AN EXPERIMENTAL INVESTIGATION OF THE EFFECTS OF SUPPLEMENTARY FOOD AND GROUND COVER ON SMALL MAMMAL POPULATION DYNAMICS AND COMMUNITY STRUCTURE IN A SWAZILAND GRASSLAND

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by

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DEDICATION

This thesis is dedicated to my wife Lynette and my son Keyan Themba.

ABSTRACT

The primary aim of this study was to investigate the role of food supply and ground cover on the community structure, population dynamics and demography of terrestrial small mammals in a subtropical grassland. This aim was achieved through a series of food supplementation and cover manipulation experiments conducted at eKundizeni Farm near Matsapha, Swaziland, over a 28 month period.

The effects of five different diets on the rodent *Mastomys natalensis* were investigated in the laboratory, and the results showed that rolled oats and rabbit pellets were suitable for growth and reproduction in this species.

The effects of supplementary food were investigated on two supplemented grids and one control over a twelve month period. Small mammal biomass increased significantly on the supplemented grids in relation to the control. This increase in biomass was the result of a twofold increase in the numbers of *M. natalensis*. Food supplementation further affected *M. natalensis* by: extending the breeding season of females; increasing body weight; increasing survival; and decreasing home range area. Food supplementation had a weak positive effect on the density of another rodent *Lemniscomys rosalia*, but did not affect any other demographic feature of this species. Food supplementation did not have a demographic effect on any other species of small mammal captured.

The effects of vegetative cover were investigated, over a twelve month period, on two control grids and four manipulated grids on which the vegetative cover was mechanically reduced. Supplementary food was added to two of the latter four manipulated grids. The biomass of small mammals, including *M. natalensis*, was lower on grids with reduced vegetative cover than on the controls. However, food supplementation resulted in a significant increase in the biomass of *M. natalensis* on one of the manipulated grids. Hence, *M. natalensis* was induced to shift to a habitat with reduced cover by the provision of supplementary food.

Additional information on the population dynamics, age structure, reproduction and diet of *M. natalensis*, *L. rosalia*, *Mus minutoides* and *Steatomys pratensis* is also presented.

PREFACE

The field work described in this thesis was conducted on eKundizeni Farm, Matsapha, Swaziland; and the laboratory work was carried out at the University of Swaziland, Kwaluseni Campus, Swaziland, from March 1995 to October 1997, under the supervision of Professor M.R. Perrin.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others it is duly acknowledged in the text.

A. Monadjem

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This study was conducted while I was a full-time lecturer in the Department of Biological Sciences at UNISWA. I am, thus, grateful to Dr. B.S. Nkosi, who was Head of the Department at the time of this study, for arranging my teaching time-table in such a manner so as to permit me to carry out this study. Departmental technicians Stan Mavuso and Mandla Magagula never turned down my requests for help, regardless of the nature of the request.

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CHAPTER 1

INTRODUCTION

General Introduction

Research into the population dynamics of northern temperate rodents began over eighty years ago (Elton 1927). Long-term monitoring programmes (Krebs 1966) together with experimental manipulation studies (Schroder & Rosenzweig 1975; Brown & Munger 1985; Lin & Batzli 1995) have led to quantification of many of the demographic features of these populations. As a result of this, population ecologists have developed a robust theoretical framework in which to study temperate rodent population dynamics and demography.

In southern Africa, small mammal population ecology and demography theory remains largely untested. The work of small mammal ecologists in the subregion has been mainly descriptive. Emphasis has been placed on geographical distributions (Smithers 1971; Rautenbach 1982), habitat selection (Rowe-Rowe & Meester 1982a; Kerley 1992a), diet (Perrin & Curtis 1980; Rowe-Rowe 1986; Kerley 1992b; Perrin *et al.* 1992a) and environmental correlates of breeding activity and demography (de Moor 1969; Mendelsohn 1982; Neal 1984; David & Jarvis 1985; Bronner *et al.* 1988). Furthermore, experimental studies (which involve manipulating environmental factors and recording population responses) are exceedingly rare (Neal 1986). Thus, although qualitative information pertaining to the demography of rodent populations in southern Africa exists, there is a need for quantitative data and an experimental approach.

This study proposes to experimentally investigate the influences of some environmental factors on rodent demography and community structure in Swaziland.

Ecology of small mammals in subtropical southern Africa

Ecological studies of small mammals in southern Africa have focused on two main subjects: population dynamics and distribution. Studies describing population fluctuations (Rowe-Rowe & Meester 1982b; de Moor 1969; Chidumayo 1980, 1984; David & Jarvis 1985; Perrin *et al.* 1992b; Monadjem in press) and reproductive cycles (Coetzee 1965; Perrin & Swanepoel 1987; Withers 1983) of southern African small mammals abound. A great many distributional studies have also been conducted. The distributions of small mammals have been documented at the geographic scale (Rautenbach 1982; Lynch 1994), habitat scale (Withers 1979; Kerley 1992a; Rowe-Rowe & Meester 1982a; Monadjem 1997a) and micro-habitat scale (Bond *et al.* 1980).

Most African species of rodents appear to be seasonal breeders whose reproductive activities are correlated with rainfall (Taylor & Green 1976; Cheeseman & Delany 1979; Delany & Happold 1979; Neal 1977a, 1977b, 1981, 1986, 1991; Perrin 1986; Perrin & Swanepoel 1987; Bronner *et al.* 1988; Christensen 1993; Leirs *et al.* 1989). The correlation with the pattern of rainfall has generally been interpreted as an indirect relationship: rainfall increases food supply which triggers and maintains breeding activity (Neal 1986). Food supply (in the form of grains, seeds and arthropods) generally increases in the wet season (Delany 1986; Lack 1986) and, thus, is also correlated with breeding activity. Further support for the food supply theory comes from the study of *Rhabdomys pumilio* on the Cape Flats where individuals breed in the dry season (David & Jarvis 1985), in contrast to conspecifics on the Transvaal Highveld which breed in the rainy season (Brooks 1982). The Cape Flats is in the winter rainfall region of southern Africa, where food supply is higher in the dry summer months than the wet winter ones (David & Jarvis 1985).

Although many studies document correlations between rainfall, food supply and rodent breeding activity, there are very few studies which have tested these ideas experimentally (Neal 1986; see below).

Ground cover appears to be an important variable in the habitat selected by rodents (De Graaff 1981). Kerley (1992a) reported that the distribution of *Gerbillurus paeba* was negatively correlated with ground cover, while Bond *et al.* (1980) reported a positive correlation between ground cover and *Rhabdomys pumilio* and *Otomys* spp.. Other workers have also documented such correlations (Jooste & Palmer 1982; Rowe-Rowe & Meester 1982a; Monadjem 1997a), although ground cover was not quantitatively measured.

Another way in which the effect of ground cover on rodent community structure has been examined has been through the monitoring of rodent populations before and after a fire has burnt through the survey grid. All such studies have documented a change in rodent community structure before and after the fire (Christian 1977; Kern 1981; Swanepoel 1981; Rowe-Rowe & Lowry 1981; Bowland & Perrin 1988; Rowe-Rowe 1995). Fire, by removing ground cover, alters the structure of the habitat. Since few rodents are thought to perish in the actual fire (Bigalke & Willan 1984), the structure of the new community is probably determined by: 1) habitat selection; 2) food availability and 3) predation pressure. The understanding of the effect of fire on the community structure of small mammals requires an experimental approach which has not yet been attempted in southern African.

Despite the relatively large number of ecological studies on southern African small mammals, these studies have tended to be patchily distributed. Vast areas of southern Africa have never even been surveyed (Skinner & Smithers 1990). Thus, for example, little literature exists on the small mammals of Swaziland (Monadjem 1997b; Monadjem 1997c; Monadjem in press).

Experimentation in ecological studies of small mammals

Manipulation of food

In the northern hemisphere, experimental studies into the demography of small mammals have been conducted since at least the 1950s (Bendell 1959). The role of food supply in population dynamics of small mammals has been experimentally studied by the addition of supplementary food. Food manipulation studies have been reviewed by Boutin (1990). The majority of these studies focussed on the effect of supplementary food on the life-history attributes of individuals or on the dynamics of the population. Furthermore, most of these studies were conducted in Europe or North America and dealt with just a handful of genera of rodents e.g. *Microtus* (Krebs & DeLong 1965; Taitt & Krebs 1981; Cole & Batzli 1978; Desy & Thompson 1983; Ford & Pitelka 1984) *Clethrionomys* (Andrzejewski 1975; Saitoh 1989), *Apodemus* (Watts 1970; Flowerdew 1972; Zubaid & Gorman 1993); *Peromyscus* (Fordham 1971; Hansen & Batzli 1979; Taitt 1981; Gilbert & Krebs 1981; Young & Stout 1986), *Sigmodon* (Doonan & Slade 1995), *Spermophilus* (Dobson & Kjelgaard 1985) and *Tamiasciurus* (Sullivan 1990). In contrast to the numerous population studies, only two studies have observed the response of the small mammal community to food supplementation (Abramsky 1978; Brown & Munger 1985). Most of the above-mentioned studies were of short-term duration, lasting 2 years or less. Only one long-term food manipulation study exists (Heske *et al.* 1994). These workers presented results covering a 13-year period.

Results from these food manipulation studies are equivocal. In many studies, individuals on grids receiving supplementary food had smaller home ranges, higher body weights, longer and more intense breeding seasons, and the population densities were two to three times higher than on the control grids. But these trends are by no means universal (see Boutin (1990) for a review of this subject).

Manipulation of cover

The importance of ground cover for the community structure and habitat selection of small mammals has been long recognized (Rosenzweig & Winakur 1969; Grant & Birney 1979; Grant *et al.* 1982). However, cover manipulation studies are far less numerous than food manipulation studies. This is probably due to the labour-intensive nature of the former. Cover manipulation studies have been conducted almost exclusively in North America and on voles (Taitt & Krebs 1983; Edge *et al.* 1995; Peles & Barrett 1996). The removal of vegatative cover in these studies appeared to have affected the density, survival and dispersal of voles.

Experimentation in Africa

Experimental manipulations of African small mammal communities have rarely been conducted (Neal 1986). Taylor and Green (1976) showed that the provision of supplementary food to *Mastomys natalensis* in Kenya did not elicit a reproductive response, although fat deposits increased significantly. Poulet *et al.* (1981) and Hubert *et al.* (1981) studied the effects of food supplementation on *Mastomys erythroleucus* and *Taterillus pygargus* in Senegal. Both studies reported an extended breeding season for those rodents on the grids receiving extra food, compared with those on a control grid, especially during years of low rainfall. Leirs *et al.* (1990), working in Tanzania, supplied a population of *Mastomys natalensis* with maize and reported a slight increase in the body weight of the individuals on the supplementary grid compared to those on the control. Neal and Alibhai (1991) and Neal (1996) investigated the effects of supplementary food, water and 6-methoxybenzoxazolinone (6-MBOA) on *Tatera leucogaster*. [6-MBOA is a plant chemical found in growing vegetation and is known to induce reproduction in *Microtus* (Berger *et al.* 1981) although its effects on African rodents are equivocal (Alibhai 1986; Linn 1991; Neal & Alibhai 1991; Leirs & Verheyen 1995; Neal 1996)]. *Tatera leucogaster* individuals which received supplementary food increased in body weight and their reproductive organs were larger than individuals that did not.

Experimental manipulation has also involved water. Christian (1979), by manipulating water supply, showed that the availability of drinking water extended the breeding activity of two (out of three) Namib desert rodents. Neal (1996) observed an increase in the uterus mass of *Tatera leucogaster* supplied with supplementary water. Little, however, is known about the water requirements of southern African rodents (Green & Rowe-Rowe 1987). It has been suggested that *Rhabdomys pumilio* is independent of drinking water (Willan & Meester 1987) and that *Mastomys natalensis* is unlikely to drink when the vegetation is lush (Green & Rowe-Rowe 1987). These studies are not conclusive and further investigation is necessary.

To date, there appear to be no studies, conducted in Africa, that have experimentally tested the influence of vegetative cover on either small mammal demography or community structure.

Aims of the study

The overall aim of the study was to ascertain the role of food and ground cover on the population dynamics and community structure of small mammals in a subtropical grassland in Swaziland by means of experimental manipulation of food supply and ground cover. Hence, the main emphasis of the study was experimentation rather than description. The aims and objectives of each chapter are stated in that particular chapter, and will not be repeated here.

Outline and format of the thesis

This thesis comprises twelve chapters of which ten (Chapters 2 to 11) form the basis of the thesis. These ten chapters have all been submitted for publication to refereed journals. Chapter 4 has been published. Furthermore, Chapter 10 has been accepted for publication, as have slightly modified versions of Chapters 9 and 11. Chapters 2 to 11 have been presented in the format in which they where sent for publication. Hence, the formats of the chapters differ, depending on the regulations of the journal to which each chapter has been sent. The only changes that have been made for the purpose of this thesis have been: 1) the addition of the chapter number which appears at the top of the first page of each chapter, 2) the addition of a note indicating the journal to which the chapter has been submitted, 3) the removal of the address(es) of the author(s), 4) the printing of figure captions on the same page as the figures, and 5) when reference has been made to publications or manuscripts included in this thesis, the chapter number has also been included in the reference.

Chapter 1 (this chapter) serves as a general introduction to the thesis. Chapter 2 provides an account of the general ecology of the small mammals inhabiting the study area. Chapter 3 describes a laboratory experiment which tests the effect of the supplementary food, used in the field experiments, on the growth and reproduction of *Mastomys natalensis* (the most numerous small mammal in the study area). Chapter 4 presents the preliminary results of the food manipulation studies. Chapters 5 and 6 deal with the effects of supplementary food and removal of cover on the community structure of small mammals in the study area. Chapters 7 to 9 deal with the effects of supplementary food and removal of cover on *Mastomys natalensis*. Chapters 10 and 11 deal with the population dynamics of some of the less numerous and less known species caught in the study area. Chapter 12 is the Conclusion.

This thesis is based on two experimental manipulations, each of twelve month duration. The chapters are not in chronological order, thus chapters 4, 5, 7, 9, 10 and 11 report on the first experiment (June 1995 to May 1996), while chapters 6 and 8 report on the second experiment (June 1996 to May 1997).

