools attached to rodent bodies are used to trace their tracks. For our GUD experiment, we chose four major sites in the forest; two representative of core habitat and two at the forest edge. Additionally, three characteristic microsites were used in the GUD experiment: dense understory, open understory and near-burrows. We hypothesised that GUDs would be lower on every succeeding observation day as rats learn to use the food patches, higher GUDs would be observed in the forest edges and open microsites, and rats would show preference for the microhabitats with least exposure to potential predators. In support of our first hypothesis, we found that GUDs were highest on the first experimental nights of every session. We also found that GUDs in the forest edges were higher than GUDs in the forest core. Lower GUDs were observed close to the rat burrows and in dense understory microsites, even though these differences were not statistically significant. Tracking of rat movements using the spool-and-line method overall revealed an even use across microhabitats, with a weak preference for those with logs, dense understory or exposed ground. Overall, our results suggest that vegetation density on a microhabitat scale has little or no effect on the perception of predation risk by African giant pouched rats.

1. Introduction

For most terrestrial birds and mammals, vegetation structure is important because of its direct or indirect effect on food abundance, as well as detection and avoidance of predators (Whelan & Maina, 2005; Abu Baker and Brown, 2010, 2014; Molokwu et al., 2010; Coleman and Hill, 2014). To avoid predation animals often show preference to foraging in or near habitats with thicker vegetation cover than those with sparse or no vegetation (Kotler et al., 1991; Hughes and Ward, 1993; Brown et al., 1998; Brown, 2000; Morris and Davidson, 2000; Mohr et al., 2003; Oyugi and Brown, 2003; Whelan and Maina, 2005; Molokwu et al., 2010).

The patch use theory (Charnov, 1976; Brown, 1988) has been widely tested and accepted as a means of understanding how animals perceive predation risk (Bedoya-Perez et al., 2013). Based on this theory, the number of food items remaining in an artificial food patch (the ‘giving up density’ or GUD) (Brown, 1988) is an index of perceived predation risk. In this theory, a complete set of costs incurred by an optimal forager before leaving a patch are incorporated into a model; the sum of these costs determines the quitting harvest rate (H) as shown below;

$$H = C + P + MOC$$

Where C = metabolic cost, P = cost of predation and MOC = missed opportunity costs (other activities an animal could be involved in instead of foraging in that patch). The quitting harvest rate (H) can be determined by GUD.

Despite the difficulty of teasing apart the individual effects of the C, P and MOC, Brown et al. (1994) successfully demonstrated that P was the major determinant of GUD. While Brown et al. (1994) focused on desert rodents, their general conclusions apply to most other animal species, because the majority of experiments which have not controlled

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for *C* and *MOC* often produced similar results (Brown and Kotler, 2004).

Although predation risk in different habitats can be inferred from GUD estimates, these inferences are more informative when combined with additional indices/techniques such as animal abundance, activity, behavioural responses, forager identity, growth measurements, handling time, morphological adaptations, mortality estimates, age structure, searching pattern, stress level and habitat use (Bedoya-Perez et al., 2013; Gallego et al., 2017). However, obtaining most of these indices/techniques in the field can be expensive and labour intensive, in contrast to the spool-line-line technique (Strauß et al., 2008) and/or camera traps (Glen et al., 2013). The spool and line method basically provide information about habitat use which may be interpreted in diverse ways depending on the context of a research.

GUD studies are most suitable for use with small mammals because of their i) propensity to show an obvious response to perceived predation risk, ii) tendency to spend time at food sources and iii) ability to select habitats (Brown, 1992; Bouskila, 1995; Arcis and Desor, 2003; Apfelbach et al., 2005; Abu Baker and Brown, 2014; Wasko et al., 2014). The ability of rodents to locate food via olfaction, vision and other sensory cues allows them to make unbiased estimates of the resource density in a patch prior to exploitation (Valone and Brown, 1989). Based on their highly efficient foraging strategies, high perception of predation risk and ability to remember rewards, most rodents can be categorised as Bayesian or prescient foragers also known as the 'smarter' and 'smartest' foragers respectively (Brown, 1999; Olsson and Brown, 2006, 2010). Bayesian and prescient foragers are able to make good decisions about the exact time to leave a patch. However, what sets prescient foragers apart is that they have immediate and continuous knowledge about the quality of a food patch (Olsson and Brown, 2010), meaning they can frequently return to a more rewarding patch that has a lower level of risk.

The most recurrent results in the majority of GUD studies involving small mammals show that open microhabitats, farther away from cover usually have higher GUDs while those close to cover have lower GUDs (Brown and Kotler, 2004). Foragers will leave lower GUDs when they are close to safety, which may be near burrows for some rodents e.g. the thirteen-lined squirrel *Spermophilus tridecemlineatus* (Thorson et al., 1998).

While most GUD studies demonstrate the importance of cover in the perception of predation risk by small mammals, a few have identified the effect of macro habitats e.g. forest edges and forest interiors on GUDs (Bowers and Breland, 1996; Wolf and Batzli, 2004; Van Der Merwe and Brown, 2008; Abu Baker and Brown, 2010). Risk of predation is often higher for small mammals at the forest edges because the scarcity of tree seeds in such habitats may increase their chances of encountering predators while foraging (Wolf and Batzli, 2004). However, Morán-López et al. (2016) theoretically argued in that degraded forest edge-habitats may be more abundant in food resources for small mammals thus lowering their seed predation and indirectly supporting plant species recruitment (Charles et al., 2019).

Given the large proportion of GUD studies that have focused on small mammals around the world, it is surprising that tropical rodents are grossly underrepresented (Menezes et al., 2017). From the few studies carried out in the tropics, it has been demonstrated that the perceived predation risk by small rodents was influenced by the presence of a predator cue (Cremona et al., 2014; Wasko et al., 2014), a light source (Bengsen et al., 2010) and vegetation density (de Arruda Bueno and Motta-Junior, 2015; Menezes et al., 2017). There is however, little or no information on the perception of predation risk by Afrotropical small mammals and this information may be useful in species and ecosystem conservation.

