

Foraging behaviour of two rodent species inhabiting a kopje (rocky outcrop) in Tsavo West National Park, Kenya

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We employed patch use theory to evaluate how several environmental factors influence the foraging behaviour of two rodent species: *Grammomys dolichurus* and *Acomys cahirinus*. Foraging efficiency was determined by measuring the remaining food in artificial food patches (giving-up densities: GUDs) from two experiments. In the first experiment, we placed patches in different microhabitat types (cover vs open) and at varying distances from cover. This experiment was conducted during three moon stages (waxing, full, waning). We found that the rodents had higher GUDs (lower foraging efficiency) in the open microhabitat. The distance from nearest shelter had a marginally significant positive effect on GUDs. GUDs were higher in both microhabitat types during the waxing and full phases, but decreased sharply once the moon began to rise after sunset. These results are likely due to higher predation risk away from cover and in more illuminated environments. In the second experiment, we examined mouse responses to seeds impregnated with plant toxins. Seeds impregnated with oxalic acid were avoided by the rodents, while seeds soaked in tannic acid did not differ significantly from control seeds. Our results highlight important ecological factors affecting the foraging behaviour of these rodents.

Key words: giving-up densities, foraging ecology, kopje, lunar.

INTRODUCTION

East African savannas contain a rich diversity of small mammals (Kingdon 1984; Keesing 2000). Small mammals play a vital role in the ecosystem as prey for various predators. However, recent studies have shown that they also affect the ecology of plants by altering biomass and patterns of seed distribution (Keesing 2000). Thus, analysing the feeding behaviour of small mammals should provide insights into the ecology of savannas.

The foraging behaviour of an animal is influenced by numerous factors, including when it feeds [e.g. time of day (Kronfeld-Schor & Dayan 2003), lunar stage (Orrock *et al.* 2004), season (Kolter *et al.* 2004)], where it feeds [e.g. habitat type and microhabitat characteristics (Kolter & Brown 1988)], and what it feeds on [e.g. plant toxins and nutrient levels (Freeland & Janzen 1974; Crawley 1983)]. Each of these factors is associated with inherent opportunities and hazards. Consequently, selection should produce flexible feeding behaviours that allow an animal to minimize foraging costs (e.g. predation, energetic demands) and maximize benefits (e.g. caloric intake, survival).

Patch use theory has been successfully employed for teasing apart environmental factors that influence foraging behaviour in many rodent species (Brown 1988; Kotler *et al.* 1993; Orrock *et al.* 2004). Patch use theory is derived from the marginal value theorem (Charnov 1976), which describes how resource quality and abundance affect an animal's use of a food patch. This theorem states that a forager should leave a patch when the rate of energetic gain falls below the average rate for its environment. Brown (1988) extended the marginal value theorem beyond energetics to consider how other fitness-enhancing behaviours (e.g. mating, grooming, avoiding predators) may affect foraging behaviour. By creating artificial food patches and manipulating specific attributes (e.g. where they are placed, what type of food is used), it is possible to identify how different factors impact foraging behaviour. Patch use studies have explored such factors as microhabitat and habitat structure (Brown 1988; Kotler *et al.* 1988), climatic conditions (Kotler *et al.* 1993; Orrock *et al.* 2004), food handling time (Garb *et al.* 2000), and plant toxins (Schmidt 2000).

Here, we applied patch use theory to study the

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foraging ecology of rodents inhabiting a kopje in Tsavo West National Park, a semi-arid bushland in Kenya. Kopjes are insular rock outcrops that disrupt the often continuous swath of savannah vegetation common in East Africa. We explored how microhabitat characteristics and location on the kopje (relative to its centre) affected foraging behaviour. Furthermore, because lunar illumination increases a rodent's conspicuousness to predators (Clarke 1983; Kotler *et al.* 1991), we tested the effects of the above spatial scales during different lunar stages. Finally, we explored the effects of two common plant secondary compounds (oxalates and tannins) on the foraging decisions of the rodents.