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CHAPTER 2*

REPRODUCTIVE BIOLOGY, AGE STRUCTURE AND DIET OF *MASTOMYS NATALENSIS* (MURIDAE: RODENTIA) AND OTHER RODENTS IN A SWAZILAND GRASSLAND

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Abstract

The timing of reproduction, monthly changes in age structure and diet of *Mastomys natalensis* were investigated in a subtropical grassland in Swaziland. Mice were collected monthly over a 25 month period. The age of *M. natalensis* individuals were estimated using eye lens weight. Pregnant females and scrotal males were recorded in the wet season only, with interannual differences in the initiation of breeding being correlated with rainfall. Monthly changes in age structure of *M. natalensis* are determined by the entry of young in the wet season and the death of adults, that were previously reproductive, in the dry season. The stomach contents of *M. natalensis* consisted predominantly of vegetative plant matter in the dry season, with seeds and arthropods having contributed significantly in the wet season. Information on reproduction and diet in *Lemniscomys rosalia* and *Steatomys pratensis* are also presented.

Introduction

The multimammate mouse *Mastomys natalensis* (A. Smith) is a widespread African murid rodent of great economic importance (DE GRAAFF 1981). The reproductive biology and population structure of *M. natalensis* has been intensively investigated at a single study site in Tanzania (TELFORD 1989; LEIRS and VERHEYEN 1995). In contrast, existing knowledge of this species in southern Africa is based on several scattered, short-term studies (COETZEE 1965; CHIDUMAYO 1984; BRONNER, RAUTENBACH and MEESTER 1988). Furthermore, the age of mice captured in these southern African studies were estimated using toothwear, a technique which is known to be inaccurate (MORRIS 1972).

The objectives of this study were to investigate the timing of reproduction, monthly population age structure and seasonal changes in diet of *M. natalensis* in a subtropical grassland in the Middleveld of Swaziland. Since other species of small mammals were also captured during this study, information on these species is presented where available.

Materials and methods

The study area was situated at eKundizeni Farm (26°33'S; 31°16'E) near Matsapha, Swaziland, approximately 1 km away from the site described in MONADJEM and PERRIN (1996; Chapter 4). This region receives most of its rainfall between October and March, but the onset of rains differs between years. 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. During the study period, rainfall was recorded monthly at eKundizeni Farm.

Small mammals were trapped monthly using Sherman live-traps and commercial back-break kill-traps set in lines. These lines were rotated on a monthly basis to avoid trapping the same line two months consecutively. Sherman traps were set on one or two nights per month from October 1995 to March 1997, whereas kill-traps were set from October 1995 to October 1997. The mice captured with Sherman traps were returned to the laboratory where they were killed with chloroform, measured and their reproductive condition assessed. Reproductive condition was assessed following LEIRS and VERHEYEN (1995). In males, the position and length of the testes, the size of the seminal vesicles and epididymal tubuli was recorded. In the females, the condition of the uterus (filiform, normal, oestrous or pregnant), the number of embryos and placental scars was recorded.

The eyes of *M. natalensis* were removed immediately after death and the eye lenses were prepared for weighing following PERRIN (1979). The eyes were fixed in 10% formalin. After fixing, the lenses were removed and oven dried for 7 days at 80°C. Each lens was weighed separately on an electronic balance. The age of each mouse was estimated using the regression line of lens weight on age in days in LEIRS and VERHEYEN (1995):

$$w = -10.46088 + (4.35076 \times \ln(a))$$

where: w = dry eye lens weight in mg; and a = age in days. Mice were assigned to one of seven age classes (<99 days, 100-159 days, 160-219 days, 220-279 days, 280-339 days, >340 days). *Mastomys natalensis* reaches first oestrous at a mean age of 104 days (JOHNSTON and OLIFF 1954) and, hence, the first age class includes mostly immature individuals. The remaining age classes were arbitrarily set at 60 day intervals.

Mice captured in the kill-traps were returned to the laboratory where their reproductive condition and stomach contents were assessed. Commencing in November 1996, the stomachs of the kill-trapped mice were removed for stomach content analysis following (KERLEY 1989; MONADJEM 1997). Four dietary categories were recognized: foliage (vegetative plant material), seeds, arthropods and unidentified material. The importance of each food type was expressed both as a frequency of occurrence and a proportional (percentage) contribution. Frequency of occurrence was calculated as the number of stomachs in which a particular food type was observed. Percentage contribution was determined by examining the stomach contents through a dissection microscope. The relative contribution of each food type in the microscope field was estimated for five randomly placed fields.

Results

Total monthly rainfall during the study period is shown in Fig. 1. The total rainfall for the period October 1995 to September 1996 was 1368 mm, and for the period October 1996 to September 1997 was 1101 mm. Rainfall during the study period was above the long-term mean (928 mm) for the area.

A total of nine species of small mammals was captured, of which only three species (*M.*

natalensis, the single-striped mouse *Lemniscomys rosalia* (Thomas) and the fat mouse *Steatomys pratensis* Peters) were captured in more than six separate months (Table 1). The results, hence, focus on these three species and in particular on *M. natalensis*. Other species of small mammal captured were: the swamp shrew *Crocidura mariquensis* Roberts, the musk shrew *Crocidura hirta* Peters, the striped mouse *Rhabdomys pumilio* (Sparrman), the pygmy mouse *Mus minutoides* A. Smith, the climbing mouse *Dendromus mystacalis* Heuglin and the angoni vlei rat *Otomys angoniensis* Thomas.

Reproduction

Mastomys natalensis was not reproductively actively throughout the study period (Fig. 2). Males were scrotal in 14 months of the study and females were pregnant in 8 months. Reproductive activity was correlated with rainfall in both males (r_{23}=0.802, $P<0.001$) and females (r_{23}=0.569, $P<0.01$). Reproductive activity in females was also correlated with rainfall one and two months previously (r_{22}=0.622, $P<0.01$; r_{21}=0.668, $P<0.001$, respectively), while in males it was only correlated with rainfall one month previously (r_{22}=0.589, $P<0.01$). There was very little sign of reproductive activity, in either sex, in the dry season between April and October. Similar trends were shown by *L. rosalia* and *S. pratensis*. Scrotal male *S. pratensis* were collected in October, December and January, and perforate females in December. Pregnant or lactating female, and scrotal male, *L. rosalia* were captured between January and April.

The initiation and intensity of breeding in *M. natalensis* varied between the two years. In the

1995/6 breeding season, all males were fully scrotal at the beginning of the study in October. In the 1996/7 breeding season, however, only 80% of the males were scrotal in October. This interannual difference was even more pronounced in females, where 75% of females were pregnant in November 1995 while none were pregnant in November 1996 (and only 33% were pregnant in December 1996). Thus, *M. natalensis* initiated breeding approximately one to two months later in the 1996/7 breeding season than in the previous season.

The litter size of *M. natalensis* was 11.4 (n=17). There were no significant differences in the litter size of *M. natalensis* between females of ages less than six months, 6 to 8 months and greater than 8 months (ANOVA, P>0.05; Table 2). Females older than 8 months, however, weighed more than females in the two younger categories. The mean litter size of *L. rosalia* was 6.1 (n=12, range: 4-10).

The ages of 146 (60 females and 86 males) *M. natalensis* were estimated using eye lens weight. It was thus possible to estimate the dates of birth for these individuals. Most mice were born between November and March (Fig. 3), with only a single (incorrectly aged?) individual being born between July and September in 1995 and none between July and November in 1996.

There was a significant, albeit weak, correlation between age and body mass in male *M. natalensis* (r_{86}=0.453, P<0.001).

Age structure

The monthly age structure of *M. natalensis*, based on the mice that were aged by the eye lens weight technique, is shown in Table 3. Immature mice (first age class) entered the population in

December in the 1995/6 season, but only in February in the 1996/7 season. This corresponds to the delay in reproductive activity recorded in the 1996/7 season (see above). Immature mice were recorded between December 1995 and July 1996 with a peak in April, but were absent between August 1995 and January 1996. Very few mice were estimated to be older than twelve months (the oldest mouse being aged at 480 days). Individuals in the last age class were captured in the wet season and the late dry season, but were absent in the late wet season and early dry season (between April and September).

Diet

The composition of the diets and the frequency of occurrence of food types of the different species are presented in Table 4. With the exception of *M. natalensis*, the sample sizes were small. The stomach contents of *O. angoniensis* and *D. mystacalis* consisted purely of foliage (vegetative plant matter), while those of *C. hirta* consisted of arthropod remains. Foliage constituted the entire stomach contents of *L. rosalia* in all months except the wet summer months when seeds formed about 50% of the contents. The stomach contents of *S. pratensis* consisted of approximately equal parts of foliage and arthropod remains, with arthropods forming a significant proportion of the contents in both the wet and the dry season. Seeds were only present in the late wet season (January to April). The stomach contents of *M. natalensis* consisted predominantly of foliage, with seeds and arthropods present at lower frequencies. Seasonal changes in the diet of *M. natalensis* are shown in Fig. 4. In the dry season (between June and October), the diet of *M. natalensis* consisted entirely of foliage. Seeds were an important component of the diet in the wet months between November and May, while arthropods were an important part of the diet only in the middle of the wet season between January and April.

Discussion

Reproduction

It has been shown throughout Africa that reproduction in *M. natalensis* is associated with rainfall (COETZEE 1965; TAYLOR and GREEN 1976; NEAL 1977; SWANEPOEL 1980; CHIDUMAYO 1984; BRONNER et al. 1988; LEIRS et al. 1989; PERRIN, SLOTOW and MENDELSOHN 1992; WIRMINGHAUS and PERRIN 1993). BRONNER et al. 1988 reported a correlation between rainfall two months previously and reproductive activity in female (but not male) *M. natalensis* in South Africa. A similar correlation was reported by LEIRS and VERHEYEN (1995). The latter study, conducted over several years, included interannual variation in rainfall which, thus, strengthened the observed correlation. In the present study, reproductive activity of both male and female *M. natalensis* was correlated with rainfall in the previous month, although the strongest correlation in females was with rainfall two months previously. This supports the suggestion that rainfall is the ultimate factor in the timing of reproduction in female *M. natalensis* (BRONNER et al. 1988). In males, by contrast, the strongest correlation was with rainfall in the same month. The reason for this is probably related to the fact that reproductive activity in females was defined by pregnancy, while in males it was defined by scrotal testes. Defined as such, males should be able to respond to rainfall more quickly than females.

The litter size of *M. natalensis* reported here (11.4, see Results) is very similar to that reported from Morogoro in Tanzania (11.3; LEIRS and VERHEYEN 1995) and that from Zambia (12.4; CHIDUMAYO 1984). There were no differences in litter size between three different age classes of *M. natalensis* supporting the findings of LEIRS and VERHEYEN (1995) that there is no age-specific fecundity in this species. Similar findings have also been reported for *Tatera leucogaster* (PERRIN and SWANEPOEL 1987). The mean litter size recorded for *L. rosalia* (6.1) in this study is higher than that reported for wild (range: 2-7; JACOBSEN 1977; SKINNER and SMITHERS 1990) and captive (mean: 4.2; SCOTT and MEESTER 1988) females.

Owing to the small sample sizes, not much should be said about reproduction in any of the other species of small mammal captured. The period of reproductive activity recorded for female *L. rosalia* in this study (between January and April), however, corresponds to the presence of juvenile *L. rosalia* in a capture-mark-release study conducted approximately 1 km from the present study (MONADJEM and PERRIN in press; Chapter 10).

Age structure

The seasonal changes in age structure of *M. natalensis* described in this study are similar to those described in Tanzania (LEIRS, VERHAGEN and VERHEYEN 1993; LEIRS and VERHEYEN 1995), and to those described by toothwear in South Africa (COETZEE 1965), Uganda (NEAL 1977) and Zambia (CHIDUMAYO 1984). *Mastomys natalensis* individuals seldom survive much beyond 12 months, and probably never breed in more than one season. Of the four mice, in this study, whose ages were estimated between 400 and 480 days, one of them was captured in July and probably would not have survived the dry season to breed in a second season. The other three mice were captured in the middle to late wet season and would, thus, have been immatures in the previous breeding season. The older age classes die off at the end of the breeding season (March/April) and are replaced by that season's offspring.

The monthly age structure of this population corresponded with the timing of reproductive activity of the mice and was dissimilar in the two breeding seasons. In the 1995/6 season, pregnant females were first captured in November and immature mice in December. In the 1996/7 season, pregnant females were first captured in December/January and immatures in February.

Diet

Mastomys natalensis exhibits gastro-intestinal and dental characteristics typical of an omnivorous murid rodent (PERRIN and CURTIS 1980). In this study *M. natalensis* appeared to be omnivorous, feeding on what food was available. In the dry season when seeds and arthropods are present in low numbers (LACK 1986; personal observation), *M. natalensis* feeds only on vegetative plant matter (probably leaves of grasses). In the wet season when most grasses seed (VAN OUDTSHOORN 1992; personal observation) and arthropod numbers increase (LACK 1986), seeds and arthropods contribute up to 50% of the identifiable stomach contents. Similar observations have been made in Tanzania (LEIRS, VERHAGEN and VERHEYEN 1994; LEIRS and VERHEYEN 1995), where the diet of *M. natalensis* was predominantly vegetative plant matter, with arthropod consumption increasing in the wet season. Seeds were an important component of the diet during the long "masika" rains when reproduction was at its peak. In Uganda, FIELD (1975) reported that over 90% of the stomachs of *M. natalensis* contained insect remains which made up 20% of the diet by weight. In Kenya, based on faecal analysis of *M. natalensis*, grass seeds contributed the bulk of food eaten (OGUGE 1995). It is likely that seeds and vegetative plant matter are not digested to the same degree (Hansson 1970), and that therefore the results of faecal analysis are skewed toward food materials that digest slowly. In Zimbabwe, seeds formed the main component of the diet of *M. natalensis*, while arthropods contributed significantly only in spring and summer (SWANEPOEL 1980). The latter study was conducted in an agricultural area, and it is thus likely that seeds would have been available throughout the year. In conclusion, it would appear that *M. natalensis* eats seeds and arthropods when available, but survives on vegetative plant matter throughout the remainder of the year.

The diet of *L. rosalia* has been anecdotally recorded as consisting of grass and seeds (DE GRAAFF 1981). The stomach contents of a small sample of *L. rosalia* taken in the wet season from the South African lowveld consisted of approximately equal amounts of seeds and vegetative plant matter (WATSON 1987 in SKINNER and SMITHERS 1990). The present study shows that *L. rosalia* feeds predominantly on vegetative plant matter, taking seeds when available (i.e. in the wet season).

Information on the diet of *S. pratensis* is scanty. *S. pratensis* has been described as an omnivorous granivore (SKINNER and SMITHERS 1990) and herbivorous granivore (MONADJEM 1997). The present study indicates that arthropods play an important role in the diet of *S. pratensis*, while seeds are seasonally important.

