Short Communications

Seed predation by nocturnal rodents in an African savanna ecosystem

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The small mammal community in *Acacia* savanna consists of three omnivorous nocturnal rodent species, *Mastomys natalensis*, *Saccostomus campestris* and *Aethomys chrysophilus*, which eat varying proportions of seed in their diet. From a seed removal experiment, it was found that rodents preferentially selected *Acacia tortilis* seeds. The annual *Acacia* seed consumption by rodents in a South African savanna ecosystem was analysed by using estimates of rodent population densities, diet composition, seed predation by captive rodents and published estimates of field metabolic rates. Total seed consumption was estimated to represent 1,6–4,1% of the annual seed crop of *A. tortilis*, 0,7–0,9% of the annual seed crop of *A. nilotica* and 9,3–25,0% of the annual seed crop of *A. karroo*. Granivory of *A. nilotica* seeds by rodents may have a negligible effect upon seedling recruitment. However, rodent predation of *A. tortilis* and *A. karroo* seeds may have important implications on seed survival and later seedling recruitment.

Die kleinsoogdier-gemeenskap in *Acacia*-savanna bestaan uit drie naglewende omnivore knaagdierspesies, nl. *Mastomys natalensis*, *Saccostomys campestris* en *Aethomys chrysophilus*. Die dieet van die spesies bestaan uit variërende proporsies van sade. Volgens die uitslae van 'n saadverwyderingsproef, het hierdie knaagdiere *Acacia*-sade verkies. Skattings van bevolkingsdigtheid, dieet-samestelling, saadpredasie deur knaagdiere in gevangenskap en gedokumenteerde metaboliese tempo's, is gebruik om die jaarlikse *Acacia*-saadverbruik deur knaagdiere in 'n Suid-Afrikaanse savannasisteem te bepaal. Die totale saadverbruik het 1,6–4,1%; 0,7–0,9% en 9,3–25,0% van die onderskeidelike saadproduksie van *A. tortilis*, *A. nilotica* en *A. karroo* uitgemaak. Die verbruik van *A. nilotica*-sade deur knaagdiere het moontlik geen effek op saailingwerwing, terwyl predasie op *A. tortilis* en *A. karroo* moontlik belangrike gevolge toon in terme van saadoorlewing en saailingwerwing.

Rodents are important seed predators in communities such as thickets of alien *Acacias* in the south-western Cape (David 1980; Holmes 1990). Seed predation may affect community structure (Brown, Davidson, Munger & Inouye 1986), e.g. seed selectivity may be critical to plant species survival. Although rodents have been reported to feed on *Acacia* seeds (Kerley 1990; 1991), their impact on the *Acacia* savanna community has not been documented.

Fluctuations in the abundance of natural food sources may determine the impact of rodents as *Acacia* seed predators. Fewer *Acacia* seeds may be consumed during summer when there are many alternative food sources and more seeds may be taken in winter when other food resources are low. Rodent densities also fluctuate considerably with changing abiotic factors such as rainfall (Christian 1977; Nel 1992), and although some rodent species breed throughout the year, densities in semi-arid communities may be higher in summer than in winter (Skinner & Smithers 1990; Kerley 1992b).

This study was designed to (1) determine rodent seed selectivity and seed removal of the umbrella thorn, *Acacia tortilis* Forsk. and the scented pod, *A. nilotica* Hayne in two different patches of *Acacia* savanna in different seasons; (2) assess the species composition and population density of seed feeding rodents and, (3) determine the importance of rodents as consumers of *A. tortilis*, *A. nilotica* and the sweet thorn, *A. karroo* (Hayne) seeds in an African savanna ecosystem.

Research was carried out in the winter of 1991 and summer of 1992 at Nylsvley Nature Reserve (24°40'S; 28° 43'E) in the northern Transvaal, South Africa. *Acacia* savanna comprises 13% of the vegetation. The total rainfall received in 1991 and 1992 was only 149,1 mm and 268,3 mm, respectively — close to the lowest rainfall ever recorded.

The study sites held three species of nocturnal, seed-eating rodents: the multimammate mouse, *Mastomys natalensis* A. Smith, the pouched mouse, *Saccostomus campestris* Peters and the red velt rat, *Aethomys chrysophilus* de Winton. No diurnal rodents were captured.