Considering the dramatic degradation of Afrotropical forest ecosystems (Ahrends et al., 2010; Craigie et al., 2010), scatter-hoarding rodents may be important in bridging seed dispersal gaps but little is known about their behaviour. The African giant pouched rat (*Cricetomys* sp. nov), being a nocturnal scatter-hoarding rodent is potentially useful in dispersing large-seeded species owing to its large size (Aliyu et al., 2014; Seltzer et al., 2015; Yadok et al., 2018, 2019). However, the presence of predators may indirectly affect the foraging behaviour of this rat thereby having an indirect effect on seed dispersal patterns within forests. In this study, our aim was to investigate the effect of predation risk on microhabitat use by African giant pouched rats (*Cricetomys* sp. nov, hereafter referred to as *Cricetomys*) in a West African montane forest—Ngel Nyaki forest Reserve. The potential predators for *Cricetomys* in Ngel Nyaki forest include African Civets (*Civettictis civetta*), African golden cats (*Caracal aurata*), barn owls (*Tyto alba*) and snakes (Yadok, 2018). We predicted that i) the rats will learn to recognize and remember food locations resulting in lower GUDs in each patch after each day of replenishment ii) GUDs will be higher in forest sites that are closer to forest edges than interior forest sites because there are potentially higher chances of encounter with predators at the forest edges than in the interior or food abundance is higher at the forest edge than interior assuming that the rats remain in their small home ranges iii) GUDs will be lower in microhabitats with dense understory vegetation if predators attack in the open or vice versa if ambush predators occur in dense understory vegetation iv) the features of microsites used by *Cricetomys* would be characteristically different from features of microsites that are most commonly available if *Cricetomys* show strong preference for microhabitat types. We expected that *Cricetomys* would show a preference for microsites with features that allow escape from predators (e.g. dense understory herb cover if the predators avoid such microhabitats or burrows) by using such sites more frequently than their availability relative to other microsites

2. Methods

2.1. Study site

Our study area was Ngel Nyaki Forest Reserve (7°5′N, 11°3′E; hereafter referred to as NNFR) in Taraba State, Nigeria. NNFR is part of the Mambilla Plateau on the Nigeria-Cameroon border; this Plateau has an elevation of ~ 1650 m asl and is mostly covered by grasslands (Adewoye et al., 2015). Although much of NNFR is grassland, several riparian forest fragments and two large continuous forest patches also occur in the reserve. The plant community in the continuous forest patches of NNFR is more diverse than any other sub-montane forest in Nigeria and consequently there is also a high diversity of animal species (Chapman et al., 2004). Mean monthly temperatures during the wet and dry seasons are 13 °C–26 °C and 16 °C–23 °C respectively (Matthesius et al., 2011). The dry season typically lasts from the end of November to March while the rest of the months are characteristically wet. The mean annual rainfall is approximately 1800 mm (Nigerian Montane Forest Project, weather data).

Our studies were limited to the continuous forest because our study species (*Cricetomys* sp. nov), a close relative of *Cricetomys emini* (see Olayemi et al., 2012), rarely occurs in other habitats of NNFR (Yadok, 2018). Two sites were selected in the largest continuous forest of NNFR (Fig. 1). The first site was a 20.28 ha plot of the recently established Centre for Tropical Forest Science-Forest Global Earth Observatory (CTFS-ForestGEO; www.forestgeo.si.edu). The CTFS plot in NNFR is among a network of 63 plots designed to produce worldwide comparable data on tree species distribution. Within the CTFS-ForestGEO plot, every tree with a diameter at breast height (DBH) > 1 cm was mapped. The second site had a similar forest composition and was sufficiently distant (> 700 m) from the first site, for the sites to be independent for studying rat behaviour (Strauß et al., 2008).

2.2. Ethical note

This research work was approved by the Nigerian Montane Forest Project (NMFP), an affiliate of the University of Canterbury, New Zealand, hence animal ethics standards of the University of Canterbury