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Table 1. Number of trap-nights and number of captures of *Mastomys natalensis*, *Lemniscomys rosalia* and *Steatomys pratensis*.

	Numbers			
Date	Trap-nights	*M. natalensis*	*L. rosalia*	*S. pratensis*
1995				
October	75	6		
November	45	10		
December	120	5		1
1996				
January	80	16	1	
February	60	5	1	
March	120	5	1	
April	60	11	1	
May	60	9		1
June	No trapping			
July	60	10	4	
August	60	8	3	
September	300	14	4	
October	150	13	1	2
November	150	15		
December	150	29		3
1997				
January	150	5	1	1
February	150	10		1
March	150	8	1	
April	40	7	4	2
May	40	8		1
June	40	8		
July	40	5	4	
August	40	4	1	
September	40	4		1
October	40	2		1

Table 2. Mean mass and litter size (± SE) of female *Mastomys natalensis* of different age classes. Row values with different superscripts indicate a significant difference (ANOVA, $P<0.05$) among age classes.

	Age class		
	< 6 months	6 to 8 months	> 8 months
Sample size	22	17	21
Mean mass	30.2 ± 2.6^{a}	30.2 ± 1.8^{a}	38.6 ± 1.8^{b}
Mean litter size	13.8 ± 2.1^{a}	10.7 ± 1.5^{a}	9.9 ± 1.6^{a}

Table 3. Seasonal changes in age class structure of *Mastomys natalensis* between October 1995 and March 1997 at eKundizeni Farm, Swaziland. Numbers are the percentage of individuals recorded in each age class.

			Age class (in days)					
Month		n	<99	100-159	160-219	220-279	280-339	>340
1995	Oct	6	-	50	17	17	17	-
	Nov	9	-	-	33	22	44	-
	Dec	4	25	-	25	25	-	25
1996	Jan	15	20	7	7	40	13	13
	Feb	4	25	25	-	25	-	25
	Mar	4	50	25	-	-	-	25
	Apr	11	73	27	-	-	-	-
	May	9	22	78	-	-	-	-
	Jun	No data						
	Jul	10	20	40	10	20	-	10
	Aug	8	-	13	25	38	25	-
	Sep	3	-	-	33	33	33	-
	Oct	13	-	-	31	46	8	15
	Nov	14	-	29	43	7	7	14
	Dec	24	-	-	4	67	17	13
1997	Jan	2	-	-	-	100	-	-
	Feb	6	83	-	-	-	17	-
	Mar	3	67	-	-	33	-	-

Table 4. Proportional contribution (± SE) and frequency of occurrence (in brackets) of food types (both figures expressed as percentages) found in the stomachs of six species of small mammals captured at eKundizeni Farm, Swaziland.

		Food type		
Species	n	Foliage	Seeds	Arthropods
Rodentia				
Otomys angoniensis	2	100±0	0	0
		(100)	(0)	(0)
Dendromus mystacalis	1	100	0	0
		(100)	(0)	(0)
Lemniscomys rosalia	10	93.2±6.8	6.8±6.8	0
		(100)	(10)	(0)
Mastomys natalensis	57	71.8±3.8	21.6±3.4	6.6±2.2
		(98.2)	(54.4)	(28.0)
Steatomys pratensis	9	47.4±14.3	10.4±5.6	42.1±15.6
		(77.7)	(100)	(0)
Insectivora				
Crocidura hirta	1	0	0	100
		(0)	(0)	(100)

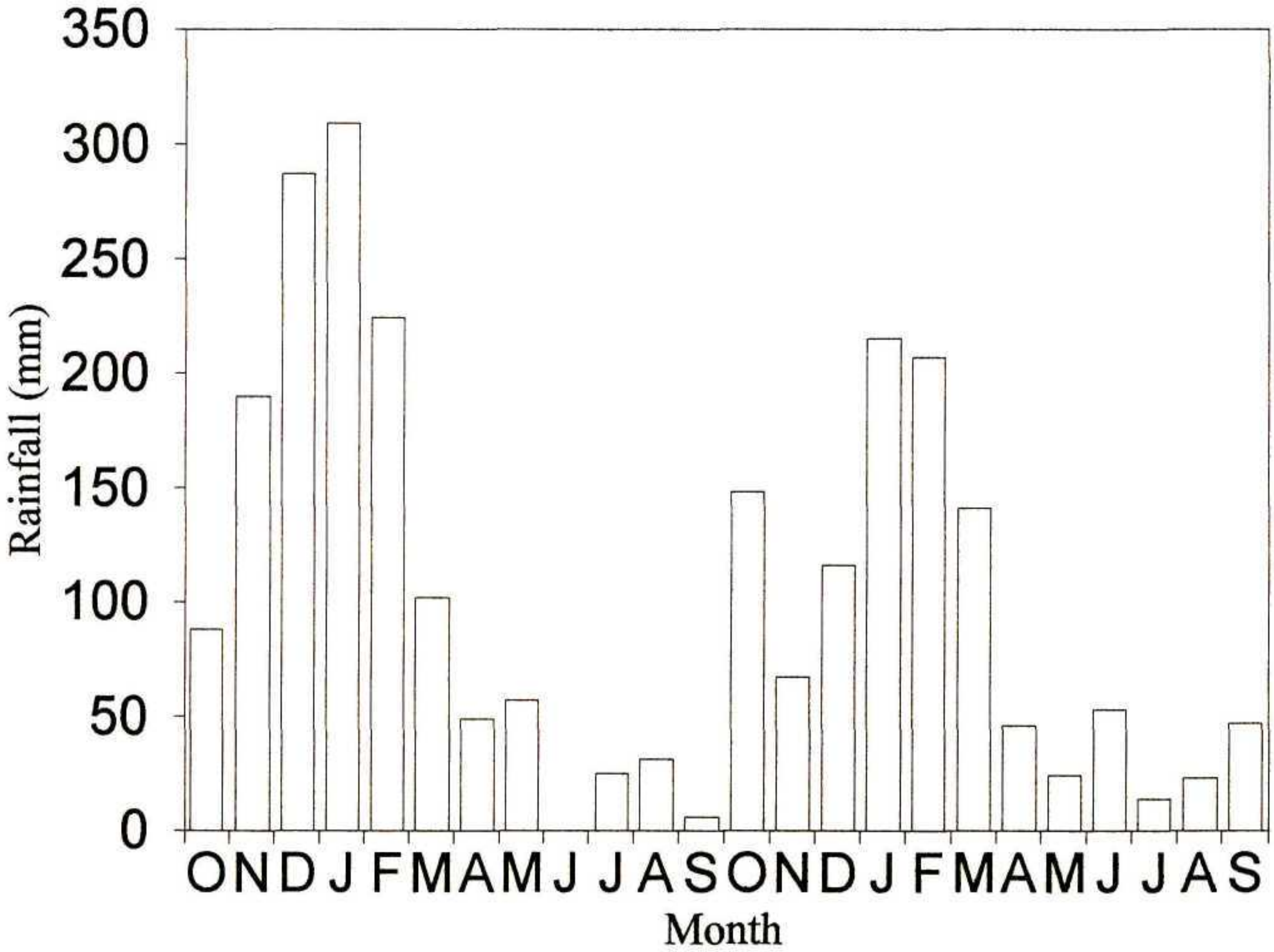

Fig. 1. Total monthly rainfall at eKundizeni Farm, Swaziland from October 1995 to October 1997.

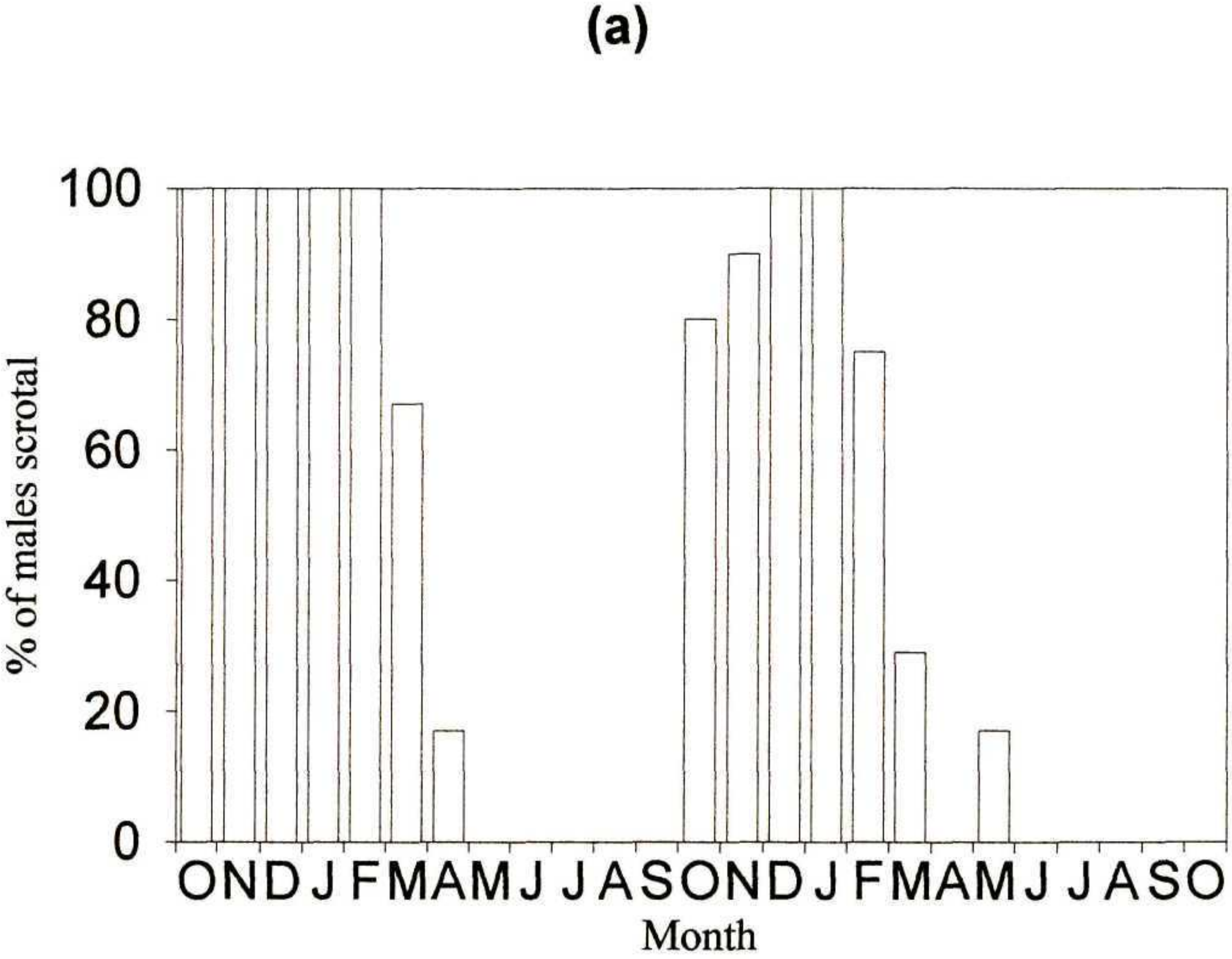

Fig. 2. The proportions (%) of *Mastomys natalensis*: (a) males with scrotal testes, and (b) pregnant females, trapped between October 1995 and October 1997.

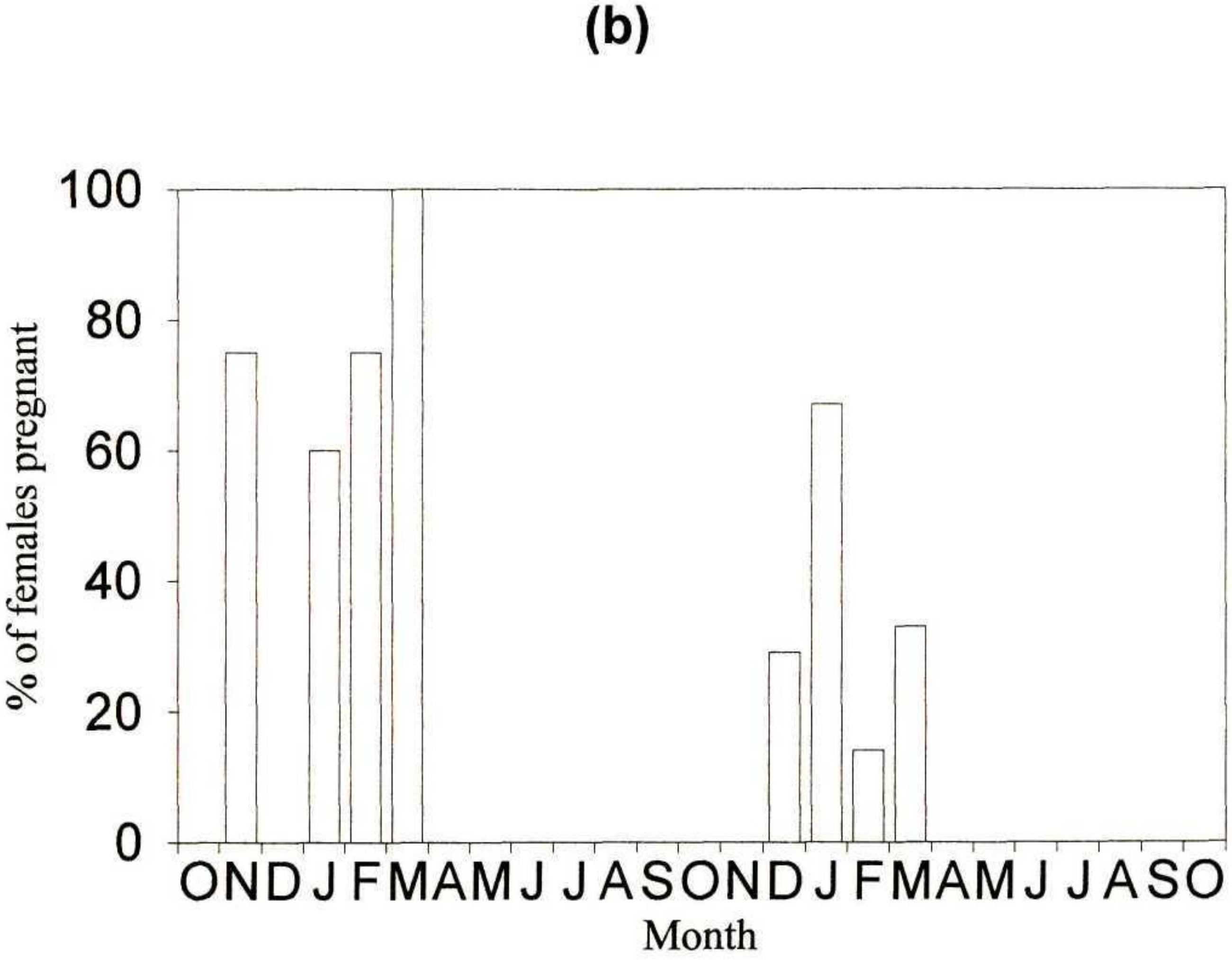

Fig. 2. The proportions (%) of *Mastomys natalensis*: (a) males with scrotal testes, and (b) pregnant females, trapped between October 1995 and October 1997.

