

Population dynamics of *Lemniscomys rosalia* (Muridae: Rodentia) in a Swaziland grassland: effects of food and fire

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The effects of food supplementation on a population of *Lemniscomys rosalia* were studied experimentally in a grassland habitat in Swaziland. Food was added bi-weekly to two 1-ha grids, while a single 1-ha grid served as the control. Rodent traps were set monthly over a 12 month period. Food supplementation may have affected the density of *L. rosalia*, but did not affect any other features of the population. Breeding commenced in September and ended in April (males) and May (females). Recruitment of juveniles occurred between January and March. Adult mean body mass increased from a low in winter (June/July) to a high in late summer (February). The drop in mean body mass in autumn was due to the disappearance of heavy adults and entry of the lighter subadults into the population. Mean survival of *L. rosalia* was low; 81% of all captured individuals disappeared within four months. An unscheduled fire burnt part of the study area and hence allowed an assessment of the effect of fire on *L. rosalia*. The fire did not cause undue mortality of *L. rosalia*, however, burnt areas were avoided for three months until grass cover had sufficiently increased.

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The role of food supply in southern African rodent communities is poorly understood (Delany 1986). Numerous studies have reported increases in rodent populations following good rainfall (Nel 1978; Perrin & Swanepoel 1987; Bronner, Rautenbach & Meester 1988). This relationship is thought to be an indirect one where increased rainfall acts to increase cover and food supply, thus enabling rodents to reproduce (Neal 1986). By experimentally manipulating food supply it is possible to ascertain the effects of food supply on various parameters of rodent populations (Boutin 1990).

Food supplementation studies have shown food to be a limiting factor of rodent populations. In the majority of studies food addition has increased rodent populations (Taitt & Krebs 1981; Flowerdew 1972; Zubaid & Gorman 1993; Doonan & Slade 1995; Monadjem & Perrin 1996). Furthermore, manipulated increases in food supply have resulted in: (1) extension of the breeding season (Hansen & Batzli 1979; Hubert, Couturier, Poulet & Adams 1981; Taitt 1981; Sullivan 1990), (2) increases in reproductive intensity (Watts 1970; Gilbert & Krebs 1981; Saitoh 1989), and (3) increases in growth rate and body weight (Fordham 1971; Leirs, Stuyk, Verhagen & Verheyen 1990; Neal & Alibhai 1991).

The population biology of *Lemniscomys rosalia* (Thomas, 1904) [formerly referred to as *Lemniscomys griselda* (Thomas, 1904), see van der Straeten 1980] is poorly known, although the closely related east African *Lemniscomys striatus* has received some attention (Field 1975; Neal 1977). Published observations on *L. rosalia* are mostly in the form of anecdotal notes (De Graaff 1981; Skinner & Smithers 1990), or as part of a study on a community of small mammals (Hanney 1965; Kern 1981; Swanepoel 1981; Gliwicz 1985; Bowland & Perrin 1988; Happold & Happold 1990, 1991).

The present study was designed to test the effect of food supplementation on the following aspects of the population of *L. rosalia*: (1) population size, (2) duration of the breeding season, (3) weight gain of individuals, (4) survival, and (5) recruitment. Furthermore, this study provides information on the population ecology of *L. rosalia* over a twelve month period.

Materials and methods

Study area

Three permanently marked grids (100 m × 100 m) were established in an ungrazed 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. Total rainfall between June 1995 and May 1996 was 1329 mm. Mean minimum temperature for July 1995 was 7.6°C, while mean maximum temperature for February 1996 was 27.3°C. The three plots, one control and two experimental (grids 1 and 3), were between 70 m and 100 m apart from each other. The vegetation was very similar on the three plots. *Hyparrhenia hirta* was the dominant grass species on all plots. The only other common grass species was *Hyperthelia dissoluta* which was abundant on the control plot and present on grid 1. No trees were present on or near any of the three plots, while a very few *Lippia javanica* shrubs (up to 1.5 m tall) occurred irregularly on each plot. The following rainfall and habitat data were collected monthly. (1) Total monthly rainfall for eKundizeni Farm was recorded using a rain gauge placed 300 m from the nearest grid. (2) Grass cover on each grid was estimated in ten randomly placed quadrats each month. The ten readings were averaged to give an estimate of grass cover on the grid. (3) Grass height was estimated in a similar way to grass cover. For each quadrat, an average grass height was estimated by measuring the height of the grass 'canopy' (i.e. emergent grass stems were not measured). This estimate presented few problems since the grass was generally thick and a 'canopy' was usually obvious. Very rarely grass within the quadrat was patchily distributed. In these situations, the 'canopy' height of the grass patch was measured. (4) Finally, the per cent of the grass that was green was estimated for each quadrat and averaged for each grid. The rainfall and temperature readings covered the whole study period

