Effects of supplemental food on the habitat selected by *Mastomys natalensis* (Muridae: Rodentia) in a subtropical grassland in Swaziland

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Mastomys natalensis, the multimammate mouse, was live-trapped on six grids varying in vegetative cover and vegetation height between June 1996 and May 1997. There were three treatments, each with two replicates: reduced cover, reduced cover with supplementary food and control. The numbers of *M. natalensis* on the grids with reduced cover were lower than those on the control. Food supplementation, however, significantly increased numbers on one of the replicates. There were also significant differences in the number and proportion of resident and adult mice among the grids. The grids with reduced cover supported a population with a lower number and proportion of adult and resident mice than those on the control. In contrast, despite the reduced cover on the food supplemented grids, the population on one of the these grids exhibited a higher number and proportion of adult and resident mice than those on the control. *Mastomys natalensis* appears to select patches with greater vegetative cover but it will abandon cover in the presence of an abundant food source.

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Habitat features such as soil type, food availability and vegetation structure may have a strong influence on the population and demographic parameters of small mammals (Fahrig & Merriam 1985; Canova, Maistrelle & Emilliani 1994; Peles & Barrett 1996). Habitat selection studies of small mammals in Africa have been mainly of a correlative nature (Happold 1975; Bond, Ferguson & Forsyth 1980; Rowe-Rowe & Meester 1982; Martin & Dickinson 1985; Iyawe 1988; Monadjem 1997a). All these studies have shown the importance of vegetation structure on the distribution and abundance of small mammals, with the amount of vegetative cover being especially important for terrestrial rodents (Bowland & Perrin 1989).

The effect of vegetative cover on the distribution and abundance of small mammals has been experimentally studied in voles of the genus *Microtus* (Taitt & Krebs 1983; Edge, Wolff & Carey 1995; Peles & Barrett 1996) and in the hispid cotton rat *Sigmodon hispidus* (Eshelman & Cameron 1996). These studies have shown that the density and recruitment of *Microtus* is lower when vegetative cover is reduced, and this has been linked to increased predation (Taitt & Krebs 1983; Kotler, Gaines & Danielson 1989). Furthermore, Eshelman & Cameron (1996) demonstrated that supplementary feeding induced cotton rats to occupy open patches which, without the food, were avoided.

Mastomys natalensis (Smith, 1834), the multimammate mouse, is a very common and widespread species of murid rodent occurring in Sub-Saharan Africa (Leirs & Verheyen 1995). It is a pioneer species that rapidly colonizes disturbed habitats (Meester, Lloyd & Rowe-Rowe 1979) such as fallow fields in which it is most successful in terms of population density and reproductive output (Telford 1989; Leirs & Verheyen 1995). It has a wide habitat tolerance (De Graaff 1981; Skinner & Smithers 1990). The abundance of *M. natalensis* has been positively correlated with vegetative cover in a number of studies (Martin & Dickinson 1985; Chidumayo 1980, 1984; Leirs & Verheyen 1995; Leirs, Verheyen & Ver-

hagen 1996; Monadjem 1997a). In other studies, however, vegetative cover apparently did not affect the distribution and abundance of *M. natalensis* (Neal 1970; Taylor & Green 1976; Cheeseman & Delany 1979), while the experimental addition of supplementary food resulted in an increase in the numbers, reproduction, and mass of *M. natalensis* (Hubert, Couturier, Poulet & Adams 1981; Leirs & Verheyen 1995; Monadjem & Perrin 1996; Monadjem & Perrin in press).

The present study was designed to test experimentally the effect of supplementary food on the habitat (defined in terms of vegetative cover) selected by *M. natalensis*. It was hypothesized that a reduction in vegetative cover would decrease the number of *M. natalensis*, but that supplementary food would increase it.