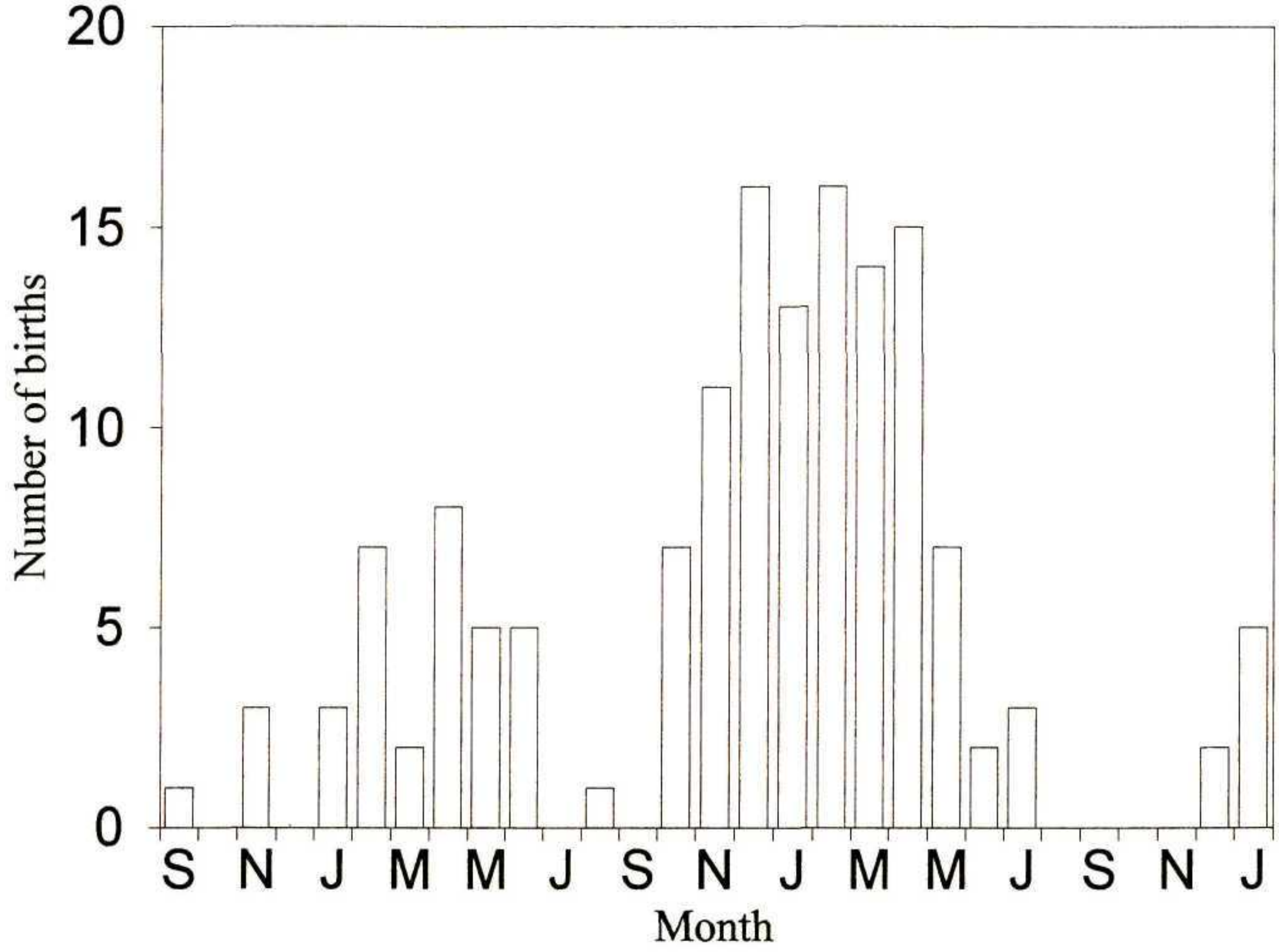

Fig. 3. Numbers of *Mastomys natalensis* born per month (based on age estimated from eye lens weight) between September 1994 and January 1997.

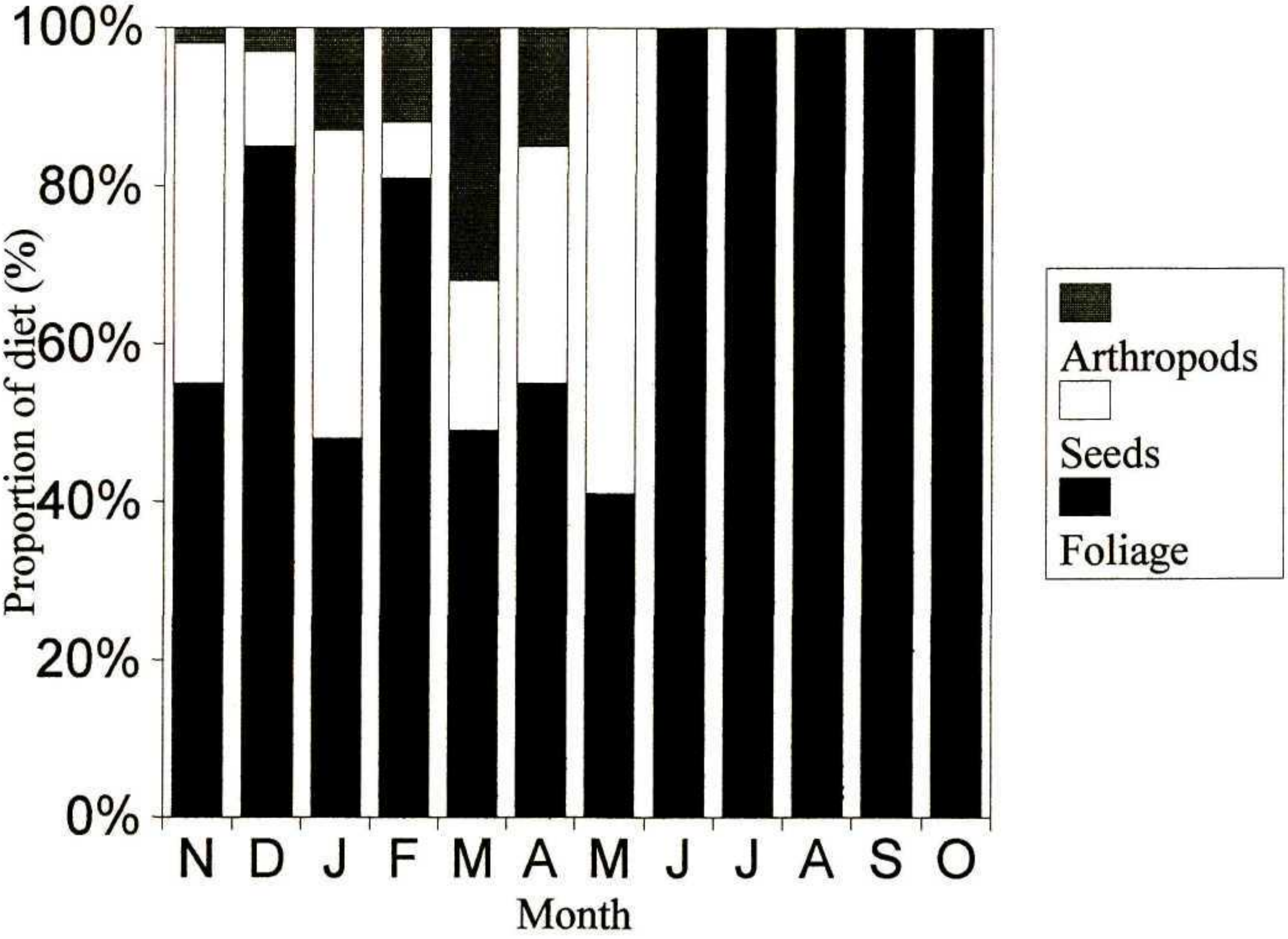

Fig. 4. Seasonal changes in (%) diet composition of *Mastomys natalensis* between November 1996 and October 1997 at eKundizeni Farm, Swaziland.

CHAPTER 3*

THE EFFECT OF VARIOUS FOOD TYPES ON GROWTH AND REPRODUCTION IN MASTOMYS NATALENSIS (MURIDAE: RODENTIA)

*Monadjem, A. Submitted. *Mammalia*

The early post-natal growth and development of the multimammate mouse Mastomys natalensis (Smith) has been studied (Meester 1960, Meester and Hallett 1970, Baker and Meester 1977), as has the growth of individuals in wild populations (Leirs et al. 1990, Christensen 1993). Mastomys natalensis has been described as an opportunistic omnivore (Leirs and Verheyen 1995; Monadjem 1997). It is, however, not known whether different food types affect the growth of M. natalensis differently.

The objectives of this study were to experimentally ascertain the effects of five different diets on the growth and reproduction of laboratory-kept M. natalensis.

Wild-born mice were captured in September 1996, immediately prior to the beginning of the breeding season, near Matsapha (26°33'S, 31°16'E) in the Middleveld of Swaziland. None of the mice were reproductively active at the time of capture. In the previous season, males were fully scrotal in October and females were perforate in November (Monadjem and Perrin 1996; Chapter 4). Two male and two female mice were randomly assigned to each of five cages. Each of these five cages was provided with a particular food type of either maize seeds, rolled oats, groundnuts, rabbit pellets or green kikuyu grass (Pennisetum clandestinum). The mice were given water ad. lib., and were fed once a week. Food was always supplied in excess of what was consumed. The amount of food consumed in each cage per week was calculated by subtracting the weight of the food remaining from that provided. Each mouse was weighed once a week for twenty-seven weeks (except the mice fed on grass, which were weighed daily).

The initial weight of the female mice assigned to the five different diets did not differ significantly (see Table 1). The initial weight of the male mice assigned to the groundnut diet was significantly higher than that of the mice assigned to the maize diet (see Table 1). The weight of the mice on the other diets neither differed from each other nor from those mice on the maize diet or groundnut diet (see Table 1). Mice that were fed a pure grass diet lost weight rapidly within three days and had to be fed rabbit pellets to prevent them from dying. This loss of body weight was not due to the mice not feeding on the grass, since the mice ate most of the grass provided. Kikuyu grass is highly nutritious and planted as a pasture for sheep and dairy cattle (van Oudtshoorn 1992). The fact that these mice lost weight suggests that M. natalensis is not able to survive on a pure grass diet.

Of the remaining four treatments, mice on the maize diet did not significantly increase their weight in the course of the twenty-seven weeks (Table 1, Fig. 1). In fact, the weight of all four mice on this diet either decreased or remained unchanged over this period. Furthermore, female mice on the maize diet did not show signs of reproductive activity and did not produce offspring. It would thus appear that a pure maize diet is not sufficient for growth and reproduction in M. natalensis. This may explain why the addition of supplementary maize had only a negligible effect on a population of M. natalensis in Tanzania (Leirs and Verheyen 1995).

The mice fed on oats, rabbit pellets and groundnuts all increased significantly during the twenty-seven weeks (Table 1, Fig. 1). At the end of the study, mice fed on these three diets weighed significantly more than those on the maize diets (see Table 1). Furthermore, female mice on the oats and rabbit pellet diets successfully produced offspring.

Studies which investigate the effect of supplementary food on small mammal populations must enure that the supplementary food provided is eaten by the animals and is suitable for their growth and reproduction. This study has shown that rolled oats and rabbit pellets are suitable foods for growth and reproduction in Mastomys natalensis.

Acknowledgements. - My sincere thanks and gratitude to Phesheya Dlamini for looking after the mice and the laboratory experiments.

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TABLE 1. - Mean weight of male and female Mastomys natalensis assigned to different diets at the beginning and the end of the 27-week experiment. Row figures with the same superscript do not differ significantly (Tukey test, P>0.05).