Acacia seed selectivity and removal by rodents was assessed at two different 1-ha patches of *Acacia* savanna (sites 1 & 2). Each site was dominated by *A. tortilis* with scattered patches of *A. nilotica* and *A. karroo*. Pods were provided on petri dishes elevated 6 cm off the ground to exclude predatory ants (Mares & Rosenzweig 1978; Parmenter, MacMahon & Van der Walt 1984). Seed removal and selectivity were quantified by supplying 20 g of *A. nilotica* and 10 g of *A. tortilis* pods (weights comprised equivalent numbers of seeds) at eight randomly selected locations within each site. Owing to a pod shortage, the seed removal experiment was not possible with *A. karroo*. The dishes were closed during the day and opened at dusk.

After four days, the remaining *Acacia* pods were collected. Since direct observations of captive rodents revealed that seeds were removed leaving an empty pod, seed removal could be determined by subtraction, knowing the dry weights of *A. tortilis* and *A. nilotica* pods and seeds. It was assumed that all removed seeds were eaten *in situ* or hoarded and consumed later.

Although fallen *Acacia* pods were only naturally available during winter, the experiment was carried out in winter and summer to determine whether *Acacia* seed predation altered the availability of alternative food sources.

Preference indices were calculated from the formula $P = (U_i / A_i) / \Sigma(U_i / A_i)$, where U_i = utilization, the weight of seeds removed, A_i = availability, the weight of seeds supplied (Kelrick, MacMahon, Parmenter & Sisson 1986).

Rodents were trapped both in summer and winter to determine approximate seasonal differences in their densities. Fifty Sherman traps (7,5 × 9 × 23 cm) were placed at both sites at intervals of 10–15 m in a grid arrangement over

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an area of 0,54 ha. Traps were baited with sunflower seeds and were checked from dawn onwards for four consecutive nights to avoid drawing in and trapping mammals from outside the study area (Hulme 1990). Captured rodents were weighed, identified to species, marked by toe-clipping and released. All faecal pellets produced by identified rodents within the Sherman traps were collected on the first day of trapping in winter for later examination (Churchfield 1984). Recaptures were noted and rodent densities were calculated (Caughley 1976).

In order to evaluate the impact of rodents on *Acacia* seeds in the wild, it was necessary to determine the diet of wild rodents, rodent predation of *Acacia* seeds in captivity, seed production and seed availability in the wild.

Dietary analysis was carried out by microscopic examination of collected faecal pellets (Churchfield 1984). Faecal remains were separated into three categories: vegetation, seeds and seed fragments and insects. The percentage area occupied on a gridded slide by each constituent within each sample (a faecal pellet) was determined by the method of Hansson (1970). Between 9 and 14 faecal pellets were sampled from pooled pellets of each species. Each pooled sample consisted of pellets from 4–6 mice. Although small, this was a suitable sample size, since the percentage of prey types levels off rapidly with pellet sample size (Churchfield 1984). There is a good correlation between the proportion of seeds in the diet and the proportion in the faecal pellet (Kerley 1990).

In total, six *S. campestris*, seven *M. natalensis* and six *A. chrysophilus* were housed in small mammal cages (30 × 20 × 20 cm) in a laboratory at Nylsvley during winter 1991 and 1992, and fed equal weights of pods of *A. tortilis*, *A. nilotica* and *A. karroo*. Daily seed consumption was recorded for 12 days. Since faecal analysis showed that the rodents were not solely granivorous, this diet was supplemented with grasses, herbaceous vegetation and seeds (from *Acacia* savanna), food pellets and sunflower seeds. Given that the captive rodents had a free choice of a variety of natural and artificial foods, all presented in excess, the data provide a crude indication of possible field consumption rates of *Acacia*. As later calculations show, major departures from these rates would be necessary to alter the conclusion of this paper.

A. tortilis, *A. nilotica* and *A. karroo* pod production was assessed within random belt transects (20 × 100 m) in *Acacia* savanna throughout Nylsvley. Although *Acacia* may be patchily distributed, since five areas were sampled throughout the *Acacia* savanna, it is considered that the data represent the reserve as a whole reasonably well. Pod production per tree was determined by a 'cage count method' (Miller 1993). From counts of the number of trees per ha, it was possible to estimate pod production per ha. Seed production per ha could be calculated from the mean number of seeds per pod (mean number of seeds per pod ±*SE*: *A. tortilis*, 6,1 ± 0,6; n = 100 pods. *A. nilotica*, 7,9 ± 0,4; n = 78 and *A. karroo*, 7,3 ± 0,4; n = 62).

