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Author(s): Benjamin G. Fanson, Kerry V. Fanson & Joel S. Brown

Source: African Zoology, 45(2):265-272. 2010.

Published By: Zoological Society of Southern Africa

DOI: <http://dx.doi.org/10.3377/004.045.0205>

URL: <http://www.bioone.org/doi/full/10.3377/004.045.0205>

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Ecological factors affecting the foraging behaviour of *Xerus rutilus*

Benjamin G. Fanson^{1*}, Kerry V. Fanson² & Joel S. Brown³

¹Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

²Department of Biological Sciences, Purdue University, 915 West State St., West Lafayette, IN 47907, U.S.A.

³Department of Biological Sciences, University of Illinois Chicago, 845 W. Taylor St., Chicago, IL 60607, U.S.A.

Received 25 November 2009. Accepted 31 May 2010

The African unstriped ground squirrel (*Xerus rutilus*) is widely dispersed across various habitats in East Africa and hence encounters a diverse suite of predators and plant communities. It is not known how different habitats and plant characteristics affect the foraging behaviour of *X. rutilus*. We used giving-up densities (GUDs) as a measure of foraging efficiency to explore the foraging costs of environmental heterogeneity. To determine foraging efficiency across spatial scales, we established food patches in two microhabitats (open and cover), which were nested within three habitats (koppie, edge and bushland). When foraging in a cover microhabitat, foraging efficiency decreased away from the koppie, but when in the open microhabitat, foraging efficiency was lowest near the koppie edge. Second, to determine foraging efficiency with common plant toxins, we presented the squirrels with seeds soaked in either tannic acid, oxalic acid or distilled water (control). Foraging efficiency did not differ between tannic-treated and control seeds, but oxalic-treated seeds had higher GUDs. Overall, our results suggest that *X. rutilus* is a remarkably efficient forager across multiple axes of environmental heterogeneity, which may have intriguing consequences for the ecological community.

Key words: foraging behaviour, GUDs, *Xerus rutilus*, koppie.

INTRODUCTION

Analysing an animal's feeding behaviour can provide a window into its ecology. Animals must constantly make decisions about when, where and what to eat. The consequences of these feeding decisions can have cascading effects through both higher and lower trophic levels (e.g. predator behaviour, seed dispersion) (Freeland & Janzen 1974; Keesing 2000). Different foraging situations possess varying costs (e.g. energetic, predation, missed opportunities) and benefits (e.g. energy, nutrients); animals should attempt to maximize the net benefits through their foraging decisions (Charnov 1976; Brown 1988). Thus, by observing foraging decisions in various environmental situations, it is possible to reveal the cost and benefits of foraging and thus obtain insights into the ecology of the animal.

One method for dissecting these costs and benefits is using giving-up densities (GUDs) in depletable foraging patches (Brown 1988; Brown 2001). As an animal forages in a depletable patch, the rate of food acquisition (harvest rate) decreases, resulting in the animal eventually quitting the patch. This quitting harvest rate indicates the point that the

animal perceives the costs of continued foraging to be more than the benefits. GUDs (the amount of food left in the patch) act as a surrogate for these quitting harvest rates (Brown 1988) and have become a common technique for assessing a species' foraging efficiency (e.g. Gutman & Dayan 2005; Perrin & Kotler 2005; Reed *et al.* 2005). Lower GUDs indicate higher foraging efficiency.

Many studies have employed GUDs to explore habitat and microhabitat preferences. With regards to microhabitat, studies generally find that when presented with identical foraging patches, GUDs are lower in cover microhabitats (under rocks, near bushes or trees) than in open microhabitats (no/minimal overhead cover) (e.g. Brown 1988; Morris 1997; Thorson *et al.* 1997). Most foraging costs are controlled for by using identical patches, so this GUD difference probably reflects a difference in predation costs. A major exception to the 'cover' preference is when snakes pose a major threat, which further supports the hypothesis that GUDs are reflecting differential predation risk (Bouskila 1995). Similarly, studies have looked at habitat preferences by placing identical patches at the boundary of distinct habitats (e.g. Brown *et al.* 1992; Morris 1997).