METHODS

Study site and study species

The study site was a single, isolated kopje in the Ngulia Rhino Sanctuary, Tsavo West National Park, Kenya (locally known as Mlima Chui) surrounded by *Commiphora-Acacia* bushland. The kopje, comprised of a granitic-gneissic rock base and littered with large boulders, was ~10 m in height by ~70 m in breadth by ~150 m in length. Vegetation was patchily distributed on the kopje.

We live-trapped for seven nights to identify which species were present and to determine their space use when no foraging patches were available. Forty Sherman live-traps (in four lines) radiated from the centre of the kopje and extended 20 m into the bushland, with traps spaced ~20 m apart. Morphological traits were used for all species identifications (B.D. Patterson, pers. comm.). Trapping suggested that *Acomys cahirinus* and *Grammomys dolichurus* were the primary foragers of the food patches (see Results).

Acomys cahirinus Desmarest, 1819 (golden spiny mouse; c. 20 g, 74–94 mm) is a well-studied nocturnal rodent that ranges from southern Morocco to Pakistan and south to northern Tanzania (Kingdon 1984; Kronfeld-Schor & Dayan 1999). *A. cahirinus* resides in semi-arid regions and frequently inhabits rocky substrates (Kingdon 1984). Gutman & Dayan (2005) showed that *A. cahirinus* foraged more during the new moon than a full moon. Their diet consists of vegetation, seeds and invertebrates (Kronfeld-Schor & Dayan 1999).

Grammomys dolichurus Smuts, 1832 (narrow-footed bush rat; c. 20 g, 85–130 mm) is a nocturnal, arboreal rodent that ranges from Central African Republic to Angola and southeastern South Africa

(Kingdon 1984). It occupies a diverse range of habitats, from tall grasses to forests, and its diet consists primarily of fruits, plant material and insects (Kingdon 1984; Wirminghaus & Perrin 1992). The life history of *G. dolichurus* has been well studied in captivity since the species has served as an experimental animal in malaria studies, but very little is known about its ecology in the wild (Yoeli *et al.* 1963; Bland 1973).

Foraging patches

In a depletable patch, an optimal forager should forage a patch until its harvest rate diminishes to the sum of energetic, predation and missed opportunity costs of foraging (Brown 1988). The remaining food in the patch (the giving-up density (GUD)) provides a surrogate for harvest rate to measure the foraging efficiencies of the rodents (Brown 1988). This technique of measuring GUDs has become a common method for assessing foraging behaviour (e.g. Gutman & Dayan 2005; Perrin & Kotler 2005; Reed *et al.* 2005). Lower GUDs indicate more efficient foraging.

For the foraging patches, circular plastic trays (6.5 cm depth × 27 cm diameter) were filled with 40 seeds (seed type depended on experiment) thoroughly mixed into 1.5 l of sifted sand (2.5 cm in depth). After smoothing the surface, two more 'bait' seeds were placed on the surface as an indicator of foraging activity. Trays were placed at dusk and collected at dawn. Upon collection, all remaining seeds were removed from the sand, cleaned, counted, and weighed. Unfortunately, the foraging medium that we used was too coarse to confidently distinguish between tracks left by *A. cahirinus* and *G. dolichurus*. Therefore, we combined the data and performed all analyses on the combined data set. Days of data collection were consecutive for each experiment, as weather permitted. A habituation session was conducted for two days prior to each experiment before we started collecting data. This session exposed the mice to the trays and to the experimental set-up. We conducted these experiments during March–April 1999.

Experiments

Spatial scales with lunar effects. To explore the effects of the kopje's spatial heterogeneity, we established four lines (~40 m apart) radiating from the centre of the kopje to the edge. There were four stations per line (~10 m apart; 0, 10, 20, or 30 m from centre), and each station had two trays filled

with 40 peanut halves ($\sim 3.0 \pm 0.1$ g). At each station, one tray was placed in 'cover' microhabitat (under a rock-ledge or bush) and another tray was placed < 2 m away in an 'open' location. For each 'cover' tray, we assessed the type of cover (bush or rock) and the degree of exposure (ranked on a five-point scale). For each 'open' tray, we measured the distance to the nearest source of cover.