The duration of *Acacia* seed availability in the wild was determined by noting the day on which mature pods were first and last present on the ground below *Acacia* trees in the two study sites.

The annual impact of rodents on *Acacia* seeds was calculated from a modification of the 'energetics approach' (Kerley 1992b). The field metabolic rate of rodents was multiplied by the winter population size to give the energy requirements (kJ/ha/d) of rodents. The energy provided by the seeds was estimated from the proportion of seeds in the diet, assuming a digestive efficiency of 85,0% (Droze 1975; Soholt 1973). The weight of seeds consumed daily was calculated using the energy value of 7,11 kJ/g (after Kerley 1989). The number of seeds of each *Acacia* species consumed on a monthly basis was then calculated using results on daily *Acacia* seed consumption by captive rodents (Miller 1993) and the average weight of *Acacia* seeds (Coe & Coe 1987). The percentage of the seed crop consumed by different rodent species was predicted from measurements of the *Acacia* seed crop (Miller 1993).

Acacia seed removal varied significantly between seasons, sites and *Acacia* species (3-way ANOVA, seasons: $F_{1,56}$ = 33,67, $P < 0,05$; sites: $F_{1,56}$ = 5,94, $P < 0,05$; and *Acacia* spp.: $F_{1,56}$ = 17,25, $P < 0,05$; Table 1). Significantly more *A. tortilis* and *A. nilotica* seeds were removed in winter than in summer at sites 1 & 2 (t_{62} = 5,80; $P < 0,05$). Significantly more *A. tortilis* seeds were taken than *A.*

Table 1 The weight (g), number and percentage of offered *A. tortilis* and *A. nilotica* pods and seeds removed by rodents in different seasons in the wild after 4 days, and rodent feeding preference for *Acacia* seeds (Kelrick *et al.* 1984)

Season	Site	*Acacia* species	Wt seeds + pods removed (g)	No. seeds removed	% of pods removed	Preference	(Variance)
Summer 1991	1	*A. tortilis*	26,9	373	33,6	0,101	(0,020)
	1	*A. nilotica*	12,9	39	8,6	0,024	(0,001)
	2	*A. tortilis*	11,5	159	14,4	0,120	(0,009)
	2	*A. nilotica*	0,9	3	0,6	0,004	(0,001)
Winter 1992	1	*A. tortilis*	64,1	889	80,1	0,087	(0,015)
	1	*A. nilotica*	55,8	612	34,9	0,038	(0,007)
	2	*A. tortilis*	36,9	171	46,1	0,078	(0,026)
	2	*A. nilotica*	44,1	136	27,6	0,047	(0,038)

nilotica seeds in summer and winter at sites 1 & 2 (t_{62} = 4,15; $P < 0,05$). Significantly more *Acacia* seeds were also removed from site 1 than from site 2 in summer and winter (t_{62} = 2,44; $P < 0,05$). *A. tortilis* was preferred to *A. nilotica* at both sites 1 & 2 (Table 1).

The community was dominated by *M. natalensis*, with lower numbers of *S. campestris* and *A. chrysophilus*. More rodents appeared to be present in site 1 than in site 2, and summer densities were apparently greater than winter densities (Table 2), although statistical comparisons cannot be carried out to confirm these apparent differences.

S. campestris, *M. natalensis* and *A. chrysophilus* consumed vegetation, seeds and insects in their natural diet (Table 3). In captivity *M. natalensis*, *S. campestris* and *A. chrysophilus* preferred *A. tortilis* seeds (Figure 1). Predicted seed loss varied among the *Acacia* species (Table 4).

The relative impact of rodents as *Acacia* seed predators clearly depends on their population density, seed composition in their diet and fluctuations in alternative food sources. Rodent densities in this study were lower than densities found by Korn (1987), and varied from 1–6 rodents per ha in unburnt *Acacia* savanna at Nylsvley. There was a severe drought at Nylsvley in 1991 and 1992, and the low rainfall may have reduced rodent population densities (Christian 1977; Nel 1992), possibly by altering foliage density (Ferreira 1992).