*Author for correspondence. E-mail: bfanson@gmail.com

Besides choosing where to forage, a forager needs to decide what to eat. Consuming plant toxins can be metabolically expensive and potentially dangerous (Freeland & Janzen 1974). Two important types of plant chemical defences include quantitative plant defences (digestibility reducers) and qualitative plant defences (physiological toxins) (Schmidt 2000). Quantitative defences diminish the physiological uptake of nutrients, whereas qualitative defences disrupt specific biochemical reactions and can cause direct fitness consequences for the forager (Rosenthal & Berenbaum 1992).

Ground squirrels in sub-Saharan Africa are limited to four species of *Xerus*, which hardly overlap in distribution (Nowak 1999). This pattern is surprising since the sub-Saharan landscape provides a wide array of habitats, from desert to savanna to forest, often associated with rich biodiversity. The African unstriped ground squirrel (*Xerus rutilus* Cretzschmar) inhabits the arid regions of East Africa (Kingdon 1984). *X. rutilus* is a conspicuous diurnal forager, despite the rich array of avian, reptilian, and mammalian predators in East African arid regions. Furthermore, across its range, *X. rutilus* encounters a diverse array of plant species and hence likely various plant chemical defences. It is not known how *X. rutilus* adjusts its foraging behaviour to mitigate these predation risks or plant defences.

In this study, we examined the foraging efficiency (using GUDs) of the African unstriped ground squirrel (*Xerus rutilus* Cretzschmar) along several axes of environmental heterogeneity in Ngulia Rhino Sanctuary, Kenya. Specifically, we explored foraging efficiencies between habitat types (bushland *vs* bushland-koppie edge *vs* koppie), microhabitat types (cover *vs* open), and plant toxin types (seeds impregnated with plant secondary compounds *vs* control seeds). Foraging efficiencies should reveal insights into the foraging costs for *X. rutilus* under different environmental conditions. Since *X. rutilus* appears to be a generalist and conspicuous diurnal forager, we predicted that *X. rutilus* should show only minor differences in foraging efficiencies across habitat, microhabitat, and toxin types.

MATERIALS & METHODS

Study site and study species

We conducted the study near the East gate of the Ngulia Rhino Sanctuary, Tsavo West National Park, Kenya. The study site consisted of a single,

isolated koppie surrounded by *Acacia-Commiphora* bushland. The koppie, an insular rock outcropping, was comprised of a granitic-gneissic rock base littered with large boulders (~10 m in height × ~70 m in breadth × ~150 m in length). The koppie hosted several plant species that were distinct from the surrounding bushland, but this vegetation was sparsely distributed. A dirt road surrounded two-thirds of the koppie's edge, providing a distinct boundary between koppie and bushland habitats. The main predators of the squirrels were avian raptors (e.g. tawny eagle (*Aquila rapax*), bateleur (*Terathopius ecaudatus*), martial eagle (*Polemaetus bellicosus*)), but several mammalian predators were also observed during the day near the koppie (e.g. African leopard (*Panthera pardus*), black-backed jackal (*Canis mesomelas*)). Almost no signs of snakes were observed at the study site.

The African unstriped ground squirrel (*X. rutilus*; c. 300 g, 200–255 mm) is an important pest species and causes economic losses to local communities (A. Noor, pers. comm.). Surprisingly, very little is known about the ecology of this conspicuous species. It is known that they forage on seeds, leaves, fruits, and insects (Coe 1972). O'Shea (1976) presents the most comprehensive study of their behaviour, focusing mainly on movement patterns and social interactions, though some foraging behaviours are noted. At our site, *X. rutilus* used ground burrows surrounding the koppie for refuge.

Measuring foraging efficiency

To quantify foraging efficiency, we established artificial foraging patches and measured the giving-up density (GUD: the amount of food left after a foraging bout). Each foraging patch consisted of a round, plastic tray (11 cm deep × 27 cm in diameter) filled with 40 pieces of popcorn thoroughly mixed into 3.0 l of sifted sand. Two extra seeds were placed on the surface of the sand as an indicator of foraging activity. Foraging sessions lasted from dawn to dusk (~12 h). At dusk, the trays were collected, the sand was sifted for remaining seeds, and the trays were recharged for the next foraging session. Remaining seeds were cleaned, counted and weighed to determine a forager's GUD.