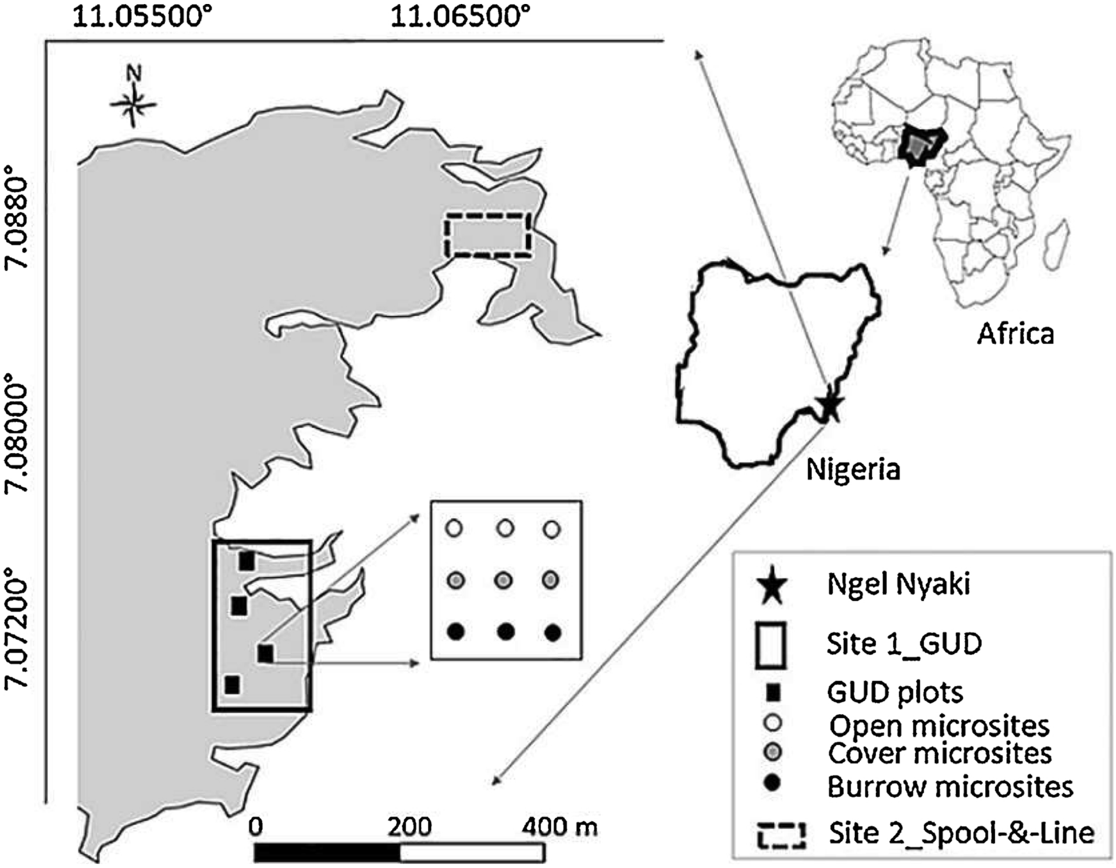

Fig. 1. Study areas in part of the largest continuous forest (large grey area) in Ngel Nyaki Forest Reserve, sites of the two experiments and the GUD experimental layout (box containing circles).

were observed during the study. The MOU between the Taraba State Ministry of Forestry (TSMF, Nigeria) and NMFP allows NMFP to directly approve research protocols on behalf of TSMF.

2.3. *Experimental design*

The two experiments carried out in this study were categorized as the ‘giving up density (GUD)’ experiment and the ‘spool-and-line’ experiment. The two experiments were carried out at the two sites shown in Fig. 1.

2.3.1. *GUD experiment*

We used the GUD experiment to estimate the perception of predation risk by *Cricetomys* in the forest between September 2016 and September 2017; specifically, September-October 2016, February-March 2017, April-May 2017 and September 2017. We established four (60 m × 60 m) plots within the Ngel Nyaki CTFS-ForestGEO plot; two at the interior (> 100 m from the grassland) and two at the at the forest edge (≤ 50 m from the grassland). Our study was limited to these four plots because of the relatively small size (20.28 ha) of the CTFS-ForestGEO plot. At each of these sites, we categorised nine microsites into three types based on understory vegetation and proximity to *Cricetomys* burrows. These microsite categories are i) open microsites with sparse understory vegetation (‘high-risk microsites’), ii) cover microsites with dense understory vegetation (‘low-risk microsites) and iii) burrow microsites that were close to active burrows (~1 m away from burrow, ‘low-risk microsites’); in most cases these burrow microsites also had sparse understory vegetation. In addition, microsites that were close to burrow in dense understory vegetation were hard to find.

For each category of microsites at each site, three plastic feeding trays (20 cm X 40 cm X 2.5 cm) were randomly placed such that nearest distance between any two trays was greater than 15 m. On each of these trays, we placed 2 litres of fine gravel (each piece being ~0.3cm long) collected and sieved from a stream bed within the reserve. Trial experiments with dried seeds of corn (*Zea mays*) and peanuts (*Arachis hypogea*) showed that *Cricetomys* removed more corn than peanut seeds at a ratio of 4:1 (as evidenced from camera trap images and footprints). Hence, corn seeds were used for the experiment. Each experimental session spanned five consecutive days. For the first two sessions, 70 g of corn seeds (each grain being ~0.8cm long) were mixed with the fine gravel on each tray, this was reduced to 25 in the third session and 20 g in the remaining six sessions. The corn seeds clearly larger than the fine gravel. We perforated the plastic feeding trays with tiny holes to allow accumulated rain water to drain out. A daily record of the weight of the remaining corn was obtained by sieving the fine gravel from the large corn seeds. After every measurement of the remaining corn in feeding trays, the mixture was replaced with another quantity as described above for each session. Because *Cricetomys* and some small mammals are known to be less active during the bright phase of the moon (Yadok, 2018; Navarro-Castilla et al., 2017), our experimental sessions were mostly carried out during the dark phase of the moon. Theoretically, the predators of the rats are supposed to synchronize their activities with those of the rats (Harmsen et al., 2011) regardless of the moonlight intensity. However, responses of *Cricetomys* to predators that depend on very low light intensities was not adequately captured in our experimental design.

To account for animals other than *Cricetomys* that may visit the traps, three motion-triggered camera traps (Bushnell® Trophy cam) were randomly placed at each of the four sites; each camera was close to one feeding tray in each microsite category. Additionally, ‘Black trakka’ paper sheets (Gotcha traps Ltd, New Zealand) were placed around each feeding tray to record footprints of visiting animals. To control for the effect of *Cricetomys* densities per plot, we sampled the burrows in each GUD site as a surrogate. Although trapping *Cricetomys* would have yielded a more precise density estimate, we did not use the method because of the cost and potential bias on behaviour of the rats. We randomly laid five 5 m x 5 m plots which were at least 20 m apart. Within each of the five plots, we laid out three smaller 2 m x 2 m plots and intensively searched for *Cricetomys* burrows within the smaller plots. Only burrows that were between 4.5 cm and 15 cm in diameter were counted, to reduce the chances including other animals' burrows (Ajayi, 1977). The mean number of rat burrows per meter square was used as an index of the density of rats for each GUD site.

2.3.2. Spool and line experiment

We used the spool and line technique (Boonstra and Craine, 1986; Pickett et al., 2005; Strauß et al., 2008) to record habitat use by *Cricetomys*. Because this method involves trapping *Cricetomys,* we set out a trapping grid (6 × 4) with a spacing of 30 m for 24 single catch cage traps (61 × 20 × 20 cm; reproduced after Havahart®) over 240 trap nights (24 traps x 10 nights). Since *Cricetomys* are most active at night, cages were opened at 1700 h when the sun was setting and the traps were checked and closed by midnight. For each trapped rat, records of sex, body length and trap location were noted. Each trapped rat was uniquely marked in its subcutaneous dorsal region with a passive integrated transponder tags (Tierchip® sterile Iso-compliant microchip with implantation device ISO-Transponder 1.4 x 8.5 mm IG) before gluing ~ 200 m cotton spool (enclosed in a heat shrink wrap) on its flank with an epoxy resin glue (Epoxy steel gum® TCM, Taiwan technology). The thread from one free end of each spool was pulled and tied to the nearest sapling before releasing the trapped rat: as the rat moves, the rest of the thread unwinds, leaving behind a trail of the rat's track. Marking and release of each rat was done at the location where it was trapped.