To assess the effect of moonlight on foraging behaviour, we recorded data during the waxing, full, and waning stages. We defined the 'waxing' phase as a waxing moon with disc illuminated 15–85%, the 'full' phase as $> 95\%$ of the moon disc illuminated, and the 'waning phase' as the waning moon with disc illuminated 15–85%. We recorded data for four nights during the 'waxing' phase, five nights during the 'full' phase, and four nights during the 'waning' phase. We initiated data collection during the waxing stage when the moon was 38% illuminated and ended during the waning stage with the moon 38% illuminated.

Plant secondary compounds – To examine the effect of toxins on diet selection, we soaked popcorn kernels in saturated solutions of tannic acid (5%, Hopkin & Williams, Chadwell U.K.), oxalic acid (15%, May and Baker, Lagos Nigeria), or 100% distilled water for the control. After soaking for two days, the popcorn kernels were sun-dried for two days. Four stations were placed at widely spaced locations on the kopje with each station containing three trays. Each tray was filled with 40 kernels ($\sim 6.2 \pm 0.2$ g) of either oxalic, tannic or control popcorn. The trays at each station were rotated every night. The experiment was conducted for six consecutive nights.

Data analysis

We performed all statistical analyses in SAS (Version 9.1 for Windows, Cary NC) using PROC MIXED. We assumed for both models that each 'station' was foraged by a single individual. This assumption was supported by the observation that when we removed an individual from the kopje, the nearest station had no foraging activity the next night (in both open and cover patches), while further stations were not affected.

We developed two models, one for the spatial scale with lunar effects experiment and the other for plant secondary compound experiment. Except for station, all variables were treated as fixed effects, and GUD (number of seeds left) was the response variable. We constructed a covariance–variance matrix for each model. For both models, the

covariance–variance matrices assumed correlation between microhabitats and among lunar stages. We compared these more complex covariance structures with simpler covariance structures, but the more complex model always performed better as determined by BIC and AICC criteria. Finally, we determined the most parsimonious model by removing fixed effects and interactions with $P > 0.10$. We tested all residuals for normality and homoscedasticity assumptions as dictated by the covariance structure. For all analyses, post-hoc comparisons were tested using least squared means with Tukey–Kramer adjustments. All values are reported as mean \pm S.E.

RESULTS

Trapping

In total, we had 46 captures in 280 trap nights. On the kopje, we trapped nine *A. cahirinus* and seven *G. dolichurus*. Only one *A. cahirinus* was trapped in the surrounding bushland, which suggests that these two species predominantly restrict their space use to the kopje. Both *A. cahirinus* and *G. dolichurus* were trapped throughout the kopje; there was no clear boundary between species. In addition to these two species, we also trapped one *Tatera sp.* and five *Aethomys chrysophilus* in the bushland surrounding the kopje; neither species was trapped on the kopje.

Spatial scale with lunar effects

Microhabitat had a strong effect on GUDs, with cover trays having significantly lower GUDs than the open trays (12.99 ± 2.28 vs 29.66 ± 2.18 seeds; Table 1). However, the intensity of the microhabitat effect depended on the lunar stage (Table 1, Fig. 1). The mean difference between open and cover GUDs did not differ significantly between waning and waxing phases of the moon ($\Delta\bar{x} = 14.15 \pm 2.38$ vs 14.67 ± 2.38 seeds, respectively; $t_{32.6} = 0.24$, $P < 0.81$), but increased significantly during the full moon ($\Delta\bar{x} = 21.19 \pm 2.38$ seeds; waxing vs full difference, $t_{32.6} = 3.22$, $P < 0.003$).