Materials and methods

Study area

Six permanently marked grids (70 m × 70 m) were established in a natural grassland on eKundizeni Farm (26°33'S; 31°16'E) near Matsapha, Swaziland. This region receives most of its rainfall between October and March, but the rains do not begin at a set time each year. The mean annual rainfall recorded over 30 years by the University of Swaziland Meteorological Station, located 8 km to the east of the study site (at a similar altitude of 650–700 m a.s.l.), is 928 mm. Mean minimum temperature for July 1995 was 7.6°C, while mean maximum temperature for February 1996 was 27.3°C. The six grids, two controls and four experimentals, were between 70 m and 100 m apart from each other, and were all on the same slope with similar aspects. The vegetation was very similar on the six grids, and consisted predominantly of grasses. *Hyparrhenia hirta* was the dominant grass species on all grids. The only other common grass species was *Hyperthelia dissoluta* which was present on the control grid 5 and on experimental grids 1 and 2. No trees were present on or near any of the six grids, while a few *Lippia javanica* shrubs

(up to 1.5 m tall) occurred irregularly on each grid. Four of the grids (grids 1, 4, 5 and 6) were situated in an ungrazed section of the farm, while grids 2 and 3 were in an area containing cattle. An uncontrolled fire swept through the study area on September 13, 1996 and completely burnt the vegetation on all the grids.

The following rainfall and habitat data were collected monthly. (1) Total monthly rainfall for eKundizeni Farm was recorded using a rain gauge placed 100 m from the nearest grid. (2) Vegetative cover on each grid was estimated in five randomly placed quadrats each month. The five readings were averaged to give an estimate of vegetative cover on the grid. (3) Vegetation height was estimated in a similar way to vegetative cover. For each quadrat, an average vegetation height was estimated. (4) Finally, the percentage of the vegetation that was green was estimated for each quadrat and averaged for each grid.

Vegetation manipulation

The vegetation on four grids (grids 1–4) was removed mechanically by mowing or manually by slashing in June 1996 prior to rodent trapping. The vegetation was cut to a uniform height of approximately 10 cm to 15 cm on all four grids. The cut grass was removed from the grids. The grass was cut again in December and again in January (grids 2 and 3) and February (grids 1 and 4). Two grids (grids 5 and 6) were not altered in any way and served as controls.

Supplementary feeding

The control grids (grids 5 and 6) and two of the cut grids (grids 3 and 4) received no supplementary food, while the two remaining cut grids (grids 1 and 2) received additional food in the form of equal amounts of rolled oats and rabbit pellets. Ten kilograms of food was added monthly to each of grids 1 and 2. Initially (between July and November) the supplementary food was placed in 25 cans (open at the side) which had been permanently arranged in a 5 × 5 grid. Each can was placed in the middle of four trapping stations. The food was placed in cans to deter birds from feeding on the food. Bird droppings were very rarely observed at the feeding stations, and it is assumed that birds removed only a small fraction of the supplementary food. Large numbers of ants were not detected at any of the feeding stations, and it is assumed that their effects were negligible. The feeding stations were checked twice monthly during which time all the cans were cleaned and refilled. Owing to the disturbance of the cans by cattle on grid 2, the cans were removed in November and the food was scattered directly onto grids 1 and 2.

Rodent trapping

Rodents were trapped monthly on the six grids from June 1996 until May 1997. Thirty-six Elliot and Sherman live-traps, baited with rolled oats, were set 10 m apart on each grid on three consecutive nights per month. The traps were checked at first light, were closed for the day and then reset in the afternoon. Each trapped rodent was uniquely toe-clipped, sexed, weighed and its reproductive condition assessed. Testes were recorded as being either scrotal or abdominal and females either as having perforate or imperforate vaginae. Juveniles were identified by a combination of body weight

and pelage colour. Juvenile *M. natalensis* had soft, grey fur, while in adults the colour changed to brown. All individuals weighing less than 20 g had grey pelage, while those above 25 g had adult pelage. Mice weighing between 20 g and 25 g were more difficult to assign to juvenile or adult age-classes and some mis-assignments may have occurred. However, very few *M. natalensis* were caught in the latter weight category. Male mice weighing more than 31 g and females more than 37 g were considered adults (Monadjem & Perrin in press). This lower body weight limit was obtained by subtracting one standard deviation from the mean weight of scrotal males and perforate females. Mice with weights between that of juveniles and adults were considered subadults. The number of individuals on each grid was estimated using the minimum number known alive method (MNA: Krebs 1966).