from June 1995 to May 1996, while grass cover was recorded from September to May and the last two grass variables from October to May. The state of the vegetation did not change noticeably between June and September (winter and early spring) when the grasses would have been dormant.

A fire swept through the study area on 22 September 1995 (shortly after the September trapping session) and burnt exactly half of the two experimental grids. It also burnt to within 15 m of the control grid. After the fire, habitat characteristics were recorded separately for burnt and unburnt sections of experimental grids 1 and 3 (i.e. five quadrats were placed in the burnt and five in the unburnt sections per grid).

Rodent trapping

Rodents were trapped monthly on all three plots from June 1995 until May 1996. One hundred 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 dawn, 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 scrotal or abdominal and females either as having perforate or imperforate vaginæ. Individuals weighing less than 21 g were classed as juveniles. Male mice weighing more than 48 g and female mice weighing more than 43 g were considered adults. 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).

Differences between the three grids were tested using analysis of variance (ANOVA). Where the variances were non-constant the data were log transformed (Zar 1984). Home ranges were estimated by calculating the mean distance between successive captures (Davis 1953). Only those individuals that were caught four or more times in non-peripheral traps were included in the latter analysis.

Supplementary feeding

The control plot received no supplementary food, while the other two received additional food in the form of equal amounts of rolled oats and rabbit pellets. Eight kilograms of food were added monthly to the first experimental plot (grid 1) from July (immediately after sampling the rodent population) until May, and also to the second experimental plot (grid 3) from July until September, after which 4 kg were added monthly until May. The supplementary food was placed in 81 cans (open at the side) which had been permanently arranged in a 9 × 9 grid. Each can was placed in the centre of four trap 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. Some of the cans attracted ants between November and January, but ants were rarely seen in other months. The feeding stations were checked twice monthly during which time all the cans were cleaned and refilled (i.e. grid 1 received 4 kg of supplementary food twice a month, totaling 8 kg of food per month).

Results

Rain and habitat variables

Monthly rainfall recorded during this study is shown in Figure 1. The rains began in October and ended in March, although some precipitation was recorded through to the end of the study. The habitat characteristics of the three grids are shown in Table 1. There were significant differences in per cent cover, per cent green grass and grass height between the grids and seasons (per cent cover: $F = 9.520$, $d.f. = 14, 39$, $p < 0.05$; per cent green: $F = 6.501$, $d.f. = 14, 39$, $p < 0.05$; grass height: $F = 5.928$, $d.f. = 14, 39$, $p < 0.05$). On the control and the unburnt sections of grids 1 and 3 grass cover was generally high, but declined slightly in October and November. Grass height increased steadily through the study, while the per cent of the grass that was green peaked between December and March. After the fire (September), the burnt sections of grids 1 and 3 had lost nearly all their cover. The new growth of grass, however, was completely green. By December there was little visual difference between the burnt and unburnt areas, although, between January and May, grass cover was still significantly higher on the unburnt sections of grids 1 and 3 and the control compared to the burnt sections ($F = 17.883$, $d.f. = 4, 24$, $p < 0.05$). However, in the same period, per cent green grass was not different between the burnt and unburnt areas (ANOVA, $p > 0.05$), while grass height was significantly taller on the burnt area of grid 1 and the control compared to the unburnt area of grid 1 and grid 3 ($F = 14.346$, $d.f. = 4, 24$, $p < 0.05$).