The lunar stage also affected the overall foraging efficiency of the mice (Table 1). Mean waxing GUDs did not differ significantly from full moon GUDs ($\Delta\bar{x} = 2.39 \pm 1.19$ seeds, $t_{30.6} = 2.01$, $P < 0.13$), but both waxing and full moon GUDs were higher than waning GUDs ($\Delta\bar{x} = 13.86 \pm 1.49$ seeds, $t_{31.2} = 9.31$, $P < 0.001$; $\Delta\bar{x} = 11.47 \pm 1.57$ seeds, $t_{31.2} = 7.31$, $P < 0.001$, respectively).

The distance from cover had a marginally significant effect on foraging efficiency (Table 1, Fig. 2).

Table 1. Results from ANOVA model for the spatial scale with lunar effects experiment. The table lists all fixed effects included in the final model ('fixed effects') and all main effects removed from the model ('removed main effects'). We treated each station as an individual mouse and consequently modelled the covariance structure accordingly (see text for details).

Source	d.f.	F-value	P-value
Fixed effects			
Lunar stage (waxing, full, waning)	2, 31.0	45.80	<0.001
Microhabitat (bush, open)	1, 17.7	80.07	0.003
Distance from cover	1, 19.0	4.14	0.056
Lunar stage \times microhabitat	2, 30.2	4.36	0.022
Removed main effects			
Cover type (rock, shrub)	1, 10.3	1.13	0.31
Cover rating	1, 13.0	0.04	0.85
Distance from Kopje centre (0, 10, 20, 30 m)	3, 10.3	1.34	0.31
Correlations			
		<i>Estimate</i>	
Microhabitat		0.19	
Lunar stage		0.35	

GUDs increased quickly with increasing distance from the nearest cover, but this relationship did not depend on the lunar stage ($F_{2,27.7} = 0.39$, $P < 0.68$). Surprisingly, we found no differences between rock and shrub cover types ($\bar{x} = 20.85 \pm 2.52$ vs 22.37 ± 3.75 seeds; Table 1) nor an effect of the degree of exposure for cover trays (Table 1). Additionally, GUDs were not affected by the distance from the centre of the kopje (Table 1).

Plant secondary compounds

Plant secondary compounds had a significant effect on GUDs ($F_{2,3.68} = 23.62$, $P < 0.0079$; Fig. 3). GUDs were lower for control seeds and tannin-treated seeds than for oxalic-treated seeds (control

vs oxalic: $\Delta\bar{x} = 16.69 \pm 3.21$ seeds, $t_{4.7} = 5.20$, $P < 0.018$; tannin vs oxalic: $\Delta\bar{x} = 9.35 \pm 2.13$ seeds, $t_{3.11} = 4.38$, $P < 0.030$). Control GUDs did not differ significantly from tannin GUDs ($\Delta\bar{x} = 7.34 \pm 3.90$ seeds, $t_{4.16} = 1.88$, $P < 0.13$).

Finally, day also affected GUDs ($F_{4,4.14} = 10.87$, $P < 0.018$) but a day by treatment interaction was not found ($F_{8,3.29} = 2.58$, $P < 0.22$). Numerous environmental factors vary from day to day (e.g. temperature, cloud cover, predator presence), and may influence GUDs on any given day.

DISCUSSION

We studied the foraging ecology of *A. cahirinus* and *G. dolichurus*, two nocturnal rodents inhabiting a