Two-way analysis of variance (ANOVA; Zar 1984) was used to test for significant differences ($p < 0.05$) among grids and between seasons for the following: (1) vegetative cover, (2) vegetation height, (3) vegetation greenness, (4) MNA of *M. natalensis*, (5) number of immigrant *M. natalensis* (defined as those mice captured for the first time on a particular grid), (6) number and proportion of resident *M. natalensis* (resident mice were defined as those that had been captured on a particular grid in the previous month and were recaptured on the same grid the following month), (7) proportion of males with scrotal testes and females with perforate vaginae, and (8) proportion of adult *M. natalensis*. The seasons were defined as follows: winter, June–August; spring, September–November; summer, December–February; autumn, March–May. For comparisons using ANOVA, separation of means was achieved using Tukey's multiple comparison (Zar 1984).

Results

Vegetation parameters

The vegetation prior to the manipulation of vegetative cover, was similar on all the six grids. The grass *Hyparrhenia hirta* was the dominant plant on all six grids. Although a quantitative vegetation survey was not conducted before the cutting of grass on the manipulated grids, vegetative cover and vegetation height appeared similar on all grids. There were subtle differences in the abundance of other grass species among the grids. *Hyperthelia dissoluta* was present on grids 1, 2 and 5. *Themeda triandra* on grid 6. *Sporobolus africana* on grid 3 and *Cymbopogon excavatus* and *Heteropogon contortus* on grid 4. These species, however, were far less abundant than, and usually occurred as single plants amongst, the dominant *H. hirta*.

There were no significant differences between replicates of the same treatment in vegetative cover, vegetation height and vegetation greenness in any of the seasons (two-way ANOVA, Tukey test, $p > 0.05$), thus only the means of these replicates are reported. After the cutting of the grass, vegetative cover and vegetation height were significantly different among the grids (cover, $F = 27.599$, $d.f. = 5, 18$, $p < 0.001$; height, $F = 31.654$, $d.f. = 5, 18$, $p < 0.001$). Mean per cent vegetative cover was approximately twice as high on the control grids as on the manipulated grids, and this difference was significant in winter, summer and autumn, but not spring (Table 1). Vegetative cover differed significantly among seasons ($F = 74.465$, $d.f. = 3, 20$, $p < 0.001$) as did vegetation height ($F =$

Table 1 Vegetation characteristics of each treatment between June 1996 and May 1997. The values are mean ± SE. Row values with different superscripts indicate a significant (p < 0.05) difference among treatments (i.e. values within the same row with the same superscript are not significantly different)

Vegetation	Season	Treatment		
		Control	Reduced cover	Reduced cover + food
Cover (%)	winter	80.2 ± 7.6^a	33.0 ± 4.7^b	39.2 ± 5.9^b
	spring	12.2 ± 6.1	8.5 ± 3.5	7.0 ± 2.9
	summer	67.8 ± 7.0^a	41.0 ± 4.1^b	37.2 ± 2.9^b
	autumn	91.5 ± 3.8^a	45.3 ± 5.9^b	42.5 ± 3.8^b
Height (cm)	winter	90.7 ± 6.0^a	7.2 ± 0.8^b	9.0 ± 1.0^b
	spring	8.7 ± 3.7	5.7 ± 2.3	5.2 ± 2.0
	summer	91.3 ± 24.8^a	26.5 ± 6.6^b	29.5 ± 9.4^b
	autumn	124.33 ± 7.7^a	21.5 ± 3.7^b	20.2 ± 3.3^b
Green (%)	winter	19.5 ± 5.3	44.3 ± 4.5	38.8 ± 5.8
	spring	66.7 ± 21.1	66.7 ± 21.1	66.7 ± 21.1
	summer	96.7 ± 2.1	100	100
	autumn	69.0 ± 3.7	90.0 ± 6.3	90.0 ± 6.3

Figure 1 Mean monthly number of *Mastomys natalensis* in control, reduced cover, and two reduced cover with supplementary food treatments between June 1996 and May 1997.

19.984, $d.f. = 3, 20$, $p < 0.001$). Similarly, there were significant differences in winter, summer and autumn with respect to mean vegetation height, which was four times taller on the control versus the cut grids (Table 1). There were no significant differences among grids in vegetative cover or vegetation height in spring. The low vegetative cover and vegetation height on the control grids in spring was due to the fire (see Materials and methods).