	Food type				
Weight	Maize	Pellets	Oats	Groundnuts	ANOVA
Males					
Initial mass	29.3^{a}	38.3^{ab}	39.6^{ab}	42.9^{b}	F=7.7748, P=0.04
Final mass	28.2^{b}	58.5^{a}	54.1^{a}	52.4^{a}	F=14.2690, P=0.01
Females					
Initial mass	22.6	25.8	28.2	30.1	F=0.4736, P>0.05
Final mass	19.5^{b}	37.4^{a}	37.7^{a}	34.1^{a}	F=22.1748, P=0.02

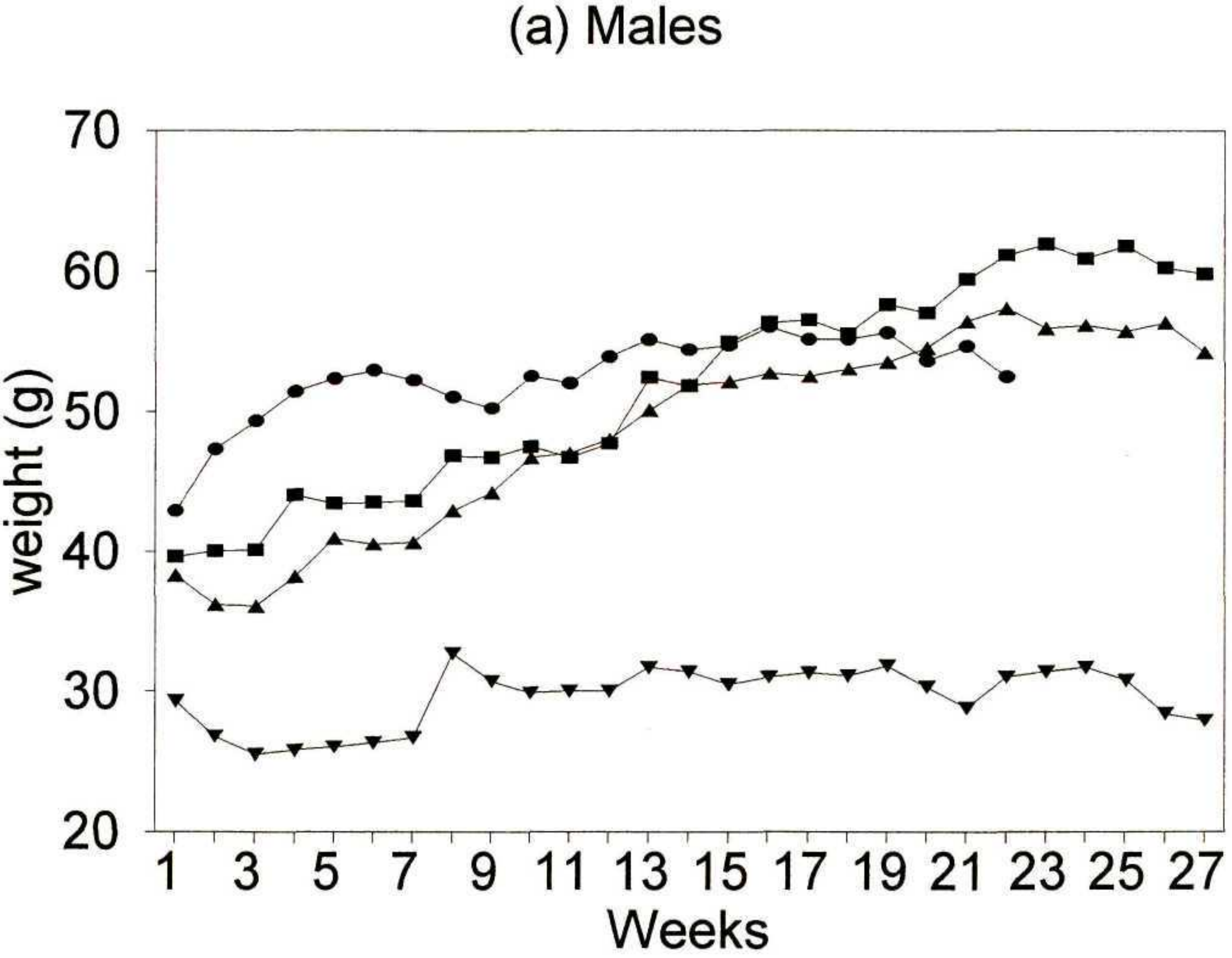

Fig. 1. - Mean weekly weights of (a) male, and (b) female Mastomys natalensis on four different diets: maize (▼), pellets (▲), oats (■) and groundnuts (●).

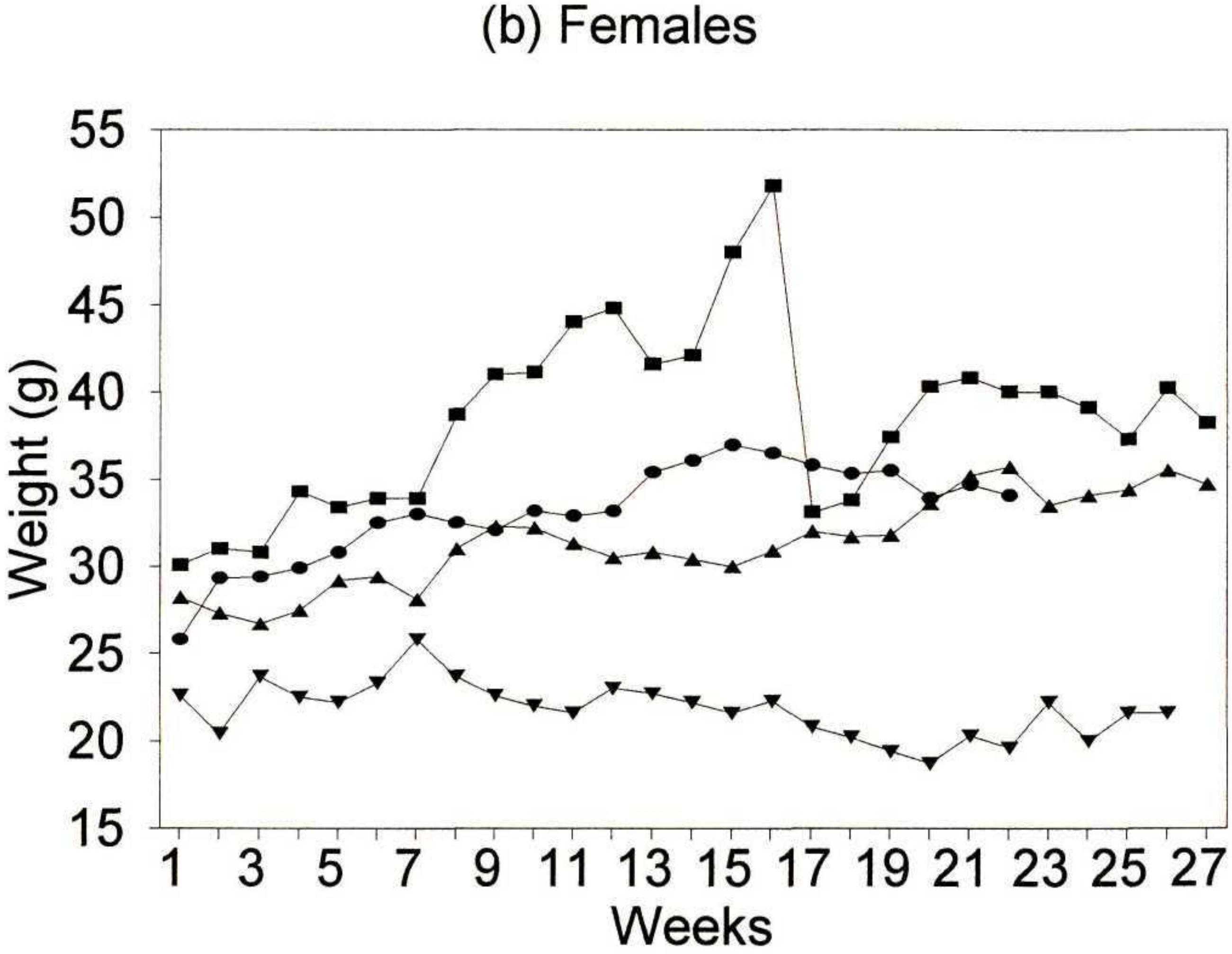

Fig. 1. - Mean weekly weights of (a) male, and (b) female Mastomys natalensis on four different diets: maize (▼), pellets (▲), oats (■) and groundnuts (●).

CHAPTER 4*

THE EFFECTS OF ADDITIONAL FOOD ON THE DEMOGRAPHY OF RODENTS IN A SUBTROPICAL GRASSLAND IN SWAZILAND

*Monadjem, A. & Perrin, M.R. 1996. *Mammalia* 60: 785-789

Although studies documenting correlations between rainfall, food supply and rodent breeding activity abound (Bronner et al. 1988, Cheeseman and Delany 1979, Christensen 1993, Leirs et al. 1989, Neal 1977, Perrin and Swanepoel 1987), there are few studies which have tested these observations experimentally (Hubert et al. 1981, Taylor and Green 1976), and none have been conducted in southern Africa. Manipulated increases in food supply have resulted in: 1) extension of the breeding season (Zubaid and Gorman 1993, Hansen and Batzli 1979, Taitt 1981), 2) increases in population size (Doonan and Slade 1995, Flowerdew 1972), 3) increases in reproductive intensity (Saitoh 1989, Taitt and Krebs 1981), 4) decreases in home range (Taitt 1981), and 5) increases in growth rate (Fordham 1971, Taitt 1981).

The objectives of the study were to experimentally ascertain the effect of addition of supplemental food on the population growth of rodents in a grassland habitat in Swaziland.

Three permanently marked grids (100m × 100m) were established, in May 1995, on an unutilized natural grassland site in the Swaziland middleveld, near Matsapha (26°33'S 31°16'E). One plot served as the control, while 8 kg of food, consisting of equal amounts of rolled oats and rabbit pellets, were added monthly to each experimental plot from July (immediately after the July sampling period) until November. Rodents were trapped monthly on all three plots from June until November. One hundred Elliot and Sherman live-traps were set 10 m apart on each grid on three consecutive nights per month. Each trapped rodent was uniquely toe-clipped, sexed, weighed and its reproductive condition was assessed. Testes were recorded as scrotal or abdominal and females either as having perforate or non-perforate vaginae. No visibly pregnant or lactating females were caught during the study. The numbers of individuals on each grid were estimated using the minimum number known alive method (MNA: Krebs, 1966).

In June and July (before food addition commenced), the initial numbers of the multimammate mouse Mastomys natalensis were similar on the control grid B and experimental grid A; the second experimental grid C had a lower number of M. natalensis during this period (Fig. 1). In August and September, however, grids A and C had populations approximately five times that of the control. The numbers of M. natalensis on the experimental grids remained higher than that on the control (about double) during October and November. Mastomys natalensis thus showed a clear increase in population density after food was added. This increase was as a result of immigration from neighbouring areas, since no juveniles had entered the population during this period.

The other two species caught in relative abundance, the single-striped rat Lemniscomys rosalia and the pygmy mouse Mus minutoides did not exhibit any population responses to the increased food (Fig. 1). Both species were caught in similar numbers on the three grids, and in the case of M. minutoides numbers declined through the study. There are three possible reasons for the lack of population increase in L. rosalia and M. minutoides. First, M. natalensis may have been denying M. minutoides access to the feeding stations, as the latter is an order of magnitude smaller than the former. Second, M. natalensis may have filled the traps earlier and more quickly and thus prevented M. minutoides from being caught. These two explanations are implausible in the case of L. rosalia, as this species is, on average, larger than M. natalensis, and it forages in the late afternoon and at dawn, while M. natalensis forages at night (De Graaff 1981, pers. obs.). Finally, L. rosalia and M. minutoides due to their solitary (and perhaps territorial) nature (Skinner and Smithers 1990) exclude other conspecifics from their territories and thus prevent an increase in numbers from occurring. Mastomys natalensis, in contrast, is a communal species and tolerates other M. natalensis in close proximity (De Graaff 1981), and as a result populations may increase in response to additional food.

The masses of those M. natalensis that were caught in either June or July and that were retrapped in at least two other months were used to calculate mean monthly masses of M. natalensis on each of the three grids. Mean mass was calculated in this way in order to avoid the biasing effects of immigrating or emigrating rodents. Mean masses were similar for June and July (before supplementation), but rose on the experimental grids in August and remained higher until the end of the study (Fig. 2). These data suggest that food supplementation accelerated growth rates of overwintering M. natalensis.

Food supplementation did not affect the time of initiation of breeding of M. natalensis (Table 1). Scrotal males were first observed on all three grids simultaneously in September. Females with perforate vaginae were first caught a month later in October. The proportions of breeding (scrotal) males and (perforate) females of M. natalensis (Table 1) were similar in all months except in November. During the latter month, no reproductively active males or females were caught on the control grid, although both experimental grids had very high proportions of breeding individuals. This may have resulted from the very small sample sizes on the control grid, however, the sample sizes on the experimental grids were also low during this month. It is likely that breeding in M. natalensis was stimulated by the rains which began in September, but only those individuals with access to additional food (ie. individuals on the experimental grids) had maintained a higher plane of nutrition and were able to maintain their reproductive condition through until November?

In conclusion, it appears that the M. natalensis population in the study area is food limited. Both the population size and the mean mass of resident individuals increased on the experimental grids immediately after food addition. In contrast, the populations of neither L. rosalia nor M. minutoides increased with the addition of extra food. In the case of M. minutoides, this may have been caused by interference competition from M. natalensis. However, the L. rosalia population may have been prevented from increasing owing to the solitary, and likely territorial, nature of the individuals of this species.

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TABLE 1. - The proportion of scrotal males and perforate females of Mastomys natalensis on two food supplemented grids (A and C) and a single control grid (B) from June to November 1995.

		Proportion (expressed as %) of reproductive individuals (sample sizes given in brackets)					
Sex	Grid	June	July	August	Sept.	Oct.	Nov.
Males	A	0 (14)	0 (12)	0 (26)	29 (31)	53 (34)	100 (8)
	B	0 (8)	0 (13)	0 (1)	33 (6)	69 (16)	0 (5)
	C	0 (5)	0 (4)	0 (33)	34 (35)	63 (24)	100 (11)
Females	A	0 (8)	0 (7)	0 (23)	0 (19)	6 (16)	58 (12)
	B	0 (6)	0 (11)	0 (3)	0 (2)	9 (11)	0 (2)
	C	0 (4)	0 (6)	0 (22)	0 (23)	0 (15)	57 (7)

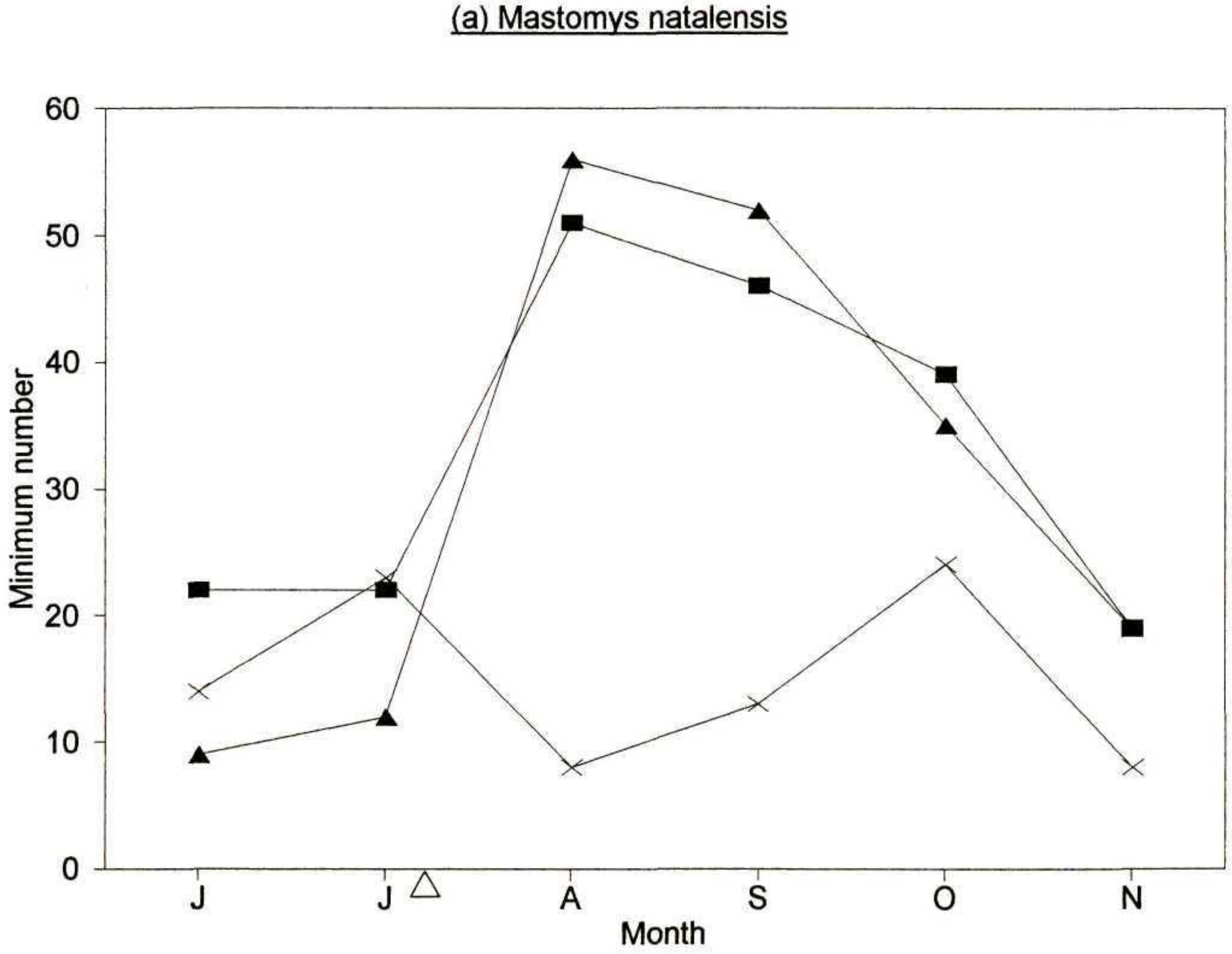

Fig. 1. - Monthly population estimates (minimum number alive) of (a) Mastomys natalensis, (b) Lemniscomys rosalia and (c) Mus minutoides on the experimental grids A (■) and C (▲), and the control grid B (✖). The △ indicates the initiation of food supplementation.