Diet composition compares favourably with other studies. *S. campestris*, *M. natalensis* and *A. chrysophilus* have all been classified as omnivorous (Watson 1987; Kerley 1989; 1992a). Studies classifying *S. campestris* as a strict granivore (e.g. De Graaff 1981) involved analyses of cheek pouches only, thus excluding any consumed material. Additionally, studies classifying *M. natalensis* as a granivore

Table 2 The population densities (no./ha) of *M. natalensis*, *S. campestris* and *A. chrysophilus* rodents at different sites and in different seasons, estimated from Caughley (1976); it is not possible to calculate *SE* using this method

		Population density (no./ha)			
Season	Site	*M. natalensis*	*S. campestris*	*A. chysophilus*	Total
Summer	1	2,93	2,50	0	5,43
	2	2,98	0	0	2,98
Winter	1	1,69	0	0,84	2,53
	2	0,43	0,86	0	1,29

Table 3 The mean (± *SD*) percentage area occupied by vegetation, seeds and seed fragments and insect components in slides of faecal pellets of rodents; *n* = number of pellets

	Percentage (mean ± *SD*)			
Species	Vegetation	Seeds and seed fragments	Insects	*n*
M. natalensis	48,3 ± 10,7	40,8 ± 10,1	11,3 ± 9,4	12
S. campestris	33,9 ± 14,6	34,9 ± 17,2	30,0 ± 19,8	14
A. chrysophilus	58,9 ± 7,5	33,9 ± 9,3	8,9 ± 5,4	9

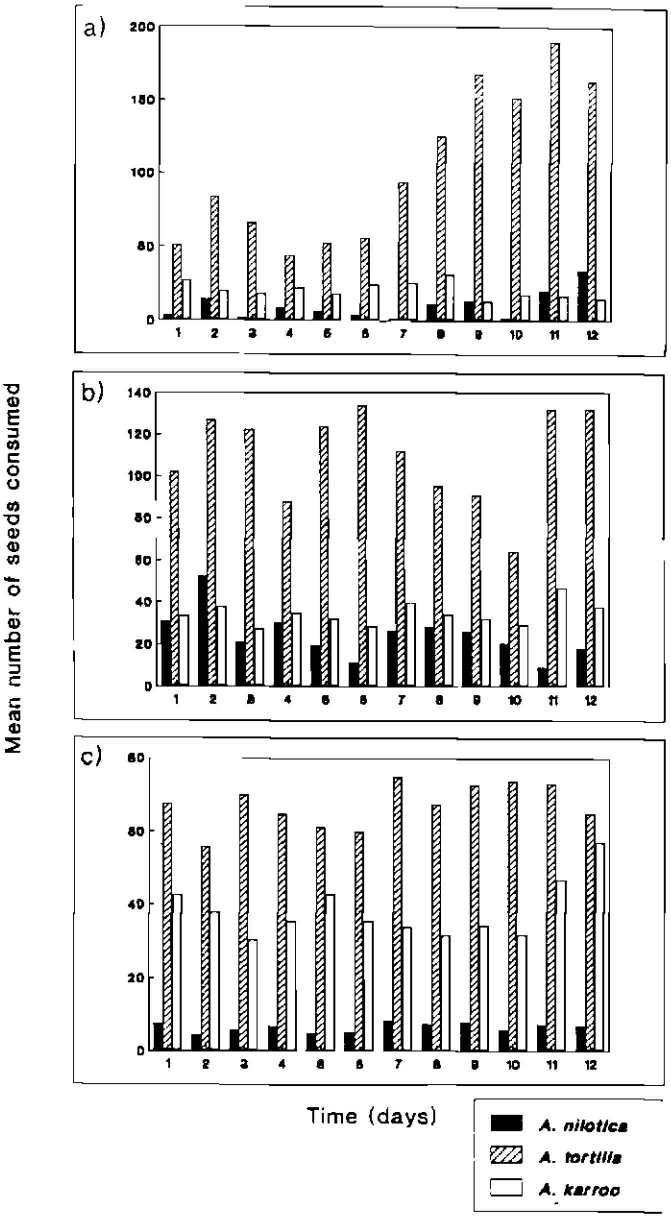

Figure 1 *Acacia* seed predation by captive (a) *Mastomys natalensis*, (b) *Saccostomus campestris* and (c) *Aethomys chrysophilus*.

Table 4 The predicted total number of *Acacia* seeds consumed by rodents during the winter season, and the percentage loss of the seed crop at two different sites

Acacia species	Site	Total no. seeds consumed	No. seeds produced/ha	% seed crop consumed
A. tortilis	1	15909	388762–391912	4,06–4,09
	2	6564		1,67–1,69
A. nolitica	1	579	59292–60731	0,95–0,98
	2	449		0,74–0,76
A. karroo	1	7567	30298–30840	24,54–24,98
	2	2868		9,30–9,47

(Swanepoel 1980; Taylor & Green 1976) were carried out adjacent to cultivated fields where seed availability was unnaturally high.