The next morning, ignoring the first 20 m of the unwound thread, which was the assumed flight response of the rat, the rat's track was traced by following the rest of the unwound thread trail. Microhabitat variables were recorded in a 1 m^2 quadrat at the centre of every 6 m point along the trail. These variables included estimated percentages of exposed ground (with no vegetation cover), understory herb cover, litter cover and dead logs in six categories (0, 0; 1, 1–20%; 2, 21–40%; 3, 41–60%; 4, 61–80%; 5, 81–100%). Also measured, were the slope and litter depth at each of these points. Additionally, within a 4 m^2 quadrat around the centre of every 6 m point along the trail, the number of *Cricetomys* burrows and trees (≥ 10 cm DBH) were recorded. For each of these points, distance to the nearest stream in five categories (1, 0–4 m; 2, 5–9 m; 3, 10–14 m; 4, 15–19 m; 5, ≥ 20 m) was recorded. In order to compare the microhabitats used by *Cricetomys* with microhabitats that were available in the immediate vicinity, we created a random trail which originated from the point which the rat was released; this trail had the same length as the rat's trail at each trap location. To ensure complete randomness of the directions in every 12 m of the random trail, we used already generated random numbers between 0 and 1 from R®, these numbers where multiplied by 360° to give an angle, which was traced from the north on a compass (Skalski, 1987). The microhabitat variables recorded on the random trail were the same as those measured on the rat's trail.

2.4. Statistical analyses

To test for the effect of time, spatial variability and abundance of large-seeded species on *Cricetomys* GUD, we used a general linear model with GUD set as the response variable. A generalised linear mixed effect model in the package 'lme4' in R® (Bates et al., 2017) was used to test for the effect of the microsites (i.e. open, cover and burrows) on *Cricetomys* GUD; observation days, locations within sites, and sites were included as random variables. Since our main objective with the GUD studies was to determine predation risk, we excluded the data from the 4th and 5th observation days from the overall data because their high frequency of zero values could potentially obscure the results of subsequent analyses assuming the rats got too used to the locations of the feeding trays. We did not include the images from the camera traps in our analyses because there were no captured images of predators and many of the feeding trays were not close to the cameras.

For all the GUD models, the data were normalized by transforming the response variable to the power of 0.35 (lambda value), which was obtained from the 'boxcox' function in the package 'MASS' (R core team, 2017). Models were checked for violation of model assumptions and significance of all tests was accepted at $\alpha < 0.05$.

A student *t*-test was used to test for the mean differences in the continuous habitat variables between trails used by the rats and the random trails. The relationship between the frequencies of understory herb cover, exposed ground cover, litter cover and dead log categories (i.e. 0,1,2,3,4,5; see previous section) in the used and random trails were tested using a Spearman's correlation test. In order to compare preferences for microhabitat types, we used Ivlev's electivity index '*E*' (Ivlev, 1961; Strauß et al., 2008).

3. Results

3.1. GUD and predation risk

The GUD results show that *Cricetomys* can easily find food sources within their home range. *Cricetomys* were essentially the sole visitors to the feeding trays because the footprints and camera trap images (213 images) were all *Cricetomys* except for three images of an unidentified mouse. GUDs were significantly affected by time within a session as GUDs continuously reduced for every consecutive observation day (Fig. 2). The session of the experiment and months had no effect and were removed from the starting model. The final model as shown in Table 1 reveals that sites and initial seed quantity had a significant positive effect on GUD. However, the interaction between the initial seed quantity (at 70 g) and observation day had a significant negative effect on GUD, showing that these rats can potentially become habituated to stay longer in a patch with abundant food resources.

Although the GUDs in sites 1 and 2 (interior sites) were lower and not significantly different from each other, the GUDs in sites 3 and 4 (edge sites) which are spatially closer, were significantly higher (see Fig. 3) than the interior sites. The interaction between site and observation day was not significant and was removed from the starting model. There was no significant effect of the interaction between site and observation day except for site 4 and initial seed quantity (70 g) ($p = 0.011$) which was negative (Table 2).

To assess the effect of site proximity from the forest edge, sites 1 and 2 were grouped together as interior sites while sites 3 and 4 were

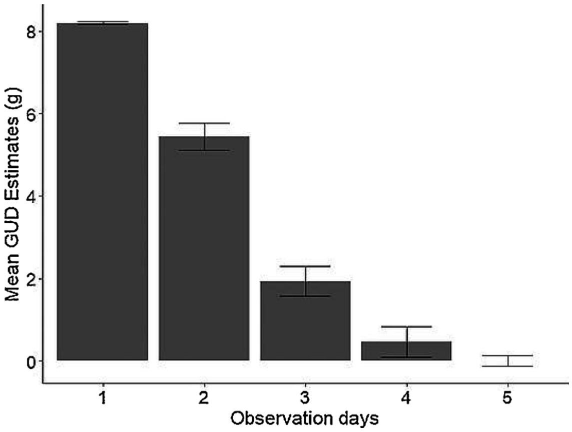

Fig. 2. GUDs for the five consecutive days within a session. GUDs become lower as the number of days increased.

Table 1
Effect of increasing number of days on GUDs. Model: GUD = observation day + site + initial seed quantity + observation day*Initial seed quantity. Overall adjusted R^2: 0.39, $F_{49,17} = 1250$.