In addition, significant interactions were observed between vegetative cover and season ($F = 3.850$, $d.f. = 1, 15$, $p < 0.001$) and vegetation height and season ($F = 3.983$, $d.f. = 1, 15$, $p < 0.001$). Vegetative cover was highest on the control grids in winter and autumn while on the manipulated grids it was approximately the same height in winter, summer and autumn. Vegetation height was tallest in autumn on the control grids, and in summer on the manipulated grids.

The per cent greenness of the vegetation was not significantly different among the grids (two-way ANOVA, $p > 0.05$), but was significantly different between the seasons ($F = 14.680$, $d.f. = 3, 20$, $p < 0.001$). The interaction between grids and season was not significant (two-way ANOVA, $p > 0.05$). The vegetation was at its peak greenness in summer and least green in winter (Table 1).

Population dynamics

A total of 223 *Mastomys natalensis* were live-trapped 640 times between June 1996 and May 1997. Where differences between replicates of the same treatment were not significant (Tukey test, $p > 0.05$), the mean of the replicates was reported. The two control grids were not significantly different from each other for any of the tests, neither were the two cut, unsupplemented grids. However, the two cut, supplemented grids were significantly different from each other and have been reported separately as grids 1 and 2.

The population fluctuations on the grids are shown in Figure 1. Numbers of *M. natalensis* were very low at the start of
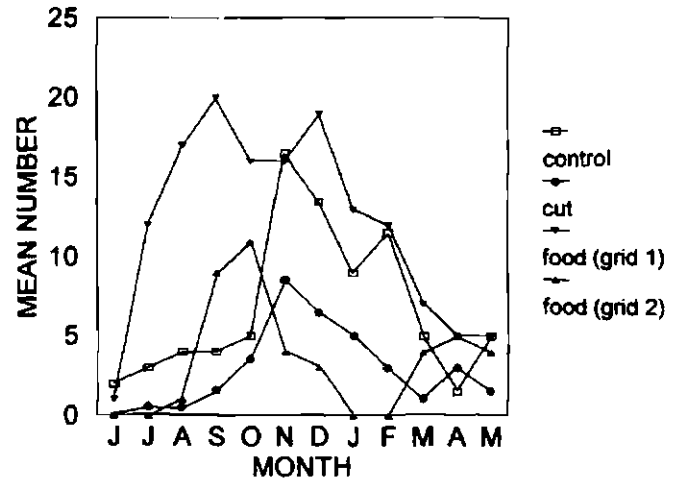
the study in June before food supplementation but after vegetation reduction. Numbers of *M. natalensis* increased significantly on grid 1 immediately after food supplementation, and remained high until February. Numbers on grid 2 did not increase immediately after food supplementation commenced, however, there was an abrupt increase observed in September but numbers dropped again in November. Numbers on the control grids were low until November when they increased and remained high until February. Numbers on the cut, unsupplemented grids were very low except for the period between November and January.

There were significant differences in the number of *M. natalensis* caught on the different grids ($F = 25.869$, $d.f. = 3, 20$, $p < 0.001$) and in the different seasons ($F = 9.620$, $d.f. = 3, 20$, $p < 0.001$). The interaction between the different grids and seasons was also significant ($F = 3.148$, $d.f. = 1, 9$, $p < 0.05$). Grid 1 supported a higher number of *M. natalensis* than the other grids in all seasons except autumn (Table 2). A higher number of *M. natalensis* were present on the control grids than on the cut, unsupplemented grids in winter, spring and summer (although the differences were only significant in the latter two seasons). The cut, unsupplemented grids supported the lowest number of *M. natalensis* in all seasons except summer. Numbers of *M. natalensis* fluctuated widely on grid 2 with an unexplained drop in summer (see Discussion).

A similar pattern is shown for the number of immigrants captured ($F = 3.951$, $d.f. = 3, 20$, $p < 0.05$). Grid 1 had significantly higher numbers of immigrants than other grids in winter, spring and summer, but not in autumn (Table 2).