Small mammals captured on the three grids

During this study 108 *L. rosalia* were captured 538 times. Other rodent species caught in the study area were *Mastomys natalensis* (310 individuals), *Mus minutoides* (75 individuals), *Steatomys pratensis* (43 individuals), *Dendromus mystacalis* (12 individuals), *Aethomys chrysophilus* (8 individuals), *Otomys angoniensis* (1 individual), and the insectivore *Crocodyra hirta* (13 individuals).

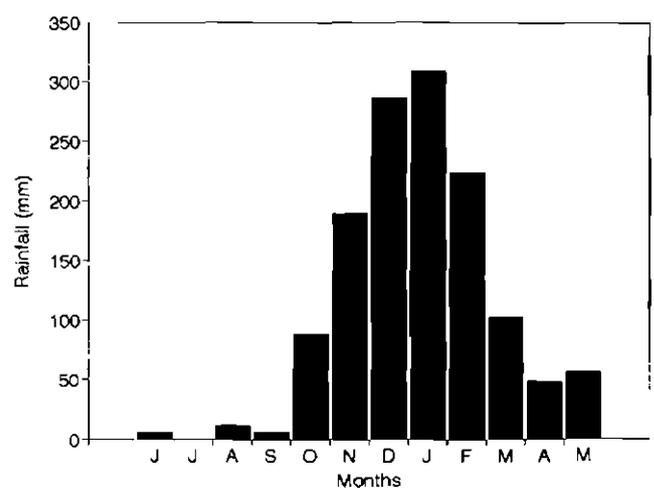


Figure 1 Total monthly rainfall at eKundizeni Farm, Swaziland from June 1995 to May 1996. Total rainfall for this period was 1329 mm.

Table 1 Vegetation characteristics of the experimental grids 1 and 3 and the control grid

Month	Grid 1						Control			Grid 3					
	Unburnt			Burnt			Cover (%)	Height (cm)	Green (%)	Unburnt			Burnt		
	Cover (%)	Height (cm)	Green (%)	Cover (%)	Height (cm)	Green (%)				Cover (%)	Height (cm)	Green (%)	Cover (%)	Height (cm)	Green (%)
Sep.	80	-	-	-	-	-	76	-	-	75	-	-	-	-	-
Oct.	59	44	16	5	5	100	74	64	11	90	72	17	5	5	100
Nov.	60	40	52	31	6	100	65	54	50	70	50	46	52	14	100
Dec.	74	45	78	40	17	100	84	61	83	79	52	76	46	35	100
Jan.	78	66	89	61	108	100	95	98	89	91	47	90	64	48	100
Feb.	81	67	71	69	110	100	93	115	88	89	72	78	62	82	100
Mar.	81	98	78	78	113	92	94	114	87	77	65	86	61	54	100
Apr.	94	100	63	73	114	68	91	119	64	80	67	65	69	72	76
May	82	75	50	84	116	65	100	135	43	98	76	46	58	96	70

Effect of food

At the beginning of the study in June and July (before food addition), the numbers of *L. rosalia* were similar on the control grid and experimental grid 1. Numbers were approximately half on the second experimental grid 3 (Figure 2). Food supplementation did not obviously affect the number of *L. rosalia*, since there was no marked increase on the experimental grids after the initiation of food supplementation. However, numbers were significantly different on the three grids between August and May (ANOVA, $d.f. = 2, 27, p < 0.05$). Tukey multiple comparison test could only differentiate between numbers on grid 1 and the other two grids, but not between grid 3 and the control. Hence grid 1 supported a higher number of *L. rosalia* than the control, but grid 3 did not. Food supplementation, however, may have affected numbers on grids 1 and 3 in a more subtle way. On both grids 1 and 3, there was no decline in numbers of *L. rosalia* through the course of the year. Numbers between June and December, were not different from numbers between January and May (t -test, $p > 0.05$ in both cases). However, there was a significant decrease in numbers on the control in the same period ($t = 7.24, d.f. = 10, p < 0.05$). Thus, food supplementation

may have prevented a decline in numbers of *L. rosalia* over mid-summer.