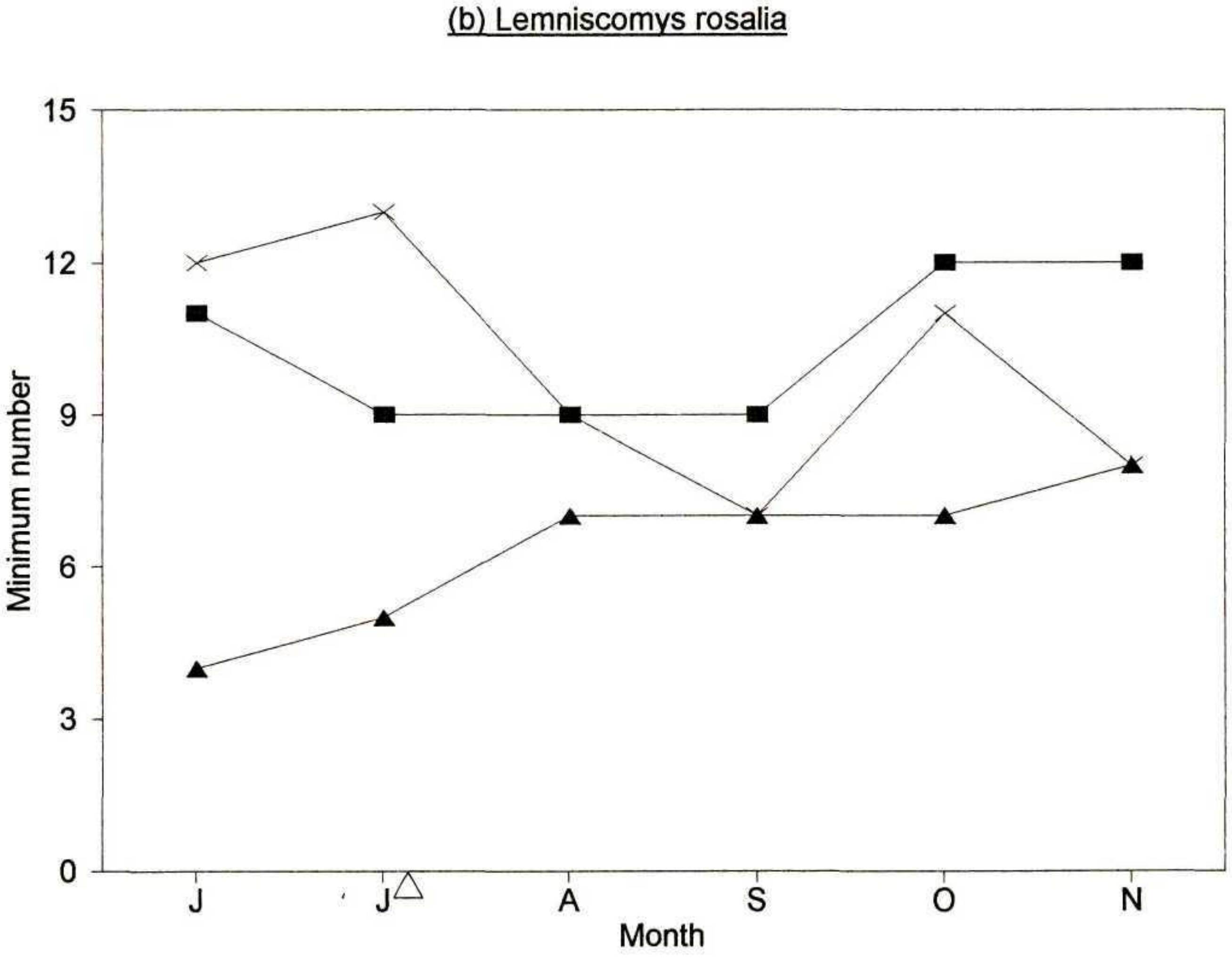
(b) Lemniscomys rosalia

Fig. 1. - Monthly population estimates (minimum number alive) of (a) Mastomys natalensis, (b) Lemniscomys rosalia and (c) Mus minutoides on the experimental grids A (■) and C (▲), and the control grid B (✖). The △ indicates the initiation of food supplementation.

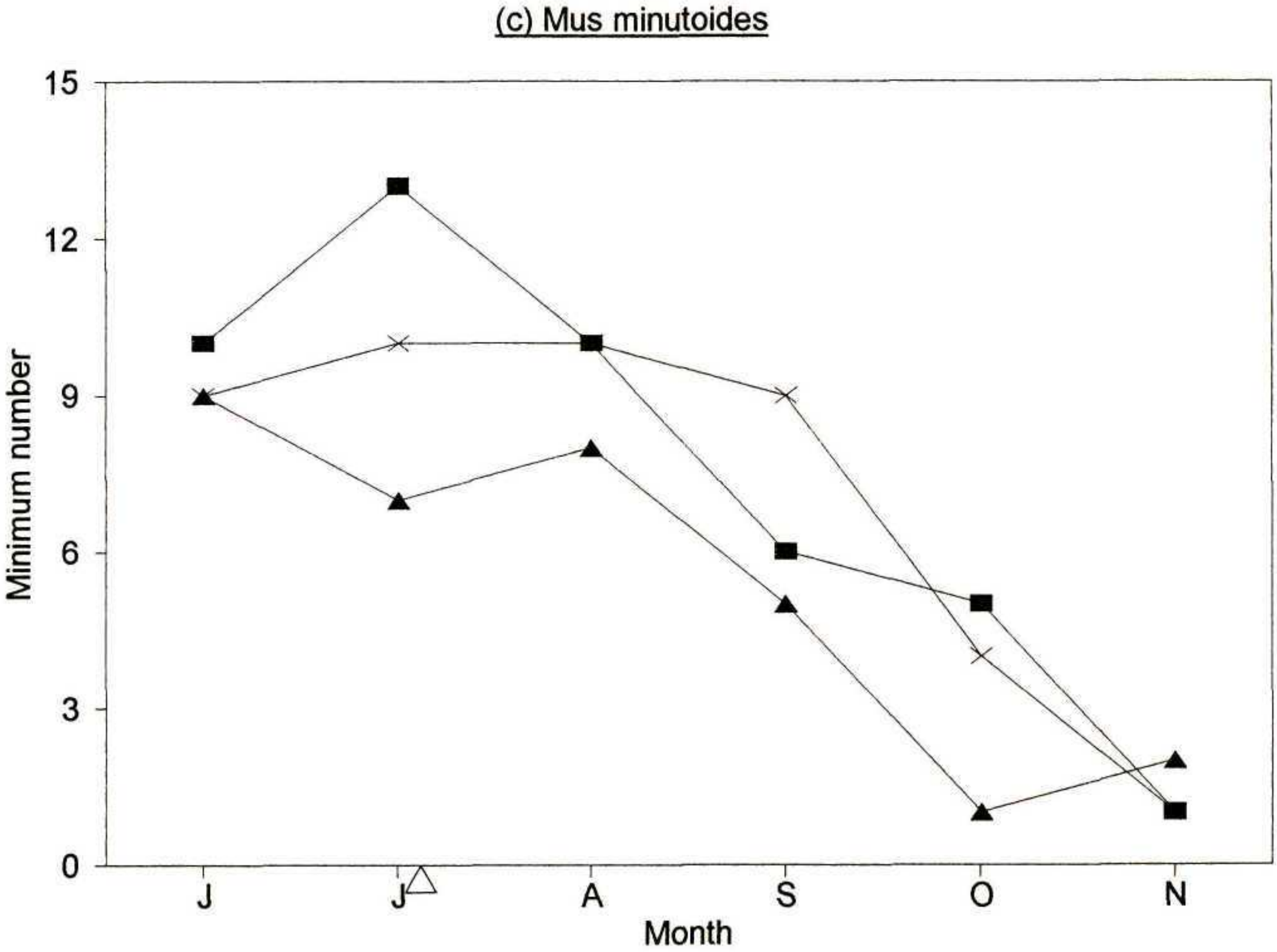

Fig. 1. - Monthly population estimates (minimum number alive) of (a) Mastomys natalensis, (b) Lemniscomys rosalia and (c) Mus minutoides on the experimental grids A (■) and C (▲), and the control grid B (✖). The △ indicates the initiation of food supplementation.

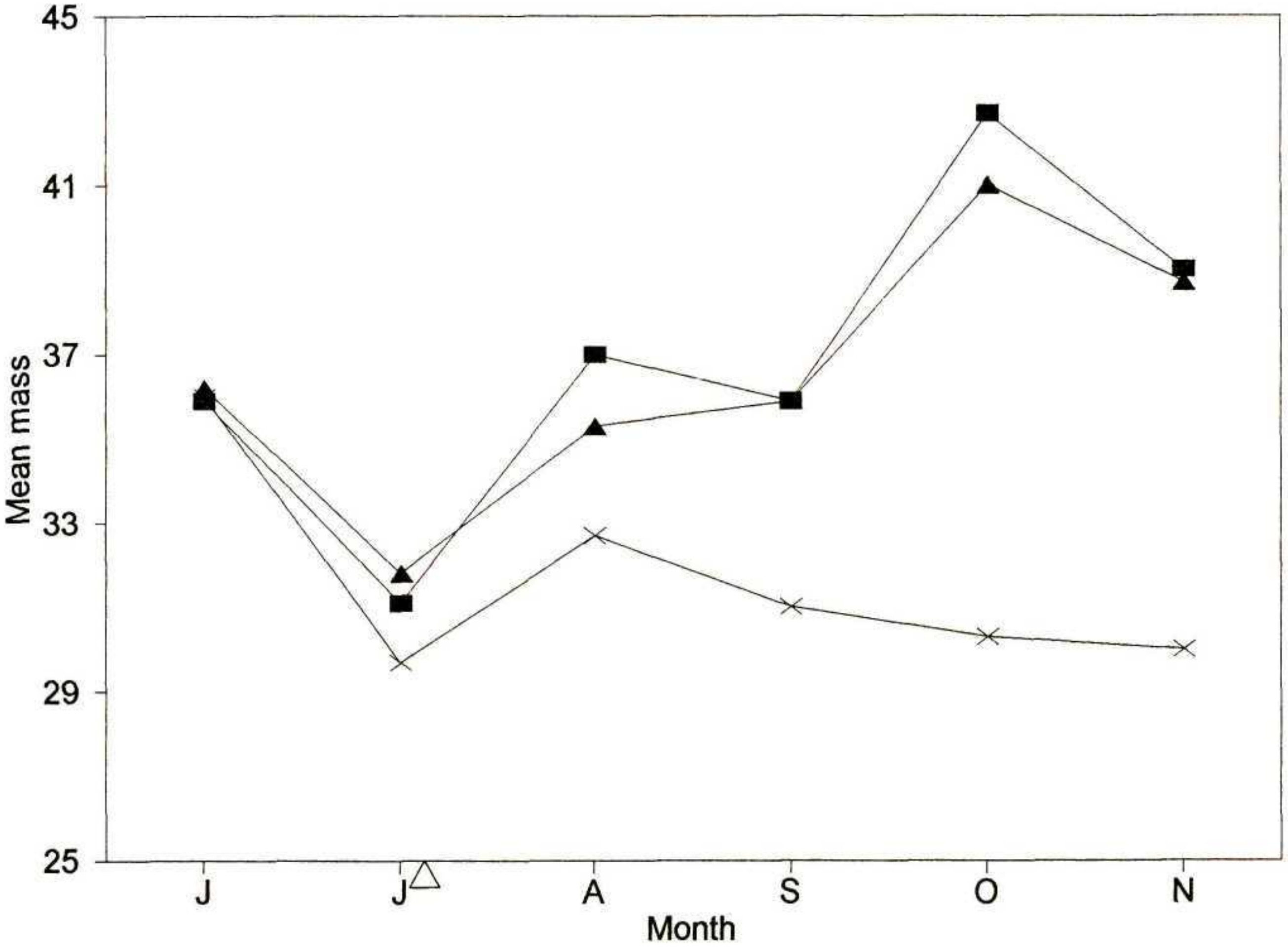

Fig. 2. - Mean monthly masses of Mastomys natalensis on the experimental grids A (■) and C (▲), and the control grid B (✖). Sample sizes are as follows: grid A, n=14; grid B, n=6; grid C, n=9.