This study was conducted during April to May 1999. Prior to each experiment, a habituation session was conducted for at least two days to expose the squirrels to the contents and location of the trays. Once experiments began, all data were collected

on consecutive days, except in a small number of instances when weather (e.g. rain) or other natural disturbances (e.g. destruction of trays by elephants) precluded data collection. In addition, general visual observations of *X. rutilus* were made from the top of the koppie between the hours of 07:30 and 11:00 and 13:30 and 17:30 almost every day. These data were used to ensure only *X. rutilus* were exploiting the trays and general foraging patterns with the trays.

Experiments

Spatial scales. To measure foraging efficiency at the habitat (koppie *vs* bushland) and microhabitat (open *vs* cover) levels, we constructed three lines that radiated from the centre of the koppie and extended into the bushland. Lines were spaced ~60 m apart and consisted of four foraging stations (-15 m, 0 m, 15 m, and 30 m). Each foraging station had two trays: one beneath a shrub (cover) and the other 1.5–2 m away in less protected location (open) (Fig 1). Each tray contained 40 popcorn kernel halves (3.0 ± 0.1 g; $\bar{x} \pm$ S.D.). After the habituation period, seven days of data were collected over a span of ten days.

Plant secondary compounds. To examine the effect of secondary compounds on diet selection, we chose two common secondary compounds: tannins (a quantitative plant defence; Swain 1979) and oxalates (a qualitative plant defence; Hodgkinson 1977). Tannins can reduce the digestibility and assimilation of protein in some vertebrate consumers. Oxalates, on the other hand, are absorbed into the blood and cause blood coagulation and renal damage.

We soaked popcorn kernels in saturated solutions of tannic acid (5% solution; Hopkin & Williams, Chadwell, U.K.), oxalic acid (15% solution; May & Baker, Lagos, Nigeria), or 100% distilled water (control). After soaking for two days, the popcorn kernels were sundried for two days. Four tray stations were then placed at widely-spaced (>50 m), covered locations in the bushland. Each station contained three trays (one tray for each treatment). Trays were charged with 40 whole popcorn kernels (6.2 ± 0.2 g). After the habituation period, data were collected for three consecutive days.

Data analysis

Using PROC MIXED (SAS, 9.1), we created two mixed linear models, one for each experiment. We constructed covariance structures for each analysis

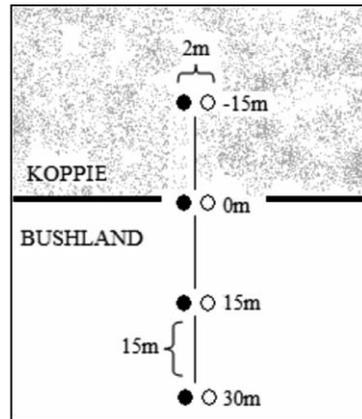


Fig. 1. Diagram of the structure of a single line in the spatial experiment. There are four station locations: -15 m (koppie), 0 m (edge), 15 m (bushland), and 30 m (bushland). Filled-in circles represent cover microhabitat trays and open circles indicate open microhabitat trays.

to accommodate correlations within an individual and across time. Based on our visual observations, we assumed that each foraging station (both open and cover microhabitats) was foraged by one individual.

In developing each model, all variables except 'individual' were treated as fixed effects: 1) microhabitat, location, and day for the spatial model, or 2) toxin treatment and day for the toxin model. The number of seeds left (instead of weight) was the response variable, because it was more normally distributed. We then constructed two separate covariance-variance matrices for each model. To deal with the microhabitat correlations, we created an unstructured covariance matrix for microhabitat for both models. To deal with correlation across time, we created a first-order autoregressive matrix across days, which reduced the correlation between days further apart in time (see Littell *et al.* 2006 for more details). We then took the Kronecker product of the two matrices for each model to obtain the final covariance matrix (Dayanand & Shantha 2001). We compared these more complex covariance structures with simpler covariance structures, but the more complex model always performed significantly better as determined by the Bayesian Information Criterion and Akaike's Information Criterion Corrected