There were no significant differences between the number of immigrants, adult body weight, timing or intensity of breeding, or survival of *L. rosalia* on the three grids, and hence for subsequent analyses the data were combined for all grids.

Population structure

The sex ratio of the *L. rosalia* population was skewed towards males. Significantly more males were trapped each month than females (t -test, $d.f. = 22, p < 0.05$; Figure 3). This may have been due to the fact that significantly more male ($n = 49$) than female ($n = 31$) immigrants were caught during the study ($\chi^2 = 4.05, p < 0.05$, Figure 3). The total number of males caught ($n = 60$) during this study, however, was not significantly different from that of females caught ($n = 47$; $\chi^2 = 1.579, p > 0.05$).

The mean adult body weight of *L. rosalia* was investigated by a two-way analysis of variance, and varied by sex and season (Table 2). Males were significantly heavier than females ($F = 28.984, d.f. = 1, 160, p < 0.05$), although males were heavier than females outside the breeding season only (the difference between male and female body weight during summer was not significant). Mean body weights varied significantly with season ($F = 16.751, d.f. = 3, 158, p < 0.05$). However, the interaction between sex and season was not significant ($F = 1.407, p > 0.05$). Mean weight of males was lower in the winter months than during other seasons, while mean weight of females was higher during the summer months (probably owing to pregnancy).

The monthly age structure of the population of *L. rosalia* is shown in Figure 4. All *L. rosalia* caught in a particular month were placed in mass classes with 5-g intervals, and the number of animals in each mass class was then expressed as a proportion of the total number caught in that month. Between January and May, there were two distinct size classes of rats in the population, presumably the larger class representing the individuals born the previous summer and the smaller class those that were born in the current summer. The proportional increase of heavy individuals in summer and their disappearance in winter suggests that, under natural conditions, *L.*

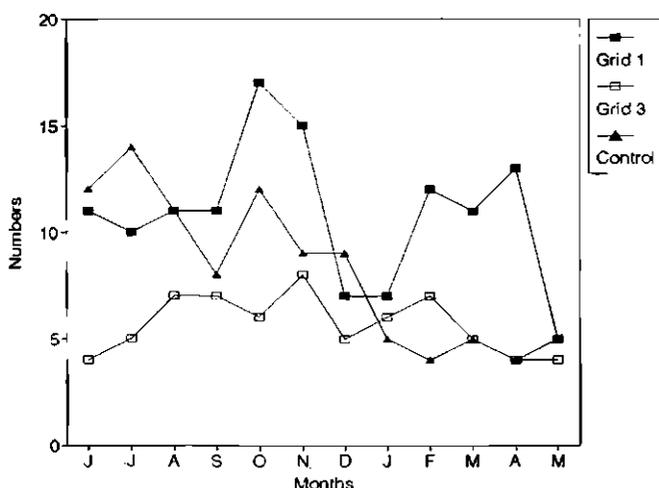


Figure 2 Minimum number of *Lemniscomys rosalia* alive on supplemented grids 1 and 3, and the control between June 1995 and May 1996.