Parameter	Estimates	SE	t-value	p-value	
Intercept	1.93395	0.06641	29.12	< 0.001	***
Day_2	−0.22209	0.0804	−2.762	0.006	**
Day_3	−0.41839	0.07843	−5.334	< 0.001	***
Day_4	−0.58673	0.0792	−7.408	< 0.001	***
Day_5	−0.59174	0.07887	−7.503	< 0.001	***
Site_2	0.06963	0.06377	1.092	0.275	
Site_3	0.33824	0.062	5.456	< 0.001	***
Site_4	0.3468	0.06172	5.619	< 0.001	***
Initial seed quantity 25g	0.40821	0.14327	2.849	0.004	**
Initial seed quantity 70g	1.88041	0.11573	16.248	< 0.001	***
Day_2: Initial seed quantity 25g	0.20947	0.20649	1.014	0.311	
Day_3: Initial seed quantity 25g	0.42744	0.2447	1.747	0.081	
Day_4: Initial seed quantity 25g	0.23487	0.24494	0.959	0.338	
Day_5: Initial seed quantity 25g	−0.4272	0.24491	−1.744	0.081	
Day_2: Initial seed quantity 70g	−0.25931	0.17677	−1.467	0.143	
Day_3: Initial seed quantity 70g	−1.00337	0.18099	−5.544	< 0.001	***
Day_4: Initial seed quantity 70g	−1.24797	0.18953	−6.584	< 0.001	***
Day_5: Initial seed quantity 70g	−1.67317	0.2007	−8.337	< 0.001	***

Significant p values are denoted by asterisk (*).
*** < 0.001.
** > 0.001 < 0.01.
* > 0.01 < 0.05.

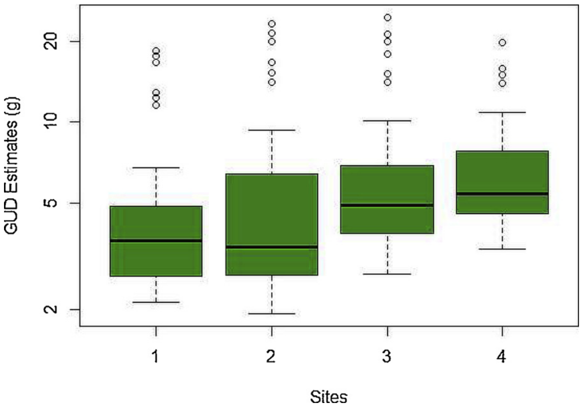

Fig. 3. Box plots showing log scaled GUD estimates in the four different sites. Sites 1 and 2 were in the forest core, and sites 3 and 4 were close to the forest edge. The 25th, 50th and 75th percentiles are shown by the lower halves, middle lines and the upper halves of the boxes in the plot while the whiskers represent the 5th and 95th percentiles of the data. The circles above the boxes represent the outlier values.

grouped as the edge sites. A *t*-test used to compare the two groups showed a significant difference ($p < 0.01$) between the two means which were 3.08 g for the interior sites and 5.12 g for the edge sites.

There was no effect of microhabitats on *Cricetomys* GUDs as revealed by the best linear mixed effect model (Table 3), although that same model showed a significant effect of the initial seed quantities and the mean densities of burrows per site. Although the GUD estimates in the open were higher than in other microhabitats within the three, different initial seed quantity categories (i.e. 20 g, 25 g and 70 g), this difference was not significant (Fig. 4).

Table 2
Effect of site on GUDs. Model: GUD = site + initial seed quantity + observation day + microhabitat + observation day*Initial seed quantity + site : microhabitat, overall adjusted R^2: 0.41, $F_{22,25} = 775$.

Parameter	Estimate	SE	t-value	p-value	
Intercept	1.569	0.068	23.116	< 2e-16	***
Site_2	0.111	0.090	1.226	0.221	
Site_3	0.175	0.087	2.002	0.046	*
Site_4	0.228	0.088	2.599	0.010	**
Initial seed quantity 25g	0.157	0.133	1.181	0.238	
Initial seed quantity 70g	1.109	0.110	10.080	< 2e-16	***
Day_2	−0.143	0.050	−2.881	0.004	**
Day_3	−0.268	0.048	−5.532	0.000	***
Burrow	0.051	0.088	0.579	0.563	
Open	0.093	0.084	1.115	0.265	
Site_2 : Initial seed quantity 25g	0.193	0.162	1.194	0.233	
Site_3 : Initial seed quantity 25g	0.118	0.161	0.734	0.463	
Site_4 : Initial seed quantity 25g	0.051	0.163	0.315	0.753	
Site_2 : Initial seed quantity 70g	0.214	0.134	1.594	0.111	
Site_3 : Initial seed quantity 70g	0.056	0.132	0.423	0.673	
Site_4 : Initial seed quantity 70g	−0.326	0.128	−2.548	0.011	*
Day_2 : Initial seed quantity 25g	0.128	0.128	1.003	0.316	
Day_2 : Initial seed quantity 70g	−0.182	0.110	−1.657	0.098	
Day_3 : Initial seed quantity 25g	0.295	0.152	1.944	0.052	
Day_3 : Initial seed quantity 70g	−0.552	0.112	−4.920	0.000	***
Site_2 : burrow	−0.134	0.123	−1.085	0.278	
Site_3 : burrow	−0.109	0.120	−0.904	0.366	
Site_4 : burrow	−0.004	0.120	−0.030	0.976	
Site_2 : open	−0.247	0.120	−2.050	0.041	*
Site_3 : open	0.064	0.117	0.544	0.586	
Site_4 : open	0.169	0.116	1.454	0.146	

Significant p values are denoted by asterisks (*)’.
*** < 0.001.
** > 0.001 < 0.01.
* > 0.01 < 0.05.

Table 3
Effect of microsites, initial seed quantity and mean number of burrows on GUDs. (R-square = 0.51. AIC: from 7554.48 to 6326.

Parameter	Estimate	SE	df	t-value	p-value	
Intercept	12.312	2.839	3.8	4.337	0.01351	*
Burrow	−1.069	1.09	793	−0.981	0.32689	
Open	1.547	1.073	793	1.442	0.14973	
Initial seed quantity 25g	6.573	1.459	793.4	4.505	7.63E-06	***
Initial seed quantity 70g	35.223	1.181	793.2	29.832	< 2e-16	***
Mean number of burrows per site	−15.608	5.953	793	−2.622	0.00891	**

Significant p values are denoted by asterisks (*).
*** < 0.001.
** > 0.001 < 0.01.
* > 0.01 < 0.05.