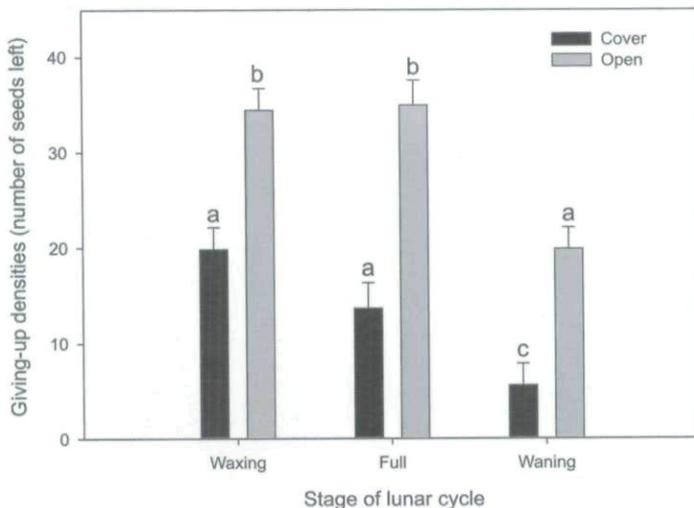


Fig. 1. Effects of lunar stage and microhabitat on mean GUDs. All error bars represent one standard error and different letters and symbols indicate significant differences at $P < 0.05$.

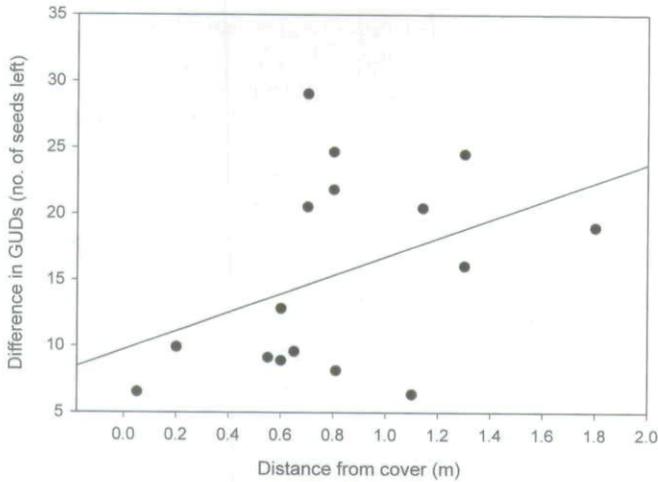


Fig. 2. Effect of distance of open tray from cover on the difference in GUDs between open and cover microhabitats. We used the difference between microhabitats as the response variable to control for inter-mouse variation. The slope of the regression line from the mixed model is 7.12 ± 3.50 seeds/m ($t_{19} = 2.03$, $P < 0.056$).

kopje in East Africa. Although we were not able to distinguish between species, we feel confident that the qualitative conclusions of this study hold for both species, though there are probably subtle quantitative differences between species. We base this conclusion on the consistency in results; foraging efficiencies were always higher 1) in covered microhabitats, 2) during the waning phase of the lunar cycle, and 3) for tannin- and water-soaked seeds. Furthermore, stations were located throughout the kopje, so it would be highly unlikely that one species foraged all of them, especially given the fairly equal population sizes and distributions

of both species on the kopje. Finally, though this study had multiple replicates on the kopje, the inferential scope is limited to just this kopje.

Spatial scale with lunar effects

Cover microhabitats appear to have lower predation risks than open microhabitats. This conclusion is based on two empirical results: the rodents exhibited greater foraging efficiency in the cover microhabitat, and mice foraging in the open microhabitat altered their GUDs in response to distance to the nearest cover. Cover can decrease predation risk by either obstructing a predator's

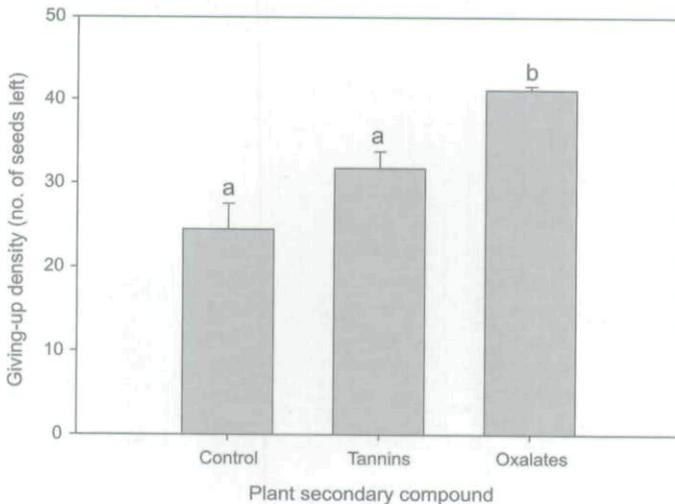


Fig. 3. Effect of plant toxin treatments on mean GUDs. 'Control' refers to seeds soaked in distilled water. All error bars represent one standard error and different letters indicate significant differences at $P < 0.05$.