Finally, we looked for the most parsimonious model by removing interactions where $P > 0.10$. We used this P -value criteria because marginally significant interactions can provide important caveats for inferences on main effects. We tested all

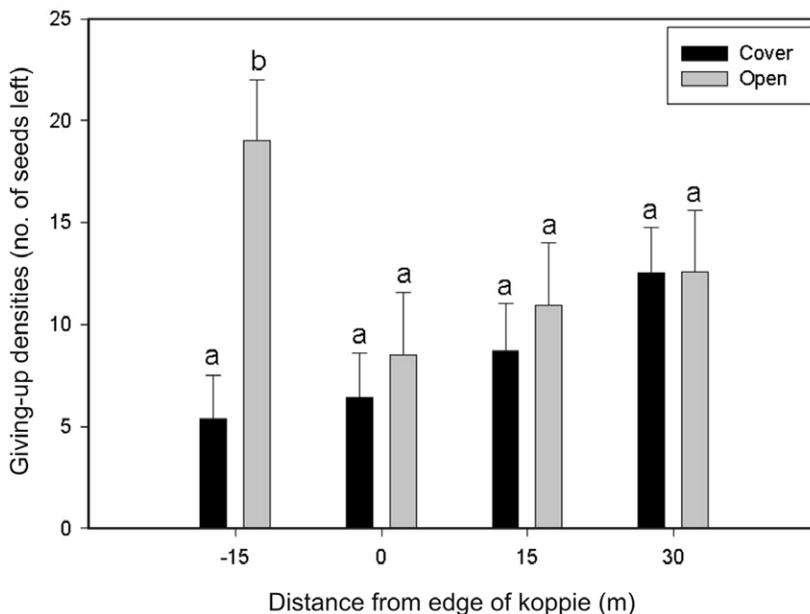


Fig. 2. GUDs for the Spatial experiment. Different letters indicate significant differences in means ($P < 0.05$). Error bars represent one standard error.

residuals for normality using the Shapiro-Wilk test and for homoscedasticity using Bartlett's test (as dictated by the covariance structure). None of these tests were significant. Means are displayed with \pm S.E., unless otherwise indicated.

RESULTS

Overall foraging efficiency

We estimated that a total of nine squirrels foraged in the trays, as determined by maximum number

Table 1. Results for the Spatial Mixed Linear Model. For the final model, all fixed effects and all interactions with $P < 0.10$ were kept. See text for description of how variances and correlation were calculated.

Source	d.f.	F-value
Fixed effects		
Microhabitat	1, 21	12.28**
Location	3, 25.2	1.04
Day	6, 52.4	2.03
Location \times microhabitat	3, 20.9	6.04**
Variances		
		Estimate
Microhabitat: cover		75.39
Microhabitat: open		140.44
Correlation		
		Estimate
Day		0.15

** $P < 0.01$.

of squirrels simultaneously seen. Overall, squirrels foraged trays to a mean GUD (\pm S.D.) of 0.73 ± 0.90 g ($n = 181$) and foraged 91% of the trays. For the spatial experiment, the mean GUD (\pm S.D.) was 0.64 ± 0.79 g (or 10.37 ± 11.36 half seeds; $n = 150$), and for the toxin experiment, 1.19 ± 1.25 g (or 7.90 ± 8.32 whole seeds; $n = 31$).

Spatial model

Microhabitat use depended on whether or not the squirrel was on the koppie ('Location by Microhabitat' interaction; Table 1). When on the koppie, squirrels foraged less in the open compared to the cover microhabitat (-15 m location: $\Delta\bar{x} = 13.68 \pm 2.49$ seeds, $t_{20.4} = 5.49$, $P < 0.001$; Fig 2). However, when in the bushland and at the edge of the koppie, microhabitat means did not differ significantly. We then tested pairwise comparisons between locations for each microhabitat type. The open microhabitat on the koppie was significantly higher than edge and bushland open microhabitats (Fig 2; *vs* 0m: $\Delta\bar{x} = 10.52 \pm 2.45$ seeds, $t_{26} = 4.29$, $P = 0.002$; *vs* 15 m: $\Delta\bar{x} = 8.1 \pm 3.24$, $t_{26} = 2.50$, $P = 0.02$; *vs* 30 m: $\Delta\bar{x} = 6.5 \pm 2.54$, $t_{26} = 2.55$, $P = 0.02$). However, none of the cover comparisons were significant, suggesting that the difference on the koppie is due to higher GUDs in the open microhabitat. To further investigate any possible trends over koppie-bushland spatial axis, we