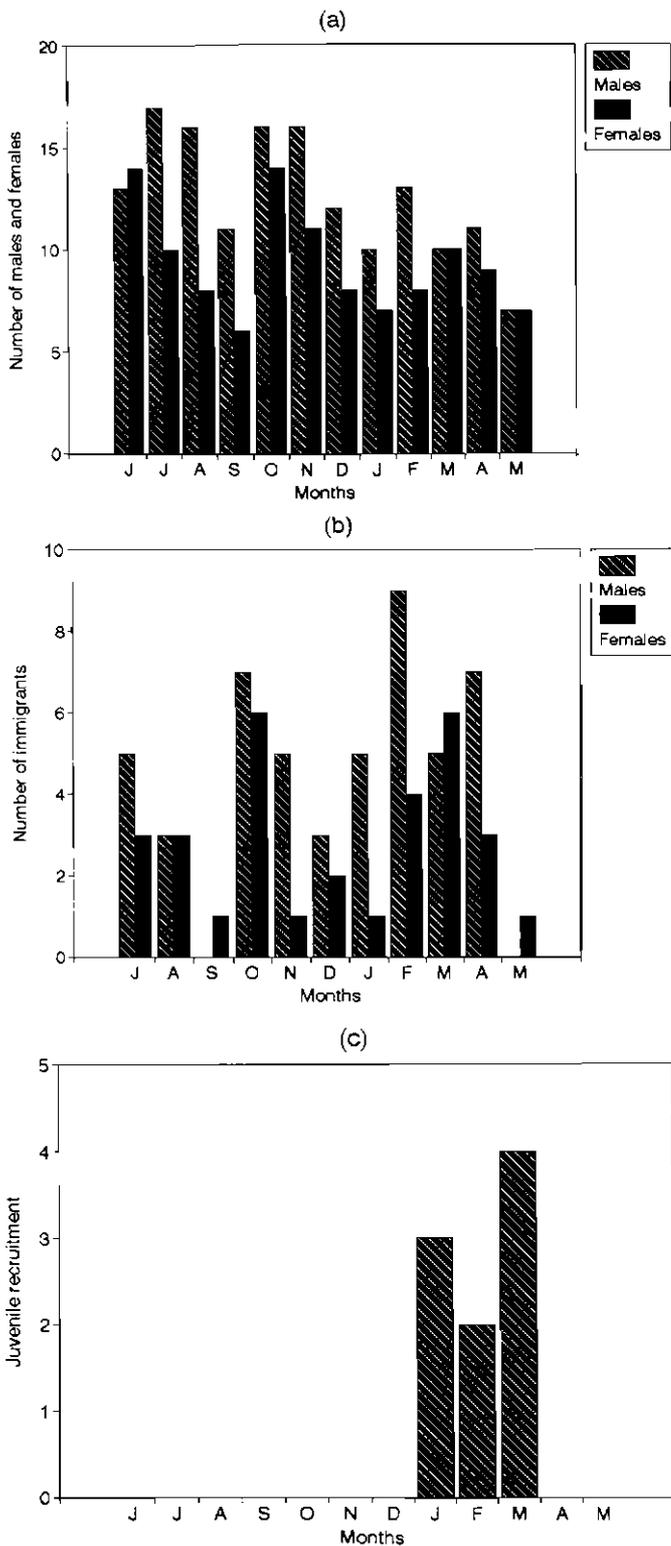


Figure 3 The number of: (a) males and females, (b) immigrants, and (c) juveniles, trapped on the three grids between June 1995 and May 1996.

rosalia do not survive for more than one year.

Reproduction

Adult male *Lemniscomys rosalia* had scrotal testes between September and April (Figure 5). However, less than 20% of adult males had scrotal testes in September and April. Thus, the majority of males were in reproductive condition only

Table 2 Monthly mean weight of adult male and female *Lemniscomys rosalia* in four seasons (winter: June–August, spring: September–November, summer: December–February, autumn: March–May) between June 1995 and May 1996. Column values with different superscripts indicate a significant ($p < 0.05$) difference between seasons (i.e. males and females considered separately, although both sexes show the same trend)

Season	Mean adult weight of <i>Lemniscomys rosalia</i> (g)	
	Males	Females
Winter 1995	53.0 (21) ^a	49.8 (14) ^a
Spring 1995	57.8 (37) ^b	51.1 (15) ^b
Summer 1995–1996	60.4 (25) ^c	57.6 (19) ^c
Autumn 1996	58.9 (14) ^b	54.1 (16) ^b