The number of resident *M. natalensis* also varied between the grids ($F = 32.271$, $d.f. = 3, 20$, $p < 0.001$). The largest number of residents were observed on grid 1 in all seasons (Table 2). The control grids had a significantly higher number of residents than grid 2 and the cut, unsupplemented grids in summer only. The proportion of *M. natalensis* that were residents varied significantly among the grids ($F = 10.441$, $d.f. = 3, 20$, $p < 0.001$), although this did not vary with season (two-way ANOVA, $p > 0.05$). Overall, grid 1 and the control grids had higher proportions of residents than the other grids. Proportions of resident *M. natalensis* were very low on grid 2

Table 2 Mean monthly MNA, number of immigrants, number and proportion of residents and proportion of adult *Mastomys natalensis* present in each treatment between July 1996 and May 1997. Row values with different superscripts indicate a significant ($p<0.05$) difference among treatments (i.e. values within the same row with the same superscript are not significantly different)

				Treatment	
			Reduced	Reduced cover + food	
	Season	Control	cover	Grid 1	Grid 2
MNA	winter	3.5 ± 0.5^a	0.5 ± 0.3^a	14.5 ± 2.5^b	0.5 ± 0.5^a
	spring	8.5 ± 2.8^a	4.5 ± 1.8^b	17.3 ± 1.3^c	8.0 = 2.1
	summer	11.3 ± 1.5^a	4.8 ± 1.1^b	14.7 ± 2.2^c	1.0 ± 1.0^d
	autumn	3.8 ± 1.2^ab	1.8 + 0.7^a	5.7 ± 0.7^b	4.3 ± 0.3^ab
Immigrants (numbers)	winter	1.8 ± 0.5^a	0.5 ± 0.3^a	11.0 ± 1.0^b	0.5 ± 0.5^a
	spring	6.5 ± 2.6^ab	4.0 ± 1.7^a	7.0 ± 2.1^b	6.3 ± 2.7^ab
	summer	4.5 ± 1.0^ab	2.5 ± 0.6^ac	63 ± 2.0^b	0.7 ± 07^c
	autumn	2.8 ± 0.8	1.3 + 0.8	2.0 = 0	4.0 ± 0
Residents (numbers)	winter	1.8 ± 0.5^ab	0^a	3.5 ± 3.5^b	0^a
	spring	2.0 + 0.3^a	0.5 ± 0.2^a	10.3 ± 0.9^b	1.7 ± 0.9^a
	summer	6.8 ± 1.6^a	2.3 ± 0.6^b	8.3 ± 1.2^a	0.3 ± 0.3^b
	autumn	1.0 ± 0.6^a	0.5 ± 0.2^a	3.7 ± 0.7^b	0.3 ± 0.3^a
Residents (proportion)	winter	0.51 ± 0.13^a	0^b	0.21 ± 0.21^b	0^b
	spring	0.37 ± 0.16^a	0.10 ± 0.05^b	0.61 ± 0.09^c	0.31 ± 0.23^a
	summer	0.58 ± 0.13^a	0.41 ± 0.12^a	0.58 ± 0.10^a	0.11 ± 0.11^b
	autumn	0.28 ± 0.09^a	0.25 + 0.05^a	0.64 ± 0.04^b	0.07 + 0.07^a
Adults (proportion)	winter	0.76 ± 0.10^a	0^b	0.60 ± 0.07^a	0^b
	spring	0.35 ± 0.07^a	0.43 ± 0.04^ab	0.59 ± 0.11^b	0.62 + 0.09^b
	summer	0.77 ± 0.12^a	0.80 ± 0.10^a	0.81 ± 0.07^a	0.33 ± 0.33^b
	autumn	0.58 ± 0.14^a	0.55 + 0.15^a	0.82 ± 0.02^b	0.72 ± 0.16^ab

except in spring (Table 2).

Proportion of male *M. natalensis* that had scrotal testes did not vary among the grids (two-way ANOVA, $p > 0.05$), but did vary among seasons ($F = 8.971$, $df - 3, 20, p < 0.05$). None of the adult males were scrotal in winter, while almost 100% were scrotal in summer. Similarly, the proportion of perforate females did not vary among the grids (two-way ANOVA, $p > 0.05$), but varied among seasons ($F = 16.935$, $df = 3, 20, p < 0.001$). Breeding commenced later in females (November) than in males (September).

The proportion of adult *M. natalensis* was significantly different among the grids ($F = 2.923$, $df - 3, 20, p = 0.05$). The proportion of adults was significantly higher on grid 1 and the control grids in winter (Table 2). Grids 1 and 2 had significantly higher proportions of adults in spring. There were no significant differences in summer (the low value for grid 2 was due to the fact that no *M. natalensis* were captured on this grid in January or February, however, all those captured in December were adults). In autumn, the proportion of adult *M. natalensis* was higher on grid 1 than on the control grids or cut, unsupplemented grids. In general, the proportions of adults remained high on grid 1, but fluctuated widely on the control grids and the cut, unsupplemented grids. The proportion of adults on grid 2 was zero in winter, but was high in spring, summer and autumn.