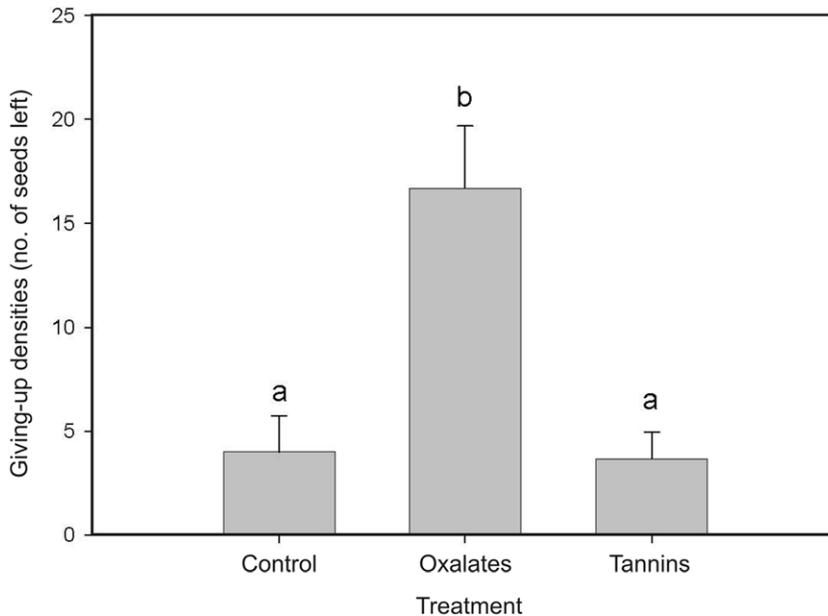


Fig. 3. GUDs for the Plant Secondary Compound experiment. Different letters indicate significant differences in means ($P < 0.05$). Error bars represent one standard error.

conducted a trend analysis testing for linear and quadratic trends across bushland location within each microhabitat (Littell *et al.* 2006). In the cover microhabitat, the trend analysis supported a linear increase in GUDs from the koppie to the bushland (Fig 2: linear, $F_{1,20.6} = 5.71$, $P = 0.03$; quadratic, $F_{1,20.6} = 0.38$, $P = 0.54$). A marginally significant quadratic relationship was found for the open microhabitat trays, due to the 0 m and 15 m locations having lower GUDs than the -15 m and 30 m

locations (Fig 2: linear, $F_{1,26.1} = 1.63$, $P = 0.21$; quadratic, $F_{1,26.3} = 4.02$, $P = 0.06$). Finally, the open microhabitat had twice the variance estimate as the cover (Table 1). This pattern was consistent across locations.

Table 2. Results for the Plant Secondary Compound Mixed Linear Model. For the final model, all fixed effects and all interactions with $P < 0.10$ were kept. See text for description of how variances and correlation were calculated.

Source	d.f.	F-value
Fixed effects		
Treatment	2, 4	17.64*
Day	2, 4	0.46
Day \times treatment	4, 5	3.46
Variances		
		Estimate
Treatment: control		54.13
Treatment: tannins		21.35
Treatment: oxalates		111.16
Correlation		
		Estimate
Day		0.68

* $P < 0.05$.

Plant secondary compounds model

Plant secondary compounds had a strong effect on GUDs (Table 2; Fig 3). Squirrels foraged much less in trays containing oxalic-treated seeds (*vs* tannins: $\Delta\bar{x} = 13.00 \pm 3.05$ seeds, $t_6 = 4.25$, $P < 0.001$; *vs* control: $\Delta\bar{x} = 12.67 \pm 3.19$ seeds, $t_6 = 3.97$, $P < 0.001$). Finally, variance estimates differed among the toxins, with oxalic-treated seeds having the highest variance and tannic-treated seeds having the lowest.