More *Acacia* seeds were removed from site 1 where the density of rodents was apparently higher. As hypothesized, fewer *Acacia* seeds were removed in summer (when rodents were apparently more abundant) than in winter, indicating that predation fluctuates with the availability of alternative food sources. Kerley (1992b) also stresses that availability of alternative resources may determine rodent seed predation.

Rodents are important seed consumers in many arid and semi-arid environments (Abramsky 1983; Morton 1985; Price & Jenkins 1986; Boyer 1987), and they can remove up to 75% of the annual seed crop of a variety of seeds (Nelson & Chew 1977; Brown, Reichman & Davidson 1979). In contrast, rodents in a southern African semi-arid region show negligible granivory (Kerley 1992b). Differences in areas of study will inevitably lead to different predation levels.

Rodents may be selective seed predators (e.g. Nelson & Chew 1977; Brown *et al.* 1986; Kerley 1990). Seed selectivity may in turn influence seed survival (Kerley 1992b), depending on the quantity of the seed crop consumed. In *Acacia* savanna, rodents preferentially selected *A. tortilis* seeds. Since *A. tortilis* seed loss to other factors is high, e.g. 68,0% of *A. tortilis* seeds may be infested and destroyed by bruchid beetles (Miller 1993; Miller 1994), seed loss to rodents may be important in reducing *A. tortilis* recruitment, depending on whether recruitment is seed-limited or not. Similarly 40% of *A. karroo* seeds may be destroyed by bruchids and thus the relatively high rodent seed predation may be sufficient to reduce *A. karroo* recruitment. In contrast, fewer (36,5%) of *A. nilotica* seeds may be infested by bruchids and as seed loss to rodents is very low, rodents may have little effect on *A. nilotica* recruitment. Further research on *Acacia* seed survival, germination and seedling establishment would be needed to assess the relative importance of rodent seed predation to seedling establishment.

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Males control the duration of copulation in the tropical millipede *Alloporus uncinatus* (Diplopoda: Julida)

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Prolonged copulation in *Alloporus uncinatus* is a form of mate guarding against sperm competition. Here we show, using a simple experiment, that males control the duration of copulation, an often overlooked assumption regarding the adaptive significance of prolonged copulation. The sex-specific evolutionary benefits of prolonged copulation are discussed in relation to the role played by sperm competition in the evolution of the mating system of *A. uncinatus*.

Lang paringstye by *Alloporus uncinatus* beskerm paargenote teen spermkompetisie. Ons dui hier met behulp van 'n eenvoudige eksperiment aan dat mannetjies die duur van paring beheer. Dit het betrekking op 'n aanname wat dikwels oorgesien word ten opsigte van die aanpassingsbelang van lang paringstye. Die geslagspesifieke evolutionêre voordele van lang paringstye word bespreek met betrekking tot die rol wat spermkompetise in die ontwikkeling van die paringstelsel van *A. uncinatus* speel.

A controversy exists over whether or not prolonged copulation has evolved through more than one suite of selective pressures (Thornhill 1984) and benefits males (e.g. Parker 1970; Sillen Tullberg 1981; Dickinson 1986), females (e.g. Wilcox 1984) or both sexes (see Walker 1980).

Clark (1988) tested two alternative hypotheses to explain the adaptive significance of prolonged copulation in the water strider *Gerris remigis*. The data refuted a female foraging hypothesis where females prolong mating to avoid interference from other males, thereby improving their foraging efficiency; but supported a male mate-guarding hypothesis in which the mating period but not genital joining is prolonged. However, implicit in both potential explanations are assumptions concerning the roles of males and females in controlling mating time.

These experiments could not determine which sex controlled copulation duration (Clark 1988). This knowledge may have relevance in determining the sex-specific benefits of prolonged copulation. For example, if it is advantageous to males to guard females, physical control of female movement would be an efficient mechanism particularly if achieved with minimal energetic cost to the male. There may also be benefits for the female though more likely there will be an associated cost which could lead to a sexual conflict of interest with selection favouring discrimination and avoidance behaviour by females especially if already mated.

Experiments that determine male and female effects on mating time may be difficult to design, and for many species observations alone are insufficient to make the distinction (but see Eberhard 1985). Consequently, most attempts to address this problem have been indirect, with a tendency to