Discussion

The results of this study support the hypothesis that vegetative cover and food availability influence the distribution and abundance of *Mastomys natalensis*. The grids with a reduced vegetative cover supported a lower number of *M. natalensis* than the control grids. However, when food was supplemented on the cut grids, the population of *M. natalensis* increased dramatically on at least one of the supplemented grids (grid 1). The population on grid 2, however, did not increase until spring, and even then for only a short period. The reasons for the lack of a rapid and significant increase on grid 2 are unclear, but are probably related to the presence of cattle on the latter grid. Grid 2 was situated in a cattle area (see Study area) and hence experienced disturbance from cattle in terms of grazing as well as trampling. Supplementary food was initially placed in 340 ml soft drink cans. These cans were trampled and destroyed in July and were replaced in August. The new cans lasted until November when they too were destroyed. The supplementary food may thus not have been available to the mice on grid 2 at the start of the study which may explain the delayed response of *M. natalensis* to supplementary feeding. The sudden decline in November may have been associated with the switch of providing supplementary food in the cans to scattering the food directly onto the grids. Although this change did not affect the population of *M. natalensis* on grid 1, the decrease in numbers on grid 2 may have been caused by the cattle taking a proportion of the supplementary food meant for the rodents. Further evidence for the suggestion that the supplementary food was not available to mice on grid 2 is that the population of *M. natalensis* on this grid and the cut, unsupplemented grids did not differ significantly in most of the parameters tested for. Thus the population of *M. natalensis* on grid 2 was behaving like those on cut, unsupplemented grids. Alternatively, the cattle were affecting the population of *M. natalensis* in another, unexplained way. Although not quantified, the cattle were spending a lot of time on grid 2 (possibly owing to the fact that, as a result of being mowed, a fresh growth of grass was usually available on this grid). Cattle, as well as wild ungulates, can influence the structure and productivity of small mammal communities (Grant, Birney, French & Swift 1982), and the population density of individual species (Bowland & Perrin 1989). The causal interactions between grazing by ungulates and the distribution and abundance of small mammals in Africa, however, require further investigation.

The results from this experiment indicate that *M. natalensis* preferentially occupy areas with high vegetative cover, but will colonize areas with low vegetative cover if an abundant supply of food is available. This finding may explain the apparently contradictory observations in the literature of *M. natalensis* both selecting high vegetative cover (e.g. Leirs & Verheyen 1995; Monadjem 1997a), and showing no preference for either high or low cover (e.g. Taylor & Green 1976). In natural habitats, open areas (with reduced vegetative cover) do not necessarily contain more food for *M. natalensis*. *Mastomys natalensis* is an omnivore (Leirs & Verheyen 1995) relying heavily on seeds (Taylor & Green 1976; Swanepoel 1980; Monadjem 1997b) and insects (Field 1975). With a lack of information on the subject, there is no *a priori* reason to expect open areas to harbour more seeds or arthro-

pods, although it has been shown that open patches support a lower abundance of orthopterans than more densely vegetated areas (Prendini, Theron, van der Merwe & Owen-Smith 1996). Thus, in natural habitats, *M. natalensis* generally selects areas with adequate vegetative cover (Chidumayo 1980, 1984; Monadjem 1997a).

On agricultural land, in contrast, open areas usually correspond to recently ploughed and planted fields which would contain a very high supply of food in the way of grains and cereals. Thus on agricultural land, *M. natalensis* may be lured away from cover by the rich supply of easily available food, as was noted by Taylor & Green (1976).

The spring fire had a very noticeable effect on both the vegetation and the population of *M. natalensis*. The fire completely burnt all above ground vegetation within at least a 3 km radius of the study area. Numbers of *M. natalensis* rose sharply on the control grids in November (two months after the fire) and remained high until February. Numbers on the cut, unsupplemented grids rose in October (one month after the fire) and declined again in January–February. The fire had no noticeable effect on the supplemented grids 1 and 2. Such an increase in numbers of *M. natalensis* after a fire have been observed elsewhere in Africa (Neal 1970; Cheeseman & Delany 1979; Martin & Dickinson 1985; Rowe-Rowe 1995), although some studies have reported no change (Bowland & Perrin 1988) or even a population decline (Kern 1981; Swanepoel 1981; Chidumayo 1984) after a fire.