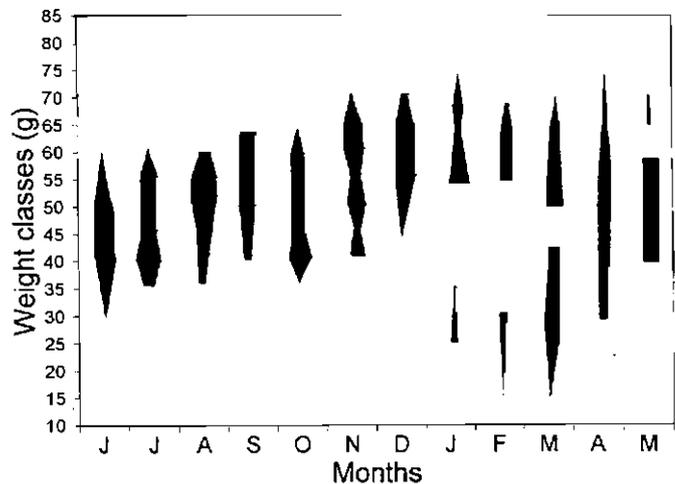


Figure 4 The monthly age structure of *Lemniscomys rosalia* captured between June 1995 and May 1996.

between October and March. In contrast, adult females had perforate vaginae between September and May (Figure 5). Recruitment of juveniles occurred between January and March (Figure 3).

Survival

Survival rates of *L. rosalia* were calculated using all individuals caught, excluding those caught in April and May. The maximum potential survival for this study was 11 months and two individuals lived that long (Figure 6). Forty-two per cent of all *L. rosalia* survived one month, while sixteen per cent survived three months. Thereafter there was a sharp drop in survival rate.

Distance between captures

A two-way ANOVA was used to test for differences in mean distance between successive captures (an index of home-range size) on the grids before and after food supplementation. The mean distance between successive captures was not different between the different grids ($F = 0.104, df = 2, 47, p > 0.05$; Table 3). Mean distance between captures did not differ before and after food supplementation ($F = 2.738, df = 2,$

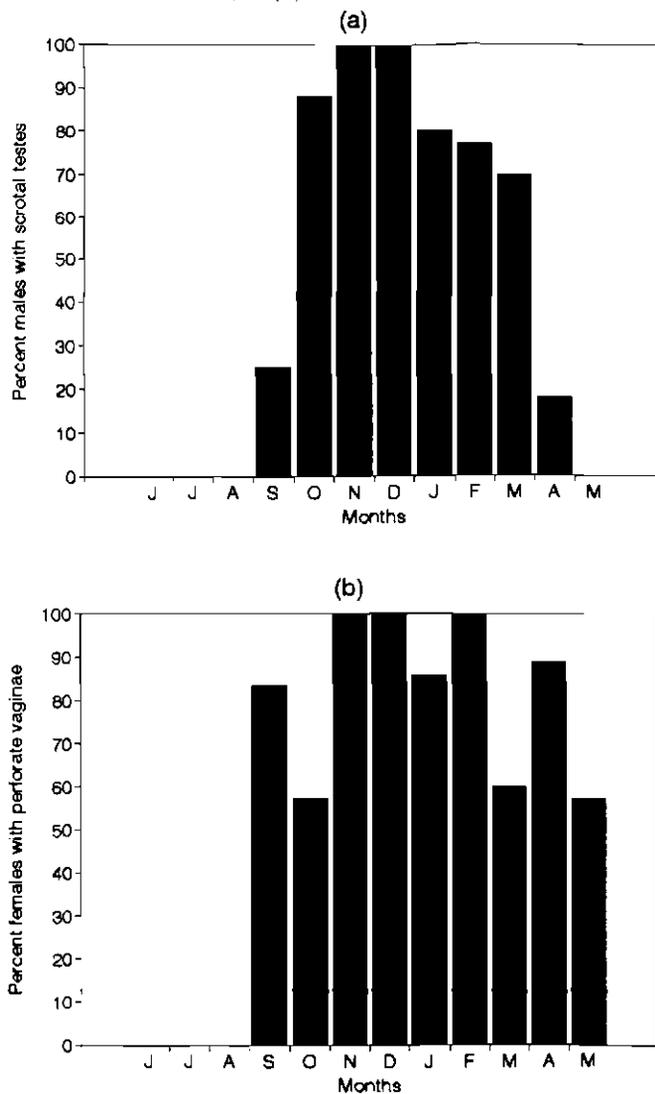


Figure 5 The proportions of: (a) adult males with scrotal testes, and (b) adult females with perforate vaginae, trapped between June 1995 and May 1996 on the three grids.