CHAPTER 5*

THE EFFECTS OF FOOD SUPPLEMENTATION AND FIRE ON SMALL MAMMAL COMMUNITY STRUCTURE IN A SWAZILAND GRASSLAND

*Monadjem, A. & Perrin, M.R. Submitted. *South African Journal of Science*

The effects of the addition of supplementary food was investigated on a terrestrial small mammal community in a Swaziland grassland. Small mammal biomass increased significantly on the supplemented grids in relation to the control. This increase in biomass was the result of an increase in the density of the rodent Mastomys natalensis. *An unscheduled fire allowed the investigation of the effect of burning on the small mammal community. The immediate effect of the fire on the small mammal community was to decrease the biomass and species diversity. After three months, however, species richness was significantly higher on the burnt grids. A greater emphasis on experimental studies is required in the study of the ecology of southern African small mammals.*

Food supplementation studies are primarily concerned with determining the role that food supply plays in the growth and development of organisms, in the dynamics of populations and in community structure[1]. Food manipulation studies involving terrestrial small mammals have mostly focused on individual or population responses. Few studies have dealt with the effects of supplementary food at the community level[1]. At the individual level, food supplementation has resulted in increased weight[2,3] (Chapter 4), while the following population responses have been recorded: increased population density[4-6]; extension of the breeding season and increased levels of reproductive intensity[7-9]. At the community level, food supplementation has resulted in increased species diversity[10], and replacement of a smaller species by a larger congeneric species[11].

Food manipulation studies have been largely biased to northern hemisphere ecosystems[1]. In Africa, the effects of food supplementation have been experimentally tested on the rodent *Mastomys natalensis* in Senegal[8], Kenya[12] and Tanzania[2] with equivocal results. To the best of our knowledge, no study experimentally examining the effect of food supply on an African small mammal community has been published. The present study was conducted with the aim of ascertaining the role of food in the shaping of a terrestrial small mammal community in Swaziland. This was achieved by increasing (perturbing) the food resource and recording the response of the small mammal community to the perturbation.

Methods and materials

Three permanently marked grids (100 m × 100 m) were established in a natural grassland, which had not been grazed by livestock for at least five years, on eKundizeni Farm (26°33'S 31°16'E) near Matsapha, Swaziland. The three grids were positioned roughly in the shape of a right-angled triangle, with the control grid at the right-angle. The control was approximately 70 m and 100 m away from each of the two experimental grids, which was far enough to prevent the movement of rodents between grids within any particular trapping session (see below). This region receives most of its rainfall between October to 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 vegetation was very similar on the three grids. *Hyparrhenia hirta* was the dominant grass species on all grids. The only other common grass species was *Hyperthelia dissoluta* which was abundant on the control and present on grid 1. No trees were present on or near any of the three grids, while a few *Lippia javanica* shrubs (up to 1.5 m tall) occurred irregularly on each grid.

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 1 m^2 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. This estimate presented few problems since the grass was generally thick and a "canopy" was usually obvious. 4) Finally, the percentage 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, 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.

An uncontrolled 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 (grids 1 and 3). It also burnt to within 15 m of the control grid. After the fire, habitat characteristics were recorded separately for the burnt and unburnt sections of grids 1 and 3 (*ie*. five quadrats were placed in the burnt and five in the unburnt sections per grid).

Rodents were trapped monthly on the three grids 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 days per month. The traps were checked at first light, were closed for the heat of the day (to prevent trapped mammals suffering or dying from heat stress) and were then reset in the afternoon. Each trapped rodent was uniquely toe-clipped, sexed, weighed and its reproductive condition assessed. Marked rodents did not move between grids within any particular trapping session. However, over the entire study period, one *Mus minutoides*, two *Steatomys pratensis*, four *Lemniscomys rosalia* and twenty-one *Mastomys natalensis* were recorded to have moved between grids between different months. These individuals represented a small proportion of the total marked population (e.g. 311 *Mastomys natalensis* were trapped and marked over the study period). Furthermore, this movement was not unidirectional *i.e.* of the twenty-one *M. natalensis* which moved between grids, thirteen moved from the control to either of the two experimental grids and eight moved from either experimental grid to the control.

The number of individuals on each grid was estimated using the minimum number known alive method (MNA)[13]. The density of small mammals was estimated as the number of individuals per hectare. Biomasses estimated were calculated by multiplying the density of each species by the average weight of that species for a particular month, and then summing the biomass figures for all the species. All biomass figures, unless stated otherwise, are quoted as g/ha (the biomass figures for the burnt and unburnt sections of grids 1 and 3 had to be adjusted accordingly). Species richness was the total number of species recorded. The Shannon index of species diversity (H') was calculated per grid per month, based on the proportional distribution of biomass among species using the following formula[14]:

$$H' = - \sum P_i \log P_i$$

where P_i represented the proportion of the total small mammal biomass contributed by the i^{th} species. Evenness (J'), which measures the equatability of the spread of biomass among species, was calculated using the following formula[15]:

$$J' = H'/\log S$$

where S represented the total number of species in the community. Values of J' range from 0 to 1, with J'=1 describing a group of species each of which contributes an equal amount to total biomass. Differences between the variances of the samples (grids) were tested using the Levene test of homogeneity of variances. Since all tested samples had equal variances ($P > 0.05$ in all cases), the differences between grids were tested using a one-way analysis of variance (ANOVA).

The control grid received no supplementary food, while the two experimental grids received additional food in the form of equal amounts of rolled oats and rabbit pellets. This choice of supplementary food was based on the fact that many species of southern African rodents have been reared in captivity on oats and pellets (Monadjem and Perrin, personal observation). Eight kilograms of food was added monthly to the first experimental plot (grid 1) from July 1995 (immediately after sampling the rodent population) until May 1996, 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 (340 ml) cans, open at the side, which had been nailed to the ground in an evenly arranged 9 × 9 grid. Rodent droppings were observed at all the feeding cans, suggesting that at least some species were feeding on the supplementary food provided. 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.

Results

Between June 1995 and May 1996 1329 mm of rain was recorded at the study site, making this a particularly wet year. Rainfall at the study site showed a clear summer peak with 1199 mm of the rain having fallen between October and March. The vegetation characteristics of the grids are shown in Tables 1 and 2. On the control and the unburnt sections of grids 1 and 3 grass cover was generally high, but declined slightly in October and November (Table 1). Grass height increased steadily through the study, while the percentage of the grass that was green peaked between December and March (Table 1). After the fire (September), the burnt sections of grids 1 and 3 had lost nearly all their cover. The new growths of grass, however, were completely green. By December there was little visual difference between the burnt and unburnt areas (Table 1). These differences in cover, grass greenness and grass height were significant between the grids and seasons (2-way ANOVA; percent cover: $F = 9.520$, *d.f.* = 14,39, $p < 0.05$; percent green: $F = 6.501$, *d.f.* = 14,39, $p < 0.05$; grass height: $F = 5.928$, *d.f.* = 14,39, $p < 0.05$).

A total of eight species of small mammal was captured on the sampling grids (Table 3). *Mastomys natalensis, Lemniscomys rosalia, Mus minutoides, Steatomys pratensis* and *Dendromus mystacalis* were captured on all grids (including on both burnt and unburnt sections of grids 1 and 3). *Aethomys chrysophilus* was only captured on grid 3, while a single individual of *Otomys angoniensis* was caught on grid 2. The only insectivore caught in this study, *Crocidura hirta*, was captured in small numbers on all grids, but not on the burnt section of grid 1 and the unburnt section of grid 3.

The biomass (adjusted to g/ha) of small mammals on the control grid was lower than on the experimental grids (Table 2) and this difference was significant between August and May ($F = 2.845$, $P < 0.05$, d.f. = 4,45). Before food supplementation, experimental grid 1 and the control had similar small mammal biomasses (Fig. 1a) and diversity indices (Fig. 1b). Experimental grid 3, prior to food supplementation, had a lower biomass (Fig. 1a), but a higher diversity (Fig. 1b) of small mammals. Food supplementation had an immediate effect on small mammal biomass. Biomass increased 2 or 3 fold on the supplemented grids between August and October, but decreased on the control (except for a small peak in October following the September fire).

Food supplementation also resulted in a sharp decrease in the species diversity on grid 3 but not on grid 1 (Fig. 1b).

Species richness was similar on all grids averaged over the duration of the study, with no statistically significant differences apparent ($P > 0.05$; Table 4). However, between December and February, the species richness was significantly higher on the burnt sections of grids 1 and 3 than on the control ($F = 4.250$, $P < 0.05$, d.f. = 4,10; Table 4). In contrast, species diversity was significantly higher on the control between August and November than on grid 1 ($F = 3.537$, $P < 0.05$, d.f. = 4,15; Table 4). Species diversity decreased on the burnt sections of grids 1 and 3 between October and December following the fire. Evenness indices were not significantly different between the grids in any season (Table 4).

Discussion

This study experimentally examined the effect of food supplementation on a community of small mammals in a Swaziland grassland. Increased food supply resulted in increased biomass of small mammals. Food is thus clearly a limiting factor in the small mammal community. However, not all species responded in an identical fashion. For example, *M. natalensis* densities increased several fold immediately after food addition, while populations of *L. rosalia, M. minutoides* and *S. pratensis* remained unchanged or even decreased[3,16] (Chapters 4,7,10 and 11). Food supplementation experiments in other studies have induced a population increase in a wide range of rodent species[4-7,17,18]. However a large number of studies have failed to induce a population increase following supplementary feeding[2,9,10,19-21]. The reasons for these differential responses to food supplementation remain speculative and deserve special attention.

The response of one species to food manipulation may be influenced by the response of a competitor or several competitors[11]. Long-term food manipulation combined with selective species removal in a North American desert ecosystem demonstrated the complexity of interactions in that rodent community[4,22]. Food addition resulted in the increase in density of one species of granivorous kangaroo rat at the expense of a smaller congeneric species. Exclusion of all kangaroo rat species resulted in the increase in density of other granivorous rodents. Thus food limitation may be mediated through interspecific interactions. Interspecific interactions of African small mammal communities have not yet been experimentally assessed.

Increased food supply also resulted in a sharp decrease in species diversity on experimental grid 3, and a smaller decrease on grid 1. On both these grids, the decline in species diversity was due to the increase in biomass of *M. natalensis*, since the populations of the other species did not change significantly with food supplementation[3,16] (Chapters 4,7,10 and 11). The larger decrease in species diversity on grid 3 in comparison with grid 1 is probably due to the fact that the *M. natalensis* density, prior to food supplementation, was far lower on grid 3 than on grid 1, but after food supplementation densities were the same on these two grids[3] (Chapter 7). Thus food supplementation resulted in a decrease in species diversity, not by decreasing species richness, but by increasing the proportional representation of one species (*M. natalensis*).

It is not clear why only *M. natalensis* responded to the supplementary food. There are a number of possible reasons. Firstly, the bait may have been unsuitable for, or not preferred by, the other species. This is unlikely to be the case in *L. rosalia*, *M. minutoides* and *S. pratensis*, all of which were maintained in the laboratory on a diet of rabbit pellets (Chapter 3; Monadjem, personal observation). Furthermore, in Swaziland, these species are primarily herbivorous granivores[27], although *M. minutoides* and *S. pratensis* also feed on arthropods (Monadjem, in preparation; Chapter 2) Secondly, *M. natalensis* may have prevented the other species from gaining access to the feeding cans. This is unlikely in the case of *L. rosalia* which is, on average, larger than *M. natalensis* and which forages earlier in the evening and later in the morning than the latter species (Monadjem, unpublished data). Food was constantly available at the feeding cans throughout the study period, making it unlikely that any particular individual or species would have dominated the supplementary food. Thirdly, the social structure of the species may have allowed, or prevented, the population of that species to increase with food supplementation. In territorial species, individual territory holders may inhibit a local population increase in the face of an increased food supply by evicting foreigners. *Mastomys natalensis* does not actively defend territories[26], which may have been the reason why the population of this species responded to food supplementation. Information on the social structure of the other rodent species is scanty, although *L. rosalia*, *M. minutoides* and *S. pratensis* occupy burrows singly or in pairs[28], suggesting that they may be territorial.

The fire resulted in a short-term decrease in biomass of small mammals. This was probably due to the small mammals avoiding the open areas, probably to reduce predation[23,24]. However, once the grass had regrown to the pre-fire height, both species diversity and biomass increased dramatically. There was, unfortunately, no control grid for the fire (*ie.* no grid was burnt and left unsupplemented), thus the effects of the fire and food will have, in part, been confounded. On both grids 1 and 3, the species richness and diversity was consistently higher on the burnt than the unburnt sections in both summer and autumn. This supports the contention that fire may be important for promoting species diversity in small mammal communities in grassland communities[25].

The ecology of terrestrial small mammal communities in Africa are still poorly known and studies have rarely progressed beyond the descriptive phase. More emphasis will need to be placed on carefully designed experimental studies to advance our understanding of the role of food supply in African small mammal communities.