It has been shown previously that supplementary food causes an increase in the density of *M. natalensis* (Monadjem & Perrin 1996; Monadjem & Perrin in press). Despite the increase in numbers on the control and unsupplemented grids, the numbers on the supplemented grid 1 were still significantly higher, supporting the hypothesis that food is an important component in the habitat selected by this species. Peak numbers of *M. natalensis* on supplemented grid 1 were recorded between August and December and ranged between 44–56 mice/ha. Peak numbers on the control grids were reached in November (46 mice/ha) and December (38 mice/ha), however, numbers on the control did not exceed 30 mice/ha in other months except February. These figures compare well with figures from a previous study at the same site (Monadjem & Perrin in press). In the latter study, the number of mice on the supplemented grids peaked at 40–56 mice/ha, while the numbers on the control reached a maximum of 28 mice/ha. These results suggest that the number of *M. natalensis* at this particular study site cannot be increased beyond approximately 60 mice/ha with food supplementation alone. The amount of supplementary food supplied in the current study far exceeded that supplied in the previous study (28 kg/ ha versus 8 kg/ha) and yet the maximum number of mice recorded in both studies was similar. Other factors, such as availability of shelter and nesting sites may be limiting in this study area, since maximum numbers of *M. natalensis* of over 400 mice/ha have been recorded (Leirs & Verheyen 1995).

The number and the proportion of resident *M. natalensis* were highest on the supplemented grid 1, intermediate on the control grids and lowest on the unsupplemented grids and supplemented grid 2. These results suggest that the *M. natalensis* captured on grid 1 were residing on that grid and not merely passing through. Furthermore, the proportion of *M. natalensis* captured that were adults was significantly higher on the supplemented grid 1. Hence, *M. natalensis* on food supplemented grid 1 were predominantly adult and resident, while those on the cut, unsupplemented grids (including the supplemented grid 2) were predominantly immature and non-resident. This suggests that adult *M. natalensis* are capable of displacing immatures from food-rich areas, and that immatures are forced to forage in suboptimal habitats.

In both sexes breeding, recorded in terms of scrotal males and perforate females, commenced on all treatments within the same month. Scrotal males, however, were recorded two months before perforate females. This observation of male *M. natalensis* becoming reproductively active before females has been recorded elsewhere (Leirs & Verheyen 1995; Monadjem & Perrin in press). There were no significant differences in the proportion of males or females that were in breeding condition among the grids (two-way ANOVA, $p > 0.05$). Hence, neither the reduction in vegetative cover, nor the presence of supplementary food had any effect on reproduction in *M. natalensis*. This is in contrast to a previous study in which female *M. natalensis* on two supplementary grids commenced breeding earlier and bred for longer than on the control (Monadjem & Perrin in press). This may have been due to the fact that the breeding season in the present study was preceded by an extraordinarily wet summer (October 1995 to April 1996). Food, in the way of grass seeds and arthropods, may thus have been present in sufficient amounts to allow the mice on all the grids to commence breeding at the same time.

The direct impact of predation on small mammals has not been studied in Africa although it has often been assumed to be significant (Happold & Happold 1986). Predation has a significant impact on vole demography (Lin & Batzli 1995), and it has even been suggested that predation may influence whether the populations will exhibit cyclic fluctuations or not (Hansson & Henttonen 1988). It is possible that *M. natalensis* avoids areas with low vegetative cover so as to reduce predation pressure. *Mastomys natalensis* skulls are commonly recorded in owl (*Tyto alba* and *T. capensis*) pellets (Vernon 1972; Perrin 1982; Wirminghaus 1989) and in small carnivore scats (Shepherd, Leman & Hartwig 1983; Bowland & Perrin 1993). Why *M. natalensis* is willing to forsake shelter for food is not known. A more important question to answer is: at what stage does the benefit derived from access to extra food in open areas override the benefit derived from remaining in shelter?

Acknowledgements

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