47, $p > 0.05$). The interaction between food supplementation and the grids was also insignificant ($p > 0.05$). Hence food supplementation did not affect the mean distances between successive captures of *L. rosalia*.

Effects of the fire

The fire completely removed all vegetation cover from the burnt sections of grids 1 and 3. By October there was a new, but short, flush of green grass (Table 1). Grass cover and height in the burnt sections, however, remained low until January. *Lemniscomys rosalia* avoided the burnt sections of both grids 1 and 3. Between October and December, there was a significant difference between numbers caught in the burnt and unburnt areas (chi-square test, $p < 0.05$ for both tests, see Table 4 for χ^2 -values). Furthermore, the three individuals caught in the burnt section of grid 1 in October and November were all caught on the edge of the burnt section (within 5 m of grass cover). After January, equal numbers of *L. rosalia* were caught in the burnt and unburnt sections of grids 1 and 3 ($p > 0.05$ for both tests, see Table 4).

The fire did not affect the survival of *L. rosalia* (Table 5). Individuals that had had home ranges in the burnt sections of

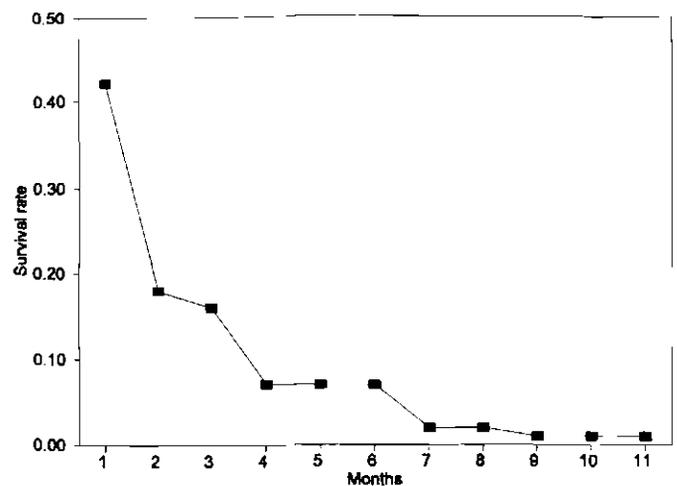


Figure 6 Survival rates of *Lemniscomys rosalia* on the three grids over an eleven-month period.

Table 3 Mean distance between successive captures (\pm standard error) of *Lemniscomys rosalia* on the three grids. Values in parentheses indicate sample sizes

Period	Mean distance between captures (m)		
	Grid 1	Control	Grid 3
June 1995–July 1995 (before supplementation)	27.4 \pm 4.2 (7)	25.2 \pm 5.1 (7)	18.3 \pm 3.1 (3)
August 1995–May 1996 (after supplementation)	26.4 \pm 2.1 (13)	25.5 \pm 3.1 (9)	34.9 \pm 3.3 (11)

Table 4 The total number of *Lemniscomys rosalia* caught in the burnt and unburnt halves of experimental grids 1 and 3

	Numbers caught					
	Grid 1		χ^2	Grid 3		χ^2
	Unburnt	Burnt		Unburnt	Burnt	
Jun. 1995–Sep. 1995*	17	24	1.195	7	16	3.522
Oct. 1995–Dec. 1995	28	6	14.236**	18	0	18.0**
Jan. 1995–May 1996	23	29	0.692	19	17	0.111

*This was the period before the fire and hence the 'burnt' areas had not yet been burnt. ** $p < 0.05$

grids 1 and 3 prior to the fire, simply shifted their home ranges to unburnt sections.

Discussion

The addition of food appeared to have affected the population of *L. rosalia* by preventing a decline in mid-summer. There was, however, no obvious increase in numbers on either of the supplemented grids. In fact, the significantly higher number of *L. rosalia* on grid 1 was due to a decline on the control, and not to an increase on grid 1. Why numbers of *L. rosalia* did not increase as a result of supplementary feeding, but responded by not declining is difficult to explain. *Lemniscomys rosalia* is a solitary species (Skinner & Smithers 1990) and may be territorial. Territorial individuals may have prevented vagrants from entering the supplemented grids.