visual detection of the rodent, or by obstructing the predator's path of attack. If mice use the cover for safety, they should be more susceptible to being caught at greater distances from cover. If the predation hypothesis is correct, the mean GUDs highlights how quickly predation risk increases with increasing distance from shelter. The preference for cover microhabitat among rodents has been well documented, and our results match several other studies (e.g. Kotler *et al.* 1991; Brown *et al.* 1992; Orrock *et al.* 2004) including studies on *A. cahirinus* (Abramsky *et al.* 1992; Jones & Dayan 2000; Jones *et al.* 2001).

It is interesting to note that the degree of cover (e.g. a rock overhang *vs* a sparsely vegetated shrub) did not have a significant effect on GUDs. This result may indicate that owls are more of a threat to the rodents than mammalian predators. The effect of cover probably depends on whether the predator has a horizontal view of the rodent (i.e. mammalian and reptilian predators) or a vertical view (i.e. avian predators). For terrestrial predators, rock overhangs and sparse vegetation may have less of an effect on their ability to detect and attack their prey, whereas dense vegetation may be more inhibitory. Conversely, for aerial predators, any overhead cover, even sparsely vegetated plants, may prevent attack due to the risk of injury in crashing through a shrub.

In the Ngulia Rhino Sanctuary, both avian (i.e. Verreaux's eagle owl (*Bubo lacteus*), spotted eagle owl (*Bubo africanus*)) and mammalian (i.e. serval (*Felis serval*), black-backed jackal (*Canis mesomelas*)) predators are common and were observed consistently at the study site. Our microhabitat results also suggest that snakes may not be playing a major role in community dynamics at the study site, at least during the time period of our study. Most snakes forage in cover microhabitats and can cause rodents to shift their activity to open microhabitats (Kotler *et al.* 1993; Bouskila 1995). In support, we observed few signs of snakes at the study site.

We also found that our rodents' foraging behaviour was affected by the lunar cycle. Lunar illumination is known to affect many animals' foraging behaviour (e.g. scorpions, Skutelsky 1996; rodents, Wolfe & Summerlin 1989; Kotler *et al.* 1991; bats, Gannon & Willig 1997). It has been suggested that rodents use illumination levels as an indirect cue of predation risk. Several studies have shown that mice have higher GUDs when exposed to higher illumination levels (Kotler *et al.* 1991, 1993; Orrock

et al. 2004). Furthermore, studies have also shown that owls forage on rodents more successfully during brighter nights (Clarke 1983; Kotler *et al.* 1991). Our results for lunar effects are similar to other rodent studies in general, but there are some unique patterns in our results.

Most studies on rodent foraging behaviour that measured foraging efficiency over the lunar cycle usually find a linear relationship between moon illumination levels and foraging efficiency (Kotler *et al.* 1993; Orrock & Danielson 2004; Orrock *et al.* 2004). In our study, mice foraged the waxing and waning moon stages differently, which is especially interesting, because the illumination levels between the two lunar stages covered the same range (38–85% of the moon disc). We believe this difference in foraging is due to different moon-rise and moon-set times between these two phases.

During the waxing phase, the moon rises during the day and sets during the night, creating a window of darkness late in the night. During the waning phase, the moon rises in the night and sets during the day, thereby creating a window of darkness early in the night. If the kopje rodents primarily foraged during the first few hours of the night, then illumination levels during the waxing and waning phases would be drastically different from a rodent's point of view. We did visually observe the kopje rodents emerging at sunset, but we did not collect any direct data on activity patterns throughout the night.