3.2. *Microhabitat use*

Of the 17 rats that were caught (14 males and 3 females) and fitted with spools, 15 made tracks greater than the assumed 20 m flight response distance. Distances along the unwound spools ranged between 24 m and 144 m, with an overall mean of 90 ± 6 m. A mean of 84 m for the three females suggest that there is no difference in movement range between males and females.

Comparing the habitat variables between the random sites and sites used by *Cricetomys* in our spool and line experiment showed that understory herb cover, dead log cover and number of burrows were significantly ($p < 0.05$) higher in the sites used by *Cricetomys* while litter cover was lower (Table 4). The sites used by *Cricetomys* were significantly closer to streams than the random sites. But there was no significant difference in the slope, elevation and number of trees between sites used by *Cricetomys* and random sites.

Spearman’s correlation test revealed a positive relationship between

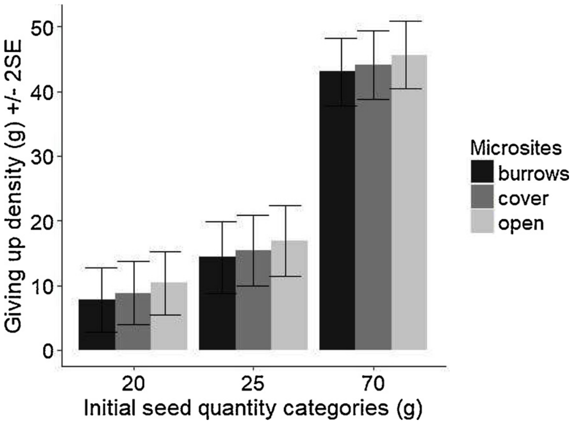

Fig. 4. Effect of initial seed quantity on GUDs. Pairwise differences between the microhabitats are not significant (p ≥ 0.05).

the frequencies of the used and random habitat variables recorded i.e. understory herb cover, exposed ground, litter cover and dead logs (Table 5). This indicated that the rats used all available microhabitats within their home ranges (Fig. 5).

Using the Ivlev's electivity index, this study showed that the rats had a slight tendency of preferring microhabitats that had more dead logs, more exposed ground and dense understory herb cover, but showed a slight tendency to avoid habitats with more litter cover (Fig. 6) in tropical forests. These preference indices were all ≤ 0.15 which is closer to 0 being the 'no preference' index rather than 1 or -1 which refer to strong active selection or avoidance respectively.

4. Discussion

Our study has shown that the perception of risk by *Cricetomys* in Afrotopical montane forest is largely affected by the proximity of the habitat to the forest edge rather than microsites with dense understory vegetation. Although there was a slight tendency for the rat to frequently use parts of the forest with denser understory herb cover, it equally foraged in open sites, which were generally perceived to be risky for rodents as shown in many similar studies (Hughes and Ward, 1993; Brown et al., 1998; Jacob and Brown, 2000; Morris and Davidson, 2000; Mohr et al., 2003) but see Bouskila (1995) and Cassini and Galante (1992) for exceptions.

An important caveat to note about this study is that we were not able to set up a perfect experiment that would provide a sufficient 'diminishing returns' scenario on each of our feeding trays despite multiple trials and communication with experts in the field. In light of the above caveat, we acknowledge that our GUD results can also be explained by the foraging activity and efficiency of *Cricetomys,* but since our study was not designed with such a question in mind, we hereby narrow our discussion to the perception of predation risk in *Cricetomys.*

Table 5
Correlation between microhabitats used by *Cricetomys* and microhabitats along randomly located tracks. LCL and UCL refers to lower confidence limits and upper confidence limits respectively.

Habitat variable	Correlation coefficient	95% LCL	95% UCL	p value	
understory density	0.827	0.046	0.981	0.042	*
exposed ground	0.983	0.849	0.998	< 0.001	***
litter cover	0.954	0.627	0.995	0.003	**
dead logs	0.993	0.936	0.999	< 0.001	***

Significant p values are denoted by asterisks (*).
*** < 0.001.
** > 0.001 < 0.01.
* > 0.01 < 0.05.

4.1. Temporal effect on Cricetomys gud

Our first hypothesis that GUDs will become lower after each succeeding night of observation regardless of food replenishment was supported by the results of this study. The continuous reduction in the amount of food remaining in all the patches for the successive observation nights in the experimental sessions, suggests that *Cricetomys* can easily identify the spatial location of food sources. This also shows that given more time in replenishing food sources, *Cricetomys* learn to either become better at harvesting food or spend more time harvesting without easily giving-up. It is also possible that *Cricetomys* are neophobic thus they may not eat much of the corn on the first two days until they get used to having the trays in their home range. The intense seed harvest by *Cricetomys* may be attributed to the relatively large sizes of the corn seeds we compared to the fine gravel provided; this may enable faster detection of seeds in the tray. However, the relatively large sizes of *Cricetomys* also mean that in a natural setting, they would require large seeds from the forest floors as shown in a study by Yadok (2018).

Tenacity—being the ability of a forager to show little or no change in its harvest rates when predation risk is increasing (Fraser and Gilliam, 1987) — may explain *Cricetomys* foraging in sites that are considered risky for rodents (Brown and Kotler, 2004). Brown and Kotler (2004) suggest three reasons for tenacity in rodents; i) relative invulnerability to predators, ii) poor predator detection abilities, and iii) behavioural modulation of predation risk e.g. though vigilance and apprehension. Of these three reasons for tenacity in rodents, *Cricetomys* fits in the first and third. Being relatively larger (~1 kg) than most other rodents in the forest, its size may reduce its vulnerability to

Table 4
T-tests for habitat variables in microsites used by *Cricetomys* and random microsites.