DISCUSSION

Overview of foraging efficiency

The overall GUD results for *X. rutilus* suggest that this species is a very efficient forager. In general, this species had extremely low GUDs (~ 0.24 g/l). In fact, when the foraging trays were filled with more desirable food types (peanuts, sunflower seeds, maize), the squirrels foraged the trays to completion. Popcorn kernels had to be cut in half to prevent the trays from being emptied by squirrels. Using the exact same tray design, study site, and popcorn kernels, *Grammomys dolichurus*

and *Acomys cahirinus* had GUDs of ~ 3.74 g/l (Fanson *et al.* 2008). We visually observed squirrels foraging in a patch up to 15 min in order to fully deplete the patch.

Spatial scale

The foraging decisions of *X. rutilus* were influenced by a combination of habitat and microhabitat factors. Looking at just the habitat scale, *X. rutilus* appeared to forage equally across the mosaic of habitat types (koppie, edge, and bushland). However, the squirrels foraged microhabitats differently depending on the location of the station (Fig. 2). At the edge and in the bushland, a squirrel's foraging efficiency was not affected by microhabitat, but once on the koppie, squirrels foraged less efficiently in the open microhabitat. There are two potential explanations for this pattern.

First, the open microhabitat on the koppie may have higher thermoregulatory costs, which would increase GUDs (Brown 1988). The rocky substrate and the lack of shade may increase surface temperatures on the koppie, thus increasing the energetic cost of foraging and decreasing the squirrel's foraging efficiency. However, open trays at the edge stations should have had similar energetic costs since they had very similar substrate and solar exposure.

We feel the more likely explanation is that predation costs may differ between the open microhabitat on koppie and all other microhabitats. Such an explanation has been advocated for a variety of rodents expressing differential use of microhabitats (e.g. Kotler & Brown 1988; Longland & Price 1991; Schmidt 2000). In support of the second explanation, we observed that the antipredator response of *X. rutilus* differed when it was on the koppie. When frightened in the bushland, *X. rutilus* would flee through the bushland in a capricious manner. On the koppie, *X. rutilus* fled directly to the bushland, rather than using the numerous rock crevices on the koppie for protection. Thus, *X. rutilus* may feel more vulnerable when in the open microhabitat on the koppie, but the cover microhabitat mitigates this perceived predation risk.

The trend analysis of GUDs from the koppie into the bushland for each microhabitat revealed a linear increase in GUDs for the bush microhabitat and a possible quadratic relationship for the open microhabitat. Thus, *X. rutilus* adjusts its foraging behaviour in relation to the koppie's edge. Our

results suggest that *X. rutilus* has the lowest GUDs on the koppie when in the bush microhabitat and near the koppie edge when in the open microhabitat. The linear pattern in cover GUDs suggests that predation risk decreases near and on the koppie. Interestingly, the quadratic pattern of GUDs from the koppie into the bushland has been found for rock hyrax (*Procavia capensis*) (Kotler *et al.* 1999). Unlike *X. rutilus*, rock hyrax use koppies as their central refuge and retreat back to the koppie when alarmed. Our koppie was similar to Kotler *et al.* (1999) site with a barren vegetation strip at the edge of the koppie and increasing vegetation further away from the koppie. Thus, *X. rutilus* may perceive lower predation risk near the edge of the koppie because greater visibility of surroundings, as suggested for rock hyrax.

Plant secondary compounds

Xerus rutilus had a much lower affinity for oxalic-treated seeds than for tannic-treated seeds or control seeds. These results suggest that tannins are not perceived as a foraging cost for *X. rutilus*, but oxalates are. Fox squirrels under low predation risk showed similar foraging patterns for these two plant toxins (Schmidt 2000).