Alternatively, if rodents forage throughout the night, it may be that foraging costs differ at different times of the night. For instance, if foraging costs (e.g. thermoregulatory costs, interference competition) increase throughout the night, then the late window of darkness experienced during the waxing phase would be qualitatively different than the early window of darkness during the waning phase. In support, Kotler *et al.* (1994) measured GUDs of gerbils every hour during the night and found that GUDs often increased during the night during a new moon. Further studies are needed to determine whether the difference in GUDs between waxing and waning lunar phases is driven by patterns of rodent activity or/and changes in foraging costs throughout the night.

A second interesting lunar result is that GUDs did not differ between the waxing and full moon stages. Several studies have found that rodents decrease their activity from quarter to full moons, suggesting that predation costs increase with

illumination levels (Clarke 1983; Falkenberg & Clarke 1998; Kramer & Birney 2001). However, our results suggest the kopje rodents perceived a threshold of lunar illumination in which predation risk did not increase. Since our GUDs measured only that point in the night that the rodent experienced the lowest foraging costs, a positive monotonic relationship between light levels and predation risk may be obscured. For instance, if energetic reserves of rodents are lower during the full moon phase because of depletion of those energetic reserves (e.g. fat or caches) during the waxing stage, then the marginal value of the food increases and GUDs decrease. Therefore, comparisons between waxing and full stages become confounded by energetic state, as the mice may perceive higher predation risk, but lower energetic state increases the value of the food resources.

We view the interaction effect between microhabitat and lunar stage as further support for the importance of energetic reserves. The difference between open and cover GUDs was greater during the full moon stage, than the waxing stage. This larger difference was due to mice foraging the cover microhabitat to lower GUDs (Fig. 1). We hypothesize that after several days of reduced foraging during the waxing stage, the rodent's energetic reserves were low. Consequently, the rodents were more willing to accept higher predation risk. If so, we would have expected the open trays to have lower GUDs as well. However, if predation risk increased with illumination levels, and more so in the open, then the added predation risk may have cancelled out the lower energetic state effect to result in open GUDs being similar.

Plant secondary compounds

The plant secondary compounds altered the foraging behaviour of the rodents. Patches containing oxalate-treated seeds had higher GUDs than tannin-treated seeds and control seeds. During the first night of the habituation period, mice actually foraged the oxalic patches to a GUD of 29.0 ± 2.04 seeds. For the remaining nights, most patches had just one or two seeds foraged. These results suggest that the mice had to learn about the toxicity of the oxalates, and subsequently, they used taste, not smell, to determine if the seed contained oxalates. In contrast to oxalates, tannin-treated seeds were foraged continuously throughout the whole experiment. Such results match the biological roles of each secondary

compound. Oxalates are a qualitative defence, which function as physiological toxins and can result in renal damage and/or in death (Hodgkinson 1977), and not surprisingly, mice almost completely avoided the oxalates. In contrast, tannins are a quantitative defence which function to reduce a food's digestibility (Swain 1979). Though not significantly different from the control, the tannin GUD mean was higher than control trays and the difference between the sample means would be biologically interesting, if found to be significant with a larger sample size.

Several considerations should be taken into account when interpreting the scope of these results. First, we did not measure the actual concentration of tannins and oxalates in the seeds. We followed a soaking procedure similar to Schmidt *et al.* 1998 which produced concentrations of each toxin in their natural ranges (1.74% for tannins and 5.3% for oxalates). However, it is not known what normal ranges the mice experience on the kopje. Second, the effect of a plant secondary compound can be affected by other factors, such as predation risk and water availability (Schmidt 2000; Dearing *et al.* 2001). All our stations were in cover locations, our inference are limited to those safer locations.

CONCLUSION

Small mammals can have profound effects on the dynamics of African savannas, but we know very little about the ecology of many of these species (Keesing 2000). Our study identified several environmental factors that strongly influence the foraging decisions of two African rodents: microhabitat, lunar stage, and plant secondary compounds. These results and further studies exploring the foraging decisions of small mammals should provide useful insights into understanding the role of small mammals in African savannas.

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