Parameter	Estimate (*Cricetomys*)	Estimate (Random)	t-value	df	p-value	
Slope	17.39	17.91	−0.828	450.99	0.4081	
understory density	2.193	1.891	2.541	450.97	0.011	*
litter cover	2.784	3.099	−3.198	441.98	0.002	**
dead log cover	0.637	0.443	2.5488	440.07	0.011	*
litter depth	2.05	2.161	−1.104	447.75	0.2701	
number of burrows	0.262	0.149	2.312	422.74	0.0211	*
number of trees	0.505	0.455	0.804	399.55	0.4217	
distance to nearest water	3.965	4.552	−4.737	397.33	< 0.001	***
Elevation	1565.54	1587.63	−2.27	236.45	0.023	

Significant p values are denoted by asterisks (*).
*** < 0.001.
** > 0.001 < 0.01.
* > 0.01 < 0.05.

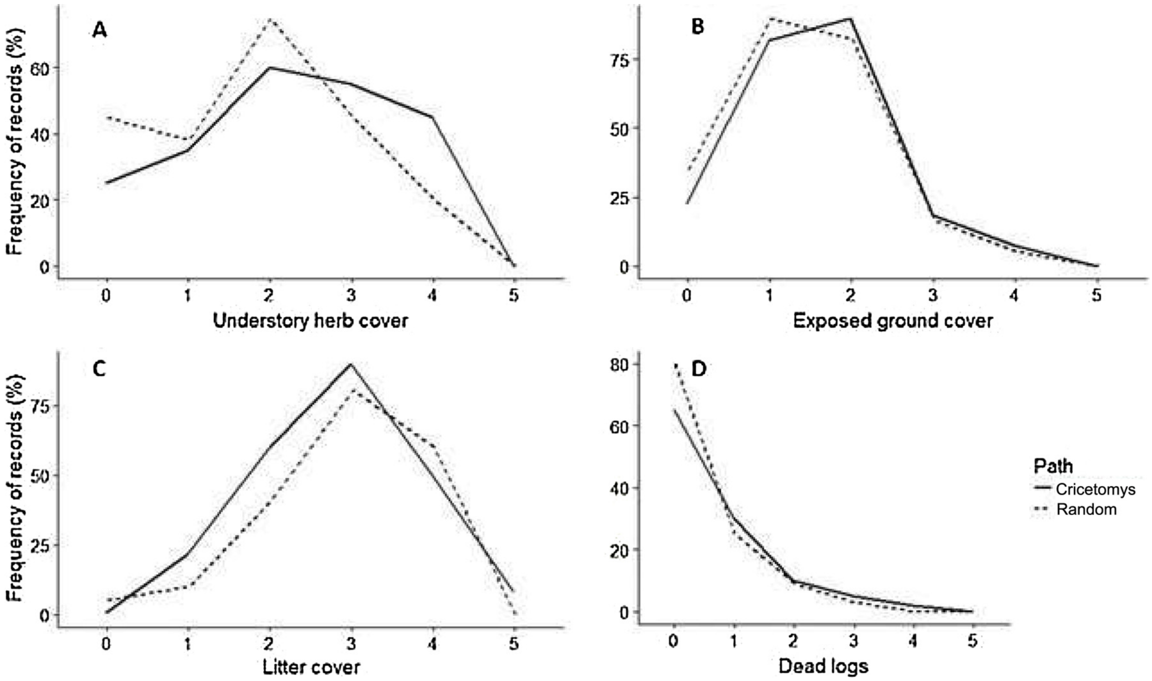

Fig. 5. Frequencies of the categories of understory herb cover (A), exposed ground cover (B), litter cover (C) and dead logs (D) in *Cricetomys* paths and random paths.

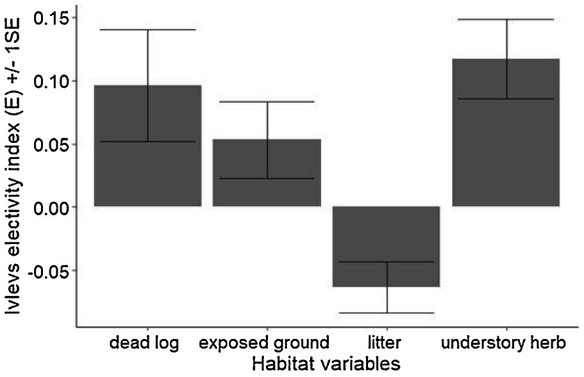

Fig. 6. Preferences for microhabitat variables by *Cricetomys*. Positive values indicate that they were used more often than available while negative values indicate they were use less often than available.

predators, allowing it to feel safe foraging in habitats that other rodents might perceive as dangerous. But its tenacity may not be attributed to size alone because the Indian crested porcupine (*Hystrix indica*) which is a far heavier rodent (~14 kg) still showed a strong sensitivity to predation risk (Brown and Alkon, 1990). The high olfaction acuity of *Cricetomys* correlates with the functional morphology of its brain (Ibe et al., 2014) and could also contribute to its modulation of predation risk through increased vigilance thus increasing its preparedness to forage in potentially risky microhabitats. Despite being quadrupedal, the hind limbs of *Cricetomys* have a slight resemblance to those of bipedal rodents in terms of musculature and length; this adaptation for escape may partly be responsible for their frequent utilization of open microsites (Taraborelli et al., 2003).

Our findings suggest that *Cricetomys* may either a Bayesian (‘smarter’) or prescient (‘smartest’) forager since its foraging behaviour conforms with Olsson and Brown’s (2010) description of foragers even though experiments with paired feeding trays having differing food quantities may be needed to confirm this. The consistent reduction in the levels of GUD over successive nights showed that these rats seem to retain information about the location of the feeding trays and searching/detection rates of the corn seeds in the feeding trays. African civets (n = 12), barn owls (n = 2) were the only possible predators observed in ~800 camera trap nights during a previous study in the same study area (Yadok, 2018); this probably indicates paucity of predators, it is likely that *Cricetomys* are already aware of the low predation risk, thus the frequent use of all microsites.