In interpreting these results, it is important to consider the biological actions of these toxins. Tannins are merely a feeding deterrent that reduces food digestibility (Swain 1979). Oxalates, on the other hand, are a physiological toxin that decreases blood coagulation, leads to renal damage, and can result in death (Hodgkinson 1977). Interestingly, *X. rutilus* was still able to forage oxalic-treated seeds (oxalic GUDs = ~ 5.7 seeds/l), but the large variance estimate suggest that the squirrels were not consistent in their foraging of the oxalic trays. Nocturnal rodents inhabiting the same area foraged only one or two oxalic-treated seeds at first and then completely avoided them (Fanson *et al.* 2008). One caveat is that we observed squirrels scatter hoarding the seeds (also noted by O'Shea (1976)). *Xerus rutilus* may be caching oxalic-containing seeds because the oxalic acid increases storability and the oxalates may degrade over time, thus providing a future resource. This hypothesis has been supported for other caching species (e.g. Steele *et al.* 1993; Dearing 1997). This hypothesis may also explain the high variance, as trays were mostly avoided unless the squirrel decided to hoard the seeds.

One potential caveat is whether the toxin-treated seeds had biologically relevant concentrations of

the plant secondary compounds. While we were not able to analyse the concentrations of the secondary compounds in our treated seeds, Schmidt *et al.* (1998) followed a similar soaking protocol and found concentrations of tannins and oxalates in their seeds to be 1.74% and 5.3%, respectively. These concentrations fall within the natural range of tannins (Swain 1979) and oxalates (Hodgkinson 1977) found in plants. However, Schmidt *et al.* used sunflower seeds which likely have different absorption properties from popcorn kernels. Using the same soaking methodology with popcorn kernels, two nocturnal rodents foraged control, tannin, and oxalic trays to GUDs of 22, 31, and 40 seeds/tray (Fanson *et al.* 2008).

Additionally, measuring foraging efficiency at only one concentration of tannins or oxalates provides only a limited perspective, as nature probably contains a gradient of concentrations. Tannins may be present at much higher quantities in Ngulia and *X. rutilus* may be sensitive to those concentrations. Furthermore, interesting interactions between secondary compounds and other environmental variables (e.g. predation risk, water) can complicate any general conclusions about oxalates and tannins (Schmidt 2000; Dearing *et al.* 2001). Thus, conclusions drawn from our secondary compound data are only limited in scope, but they provide potential directions for future research.

CONCLUSION

Xerus rutilus displays impressive foraging efficiency across both space and plant toxin. Most squirrels in North America studied so far have shown strong preference for cover microhabitat (e.g. *Ammodramus*, *Spermophilus harrisi*, *Spermophilus tereticaudus*: Brown 1988; *Spermophilus tridecemlineatus*: Thorson *et al.* 1997; *Sciurus niger*: Schmidt 2000). Thus, the ability of *X. rutilus* to exploit both microhabitats in the savanna equally may be uncommon among squirrels. Though, foraging efficiencies were lower in the open on the koppie, *X. rutilus* still foraged the patches to modestly low densities. Additionally, *X. rutilus* appears unaffected by tannins and modestly foraged oxalic containing foods. The degree to which *X. rutilus* excels at being a generalist probably has interesting ecological consequences. Seed predation by rodents can strongly affect patterns of seed distribution (Keasing 2000). Additionally, varying foraging efficiencies across environmental axes have been suggested to facilitate species coexistence

(Kotler & Brown 1988; Guerra & Vickery 1998). Thus, further research exploring the consequences of *X. rutilus* foraging behaviour should prove insightful.

ACKNOWLEDGEMENTS

We wish to express our thanks to the Kenya Wildlife Services (KWS) for providing permission and logistical support for his research. Without the financial support Kalamazoo College this study would not have been possible. Additionally, we greatly appreciate the invaluable assistance of the KWS staff at the Ngulia Rhino Sanctuary in Tsavo West National Park, especially, Adan Noor, Gabriel, Mzee, and Dave. We thank Burt Kotler and an anonymous reviewer for insightful comments on the manuscript. Finally, we express our gratitude to the Biology Department of the University of Nairobi for conceptual guidance.

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Responsible Editor: G.N. Bronner