Table 5 Survival rates of *Lemniscomys rosalia* on burnt and unburnt areas in a Swaziland grassland. Parenthetical values indicate sample sizes

Area	Per cent survival								
	Aug.–Sep. (before fire)	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
Unburnt	(14)	57 (8)	50 (7)	35 (5)	14 (2)	14 (2)	14 (2)	7 (1)	7 (1)
Burnt	(14)	64 (9)	57 (8)	29 (4)	21 (3)	7 (1)	7 (1)	–	–

Rodent home ranges often decrease in the presence of supplementary food (Taitt 1981; Boutin 1990; Sullivan 1990), presumably owing to the increased pressure by non-territory holders attempting to establish new territories. The home ranges of *L. rosalia*, however, did not decrease with supplementary feeding. The absence of a numerical increase in the *L. rosalia* population is in contrast to *Mastomys natalensis* whose population responded strongly to food supplementation (Monadjem & Perrin 1996). A few studies have reported a lack of population increase following supplementary feeding (Hansen & Batzli 1979; Young & Stout 1986), while Krebs & DeLong (1965) observed no response at all by *Microtus californicus* to extra food.

In this study *L. rosalia* was a seasonal breeder. In Uganda, the closely related *Lemniscomys striatus* has been shown to be a seasonal breeder, breeding during the rains (Field 1975; Neal 1977). In Malawi, *L. griselda* (which has been renamed *L. rosalia*, see van der Straeten 1980) appeared to breed during the summer wet season (Hanney 1965). In the former Transvaal, Rautenbach (1982) caught pregnant female *L. rosalia* between October and April, and Kern (1977 in De Graaff 1981) caught scrotal males and pregnant females between November and April. Finally Swanepoel (1972 in De Graaff 1981), working in northern KwaZulu-Natal, caught pregnant female *L. rosalia* between September and February and scrotal males between September and May.

Food supplementation neither affected the initiation nor the length of the breeding season. This may have been due to a number of factors. First, *L. rosalia* may not have been receiving sufficient quantities of the supplemented food. This is highly unlikely since food was present in the cans for most of the days of a month except for a few days during the monthly trapping sessions. Furthermore, *L. rosalia* was active in the late afternoon and early morning, at a time when the numerically dominant *M. natalensis* was inactive (pers. obs.). Hence *L. rosalia* would not have been denied access to the feeding cans. Second, the supplementary food (rolled oats and rabbit pellets) may have been inappropriate for *L. rosalia*. Again this is unlikely, since one of us (A.M.) has successfully maintained *L. rosalia* on such a diet in captivity. A third reason may be physiological in nature. Green vegetation (more specifically 6-methoxy-2-benzoxazolinone or 6-MBOA) has been linked with the initiation of breeding in rodents (Negus & Pinter 1966; Reichman, Kent & Van De Graaff 1975; Neal & Alibhai 1991). It may well be that *L. rosalia* requires a hormonal stimulus to initiate breeding. Further experimental studies are required to answer this question.

Lemniscomys rosalia avoided the burnt sections of both

experimental grids for three months after the fire. This was despite the rapid recovery of the vegetation in response to the high rainfall during this period. That *L. rosalia* does not remain in burnt areas has been reported before (Kern 1981; Swanepoel 1981; Bowland & Perrin 1988). The fire was not a cause of significant mortality to *L. rosalia*. Of the fourteen mice that were caught in the two months before the fire (in areas that subsequently burnt) nine were re-trapped in unburnt areas in the month after the fire, while in the unburnt areas eight out of fourteen mice were re-trapped over the same period. Thus, *L. rosalia* is able to escape the direct effects of fire, but does not remain in burnt areas. Owing to its diurnal habits (Skinner & Smithers 1990; pers. obs.) *L. rosalia* may be particularly prone to predation by birds of prey. Rank grass provides valuable cover which probably significantly reduces the chances of detection by aerial predators. It is perhaps for this reason that *L. rosalia* selects areas with abundant cover.

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