4.2. Effect of spatial and habitat variation

Our second hypothesis that GUDs will be higher at sites that are closer to the forest edges because of increased perception of predation risk at such sites is supported by our results. Spatial variation in the perception of predation risk may exist as a result of differences in habitat structures (Abu Baker and Brown, 2010). This suggests that there may be a large scale spatial effect on either the perception of predation risk by *Cricetomys* or their density distribution. Additionally, forest edges have been demonstrated to have lower food quality and higher risk of predation (Wolf and Batzli, 2004), but this this is yet to be examined in our study site. Food competition by the rats in the forest edges may be lesser (Morán-López, et al., 2016), plus the disparity in food abundance between the forest core and edges may also explain the higher GUDs observed in forest edges but measuring the food/rodent abundance was beyond the scope of this study. Following Yadok’s (2018) estimation of *Cricetomys* core home range (~0.31 ha) it is unlikely that the rats living in the core will access the trays in the edge habitat.

While the observed spatial difference in GUDs from this study cannot be directly linked with background food sources, it is important to note that fruit production in tropical forests is often seasonal and fruit availability in tropical montane forests is usually lower than in lowland forests (Chapman et al., 2016). Consequently, being able to retain information about the location of food sources may be important for the survival of animals in highland forests. This study suggests that *Cricetomys* easily learns about food sources which may potentially include trees with ripe and falling fruits. Higher GUDs at the start of every session suggest that these rats do not retain the information of foraging locations for a long period (> 3 weeks). However, because experimental sessions lasted for only five days, this could not be ascertained, and it could be that a longer experimental session would enable a longer lasting memory of food sources for these rats.

4.3. Effect of microsites on GUDs

Although many studies have stressed the importance of covered (‘bush’ or ‘dense vegetation’) microsites in the perception of predation risk of many small mammals (see Verdolin, 2006 review and the references therein), our study showed no apparent effect of dense understory (bush) cover on the perception of predation risk by *Cricetomys*. Therefore, our third hypothesis that higher GUDs will be observed in open microsites as a result of increased perception of predation risk was not supported. The consistent slightly higher GUDs in the open microhabitats in this study were not significantly different from GUDs in the microhabitats with dense understory or near burrows. This may suggest that there is a higher predation risk in the open microhabitats. However, *Cricetomys* can potentially modulate the risks and still utilize open areas. The consistently lower GUDs at microsites near rat burrows also suggest that the rats probably felt safer when closer to their burrows than elsewhere. While our results clearly show the indifference in GUDs among microsites we acknowledge that the zero GUD values in the fourth and fifth days of our experiments allow our results to be interpreted in other ways (e.g. time allocation and foraging efficiency), in addition to the perception of predation risk by *Cricetomys*.

The few GUD studies carried out in the tropics mostly agree with the global pattern at the microhabitat level (Wasko et al., 2014; Menezes et al., 2017). Unfortunately, there are no previous tropical African GUD studies on rodents, which this study can be compared with and because *Cricetomys* are larger than most tropical African rodents our results cannot be generalized for other rodents. It is also important to note that carrying out our experiment during the dark phases of the moon may have caused us to inadvertently undermine *Cricetomys* responses to visual predators. We are also aware of the fact that ambush predators may frequently occur in areas with dense understory vegetation (Bouskila, 1995) thus the rats may perceive it to be risky too but we do not have evidence to support this claim.

In this study, the initial seed quantity and the abundance of *Cricetomys* burrows were observed to have the most significant effect on *Cricetomys* GUD. This is surprising because a mere 5 g difference in the initial seed quantity still resulted in a lower GUD. The conventional expectation is that the initial seed quantity may not be important if the animal can hoard or collect food from the patch (Morgan et al., 1997) and so, the GUD should be the same even when the initial seed quantity is different. Although *Cricetomys* often carry excess food to their burrows or caches, they seem to have higher GUDs when the seed quantity is higher.

The abundance of burrows, which is an indirect measure of *Cricetomys* abundance was significant in lowering the GUDs of *Cricetomys*. Though this may partly reflect *Cricetomys* abundance, it is important to note that *Cricetomys* is a lone forager (Ray & Duplantier, 2013). The abundance of rat burrows may however be an indication of *Cricetomys* home ranges that are closer to these sites, thus the few *Cricetomys* foraging in those sites may have good knowledge of resources within their home range and know where to harvest food when available. Moreover, conspecific competition due to high density of individuals may enable high foraging efficiency among *Cricetomys*.

4.4. Microhabitat use

Rats frequently use microhabitats that allow minimum access to predators (Strauß et al., 2008), and this is consistent with our fourth hypothesis: our spool and line data demonstrate the frequent use of dense understory herb cover by *Cricetomys* in this study. Although our study showed that *Cricetomys* use all levels of dense understory herb cover, they frequently used more microhabitats with denser understory vegetation. In this study, *Cricetomys* seemed to use all available microhabitats within their small home ranges, which are frequently closer to streams. While *Cricetomys* rarely used microhabitats with smaller dead logs, there was a less frequent use of microhabitats with large dead trunks of trees because they were not commonly available. *Cricetomys* seem to actively select microhabitats with more understory herb cover, exposed ground, and larger dead logs or wood while microhabitats with more leaf litter seem to be slightly avoided. However, the slight habitat preference or avoidance tendencies of *Cricetomys*, as evidenced by the narrow range of Ivlev’s electivity values in this study suggest that they do not show a strong preference or avoidance of microhabitats within their home range.

4.5. Conclusion and recommendation

Overall, this study has shown that predation risk has little or no effect on the foraging behaviour of *Cricetomys* at a microhabitat scale but may be important on a larger spatial scale. Therefore, predation risk may influence seed dispersal through scatter-hoarding on a larger spatial scale. Our study also demonstrates that *Cricetomys* use all the available microhabitats within their home range with slight preference for some microhabitat structures. We recommend that a similar study be carried out in lowland tropical forests in Africa in order to determine the consistency of this behaviour across different forest types. We also recommend that a similar study be carried out with a view of ensuring a perfect diminishing returns scenario on the feeding trays in order to clarify the predation risk on *Cricetomys* foraging patterns

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