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Table 1. Monthly vegetation characteristics of the experimental grids 1 and 3 and the control grid

	Grid 1						Control			Grid 3					
	Unburnt			Burnt						Unburnt			Burnt		
Month	Cover (%)	Height (cm)	Green (%)	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

Table 2. Summary of the habitat and small mammal characteristics of the study grids

Site	Area (ha)	Plant community[1]			Small mammal community		
		Cover index (%)	Height (cm)	Green (%)	Species richness[2]	Species diversity[3]	Biomass[4] (g/ha)
Grid 1							
Burnt	0.5	55	74	91	5	0.39	1615
Unburnt	0.5	77	67	62	6	0.39	1343
Grid 2 (Control)	1	86	95	64	7	0.43	901
Grid 3							
Burnt	0.5	52	51	93	7	0.53	1209
Unburnt	0.5	83	63	63	6	0.47	1386

[1] These values represent the mean of the monthly figures
[2] Total number of species captured over the entire study period
[3] Mean monthly species diversity
[4] Mean monthly biomass adjusted to g/ha for burnt and unburnt sections of grids 1 and 3

Table 3. Total numbers of small mammal species captured between June 1995 and May 1996 on the three grids at eKundizeni Farm, Swaziland. Note that the area of each of the burnt and unburnt sections of grids 1 and 3 was 0.5 ha, while that of the control was 1 ha

	Grid 1		Grid 2	Grid 3	
Species	Burnt	Unburnt	(Control)	Burnt	Unburnt
Rodentia					
Mastomys natalensis	80	94	80	69	63
Lemniscomys rosalia	36	37	30	21	23
Mus minutoides	6	22	29	17	8
Steatomys pratensis	16	6	6	16	9
Dendromus mystacalis	1	4	3	5	4
Aethomys chrysophilus				8	3
Otomys angoniensis			1		
Insectivora					
Crocidura hirta		2	9	2	

Table 4. Mean monthly biomass, species richness, species diversity and evenness of the sampling grids. Each of these estimates is calculated as a mean value for the duration of the manipulation study (*ie*. August 1995-May 1996), in late winter-spring (August-November), Summer (December-February) and Autumn (March-May)

		Grid 1		Grid 2	Grid 3		Statistics		
		Unburnt	Burnt	(Control)	Unburnt	Burnt	F-value	*P*-value	d.f.
Biomass[1]	mean	1725	1337	828	1294	1453	2.850	0.035	4,45
	spring	2426	1234	1090	2051	1890	3.874	0.024	4,15
	summer	1451	1644	684	1171	1117	1.84	n.s.	4,10
	autumn	1064	1168	623	596	1057	4.874	0.019	4,10
Richness	mean	3.1	2.8	3.6	3.2	3.9	1.519	n.s.	4,45
	spring	3.8	2.5	4.5	4.3	4.5	2.568	n.s.	4,15
	summer	2.3	3.0	2.0	2.7	3.0	4.250	0.029	4,10
	autumn	3.0	3.0	4.0	2.3	4.0	1.469	n.s.	4,10
Diversity	mean	0.30	0,33	0.39	0.37	0.39	1.731	n.s.	4,45
	spring	0.29	0.23	0.40	0.38	0.36	3.537	0.032	4,15
	summer	0.30	0.32	0.32	0.38	0.41	0.878	n.s.	4,10
	autumn	0.32	0.34	0.39	0.46	0.49	2.512	n.s.	4,10
Evenness	mean	0.69	0.75	0.68	0.81	0.68	1.048	n.s.	4,45
	spring	0.51	0.62	0.56	0.63	0.56	0.546	n.s.	4,15
	summer	0.83	0.85	0.77	0.91	0.67	1.217	n.s.	4,10
	autumn	0.78	0.82	0.75	0.95	0.84	1.056	n.s.	4,10

[1] Biomass figures are in g/ha (biomass for burnt and unburnt sections of grids 1 and 3 had to be adjusted)

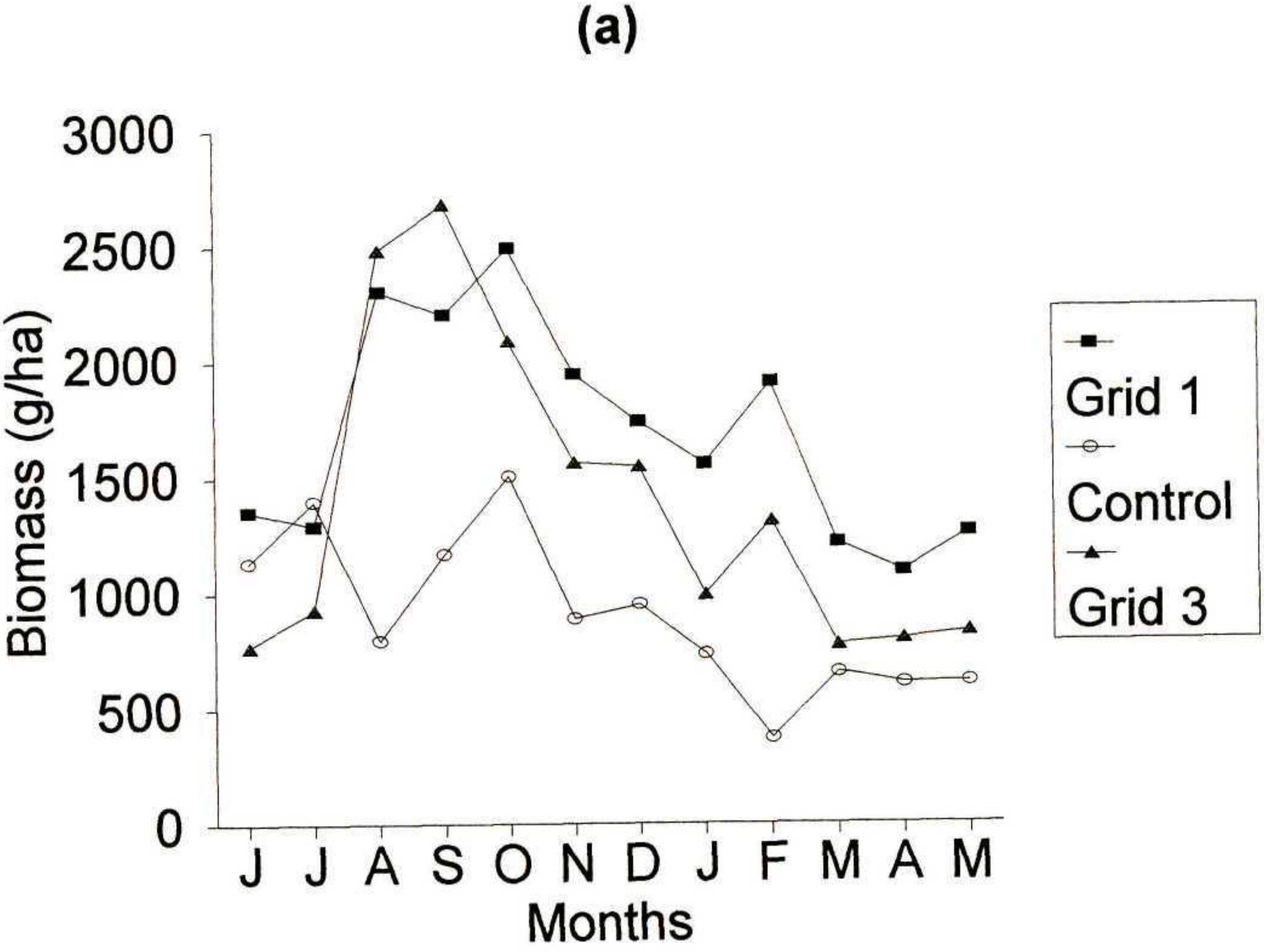

Fig. 1. Monthly biomass per hectare (a), and species diversity (b) of small mammals on the study grids between June 1995 and May 1996 at eKundizeni Farm, Swaziland.

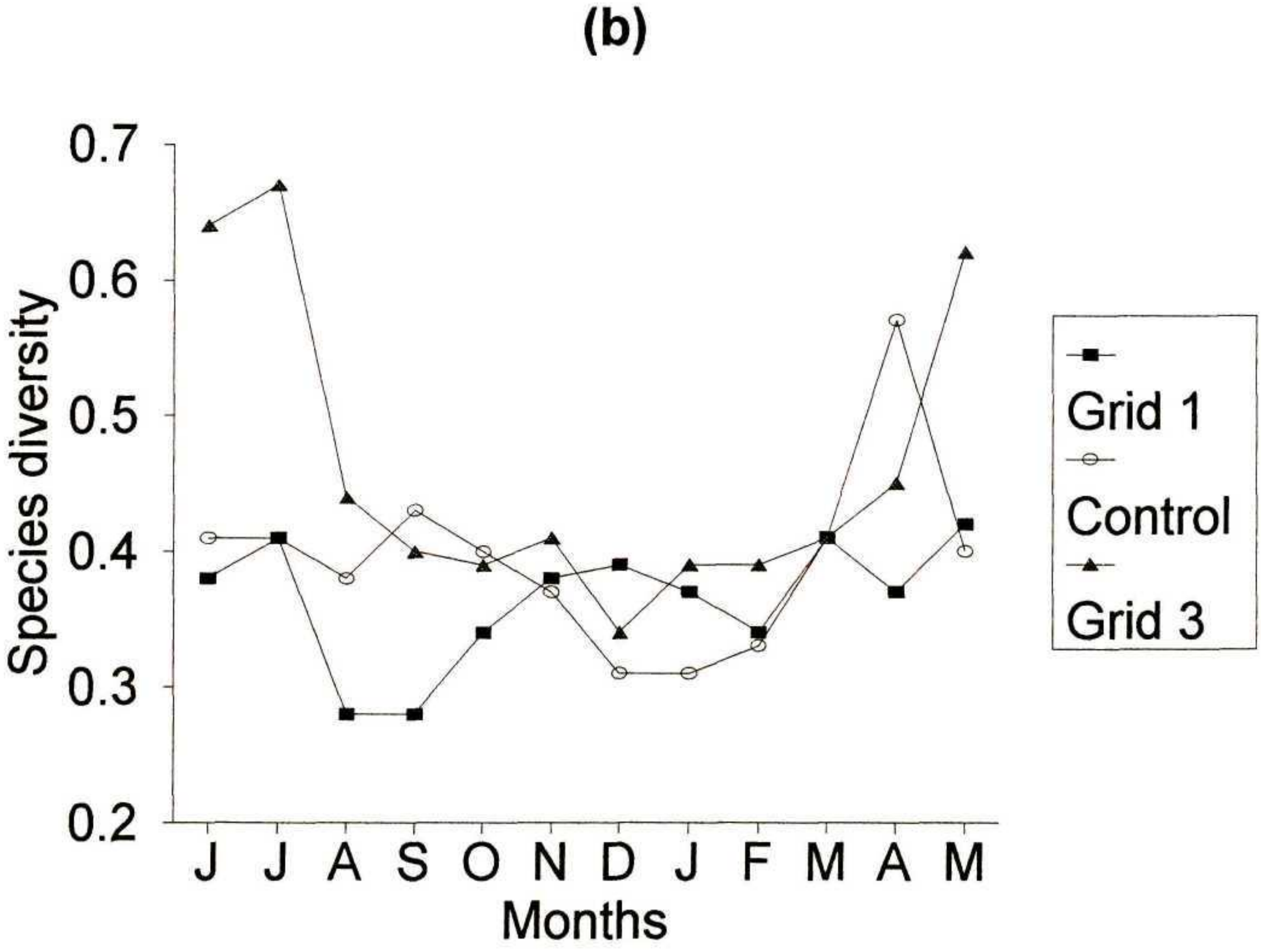

Fig. 1. Monthly biomass per hectare (a), and species diversity (b) of small mammals on the study grids between June 1995 and May 1996 at eKundizeni Farm, Swaziland.

CHAPTER 6*

THE EFFECT OF VEGETATIVE COVER AND SUPPLEMENTARY FOOD ON THE COMMUNITY STRUCTURE OF SMALL MAMMALS IN A SUBTROPICAL GRASSLAND IN SWAZILAND

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The effects of vegetative cover and supplementary food was investigated on a small mammal community in a Swaziland grassland. Three experimental treatments were conducted on six grids: two control grids and four manipulated grids on which the vegetative cover was mechanically reduced. Supplementary food was added to two of the latter four manipulated grids. A total of eight species of small mammals were captured on the six grids. The biomass of small mammals was lower on grids with reduced vegetative cover than on the controls. However, food supplementation resulted in a significant increase in biomass on one of the manipulated grids. Species richness and species diversity were highest on the control grids, intermediate on two manipulated grids in a cattle-free area, and lowest on two grids in an area containing cattle. The influence of vegetative cover and supplementary food is discussed for the different species of small mammals captured at the study site.

KEY WORDS: small mammals, vegetative cover, supplementary food, community structure.

INTRODUCTION

In North America, several studies have shown small mammal communities to be affected by both vegetative cover (Grant & Birney 1979, Grant et al. 1982) and food supply (Abramsky 1978, Brown & Munger 1985). In Africa, community ecology studies of small mammals have mainly been of a descriptive nature (Rowe-Rowe & Meester 1982, Martin & Dickinson 1985). Several African studies have experimentally manipulated food supply and observed the effects of this manipulation on single species of small mammals (Taylor & Green 1979, Hubert et al. 1981, Poulet et al. 1981, Leirs et al. 1990, Neal & Alibhay 1991, Monadjem & Perrin 1996; Chapter 4). However, to the best of our knowledge, the effect of food supplementation on the community structure of small mammals has only been experimentally investigated in Swaziland (Monadjem & Perrin in preparation; Chapter 5). The effects of vegetative cover on the community structure of small mammals have been investigated experimentally in only a single South African study (Bowland & Perrin 1989), although numerous studies have suggested that the distribution and abundance of small mammal species are influenced by vegetative cover (Bond et al. 1980, Kerley 1992, Oguge 1995, Monadjem 1997a).

Grazing by large African mammalian herbivores affects vegetative cover (McNaughton 1976) which may, in turn, affect the small mammal community (Delany 1964, Bowland & Perrin 1989). Both Delany (1964) and Bowland & Perrin (1989) observed a greater biomass and species diversity of small mammals in areas with reduced grazing pressure than in areas with increased pressure. The reason for this observation was attributed to the fact that increased grazing pressure resulted in decreased vegetative cover. It was suggested that the small mammal community was responding to changes in vegetative cover rather than grazing *per se*.

The present study was designed to experimentally investigate the effect of vegetative cover and supplementary food on a community of small mammals in a Swaziland grassland.

METHODS

Study area. Six permanently marked grids (70m × 70m) 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, while the rainfall during the study period (June 1996 to May 1997) was 1026 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. 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.

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) Vegetative cover on each grid was visually 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. Since grass height was usually homogenous within a particular quadrat, a "canopy" could be discerned which was measured and averaged for each a grid. 4) Finally, the percentage of the vegetation that was green was estimated for each quadrat and averaged for each grid.

An uncontrolled fire swept through the study area on September 13, 1996 (four months after the initiation of the study) and completely burnt the vegetation on all the grids.

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 the 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. The feeding stations were checked twice monthly during which time all the cans were cleaned and refilled. Due 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.

A summary of the experimental treatments appears in Table 1.

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 days 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. The number of individuals on each grid was estimated using the minimum number known alive method (MNA: Krebs, 1966). Biomasses estimated were calculated by multiplying the density of each species by the average weight of that species for a particular month, and then summing the biomass figures for all the species. Species richness was the total number of species recorded. Species diversity (H') was calculated per grid per month, based on the proportional distribution of biomass among species using the following formula (Begon et al. 1986):

$$H' = - \sum P_i \log P_i$$

where P_i represented the proportion of the total small mammal biomass contributed by the i^{th} species. Evenness (J') was calculated using the following formula (Pielou 1966):

$$J' = H'/\log S$$

where S represented the total number of species in the community. Significant differences ($P < 0.05$) among the grids and between the seasons were tested by way of a two-way analysis of variance (ANOVA; 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, $F = 27.599$, $P < 0.001$; height, $F = 31.654$, $P < 0.001$). Mean percent 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 2). Vegetative cover differed significantly among seasons ($F = 74.465$, $P < 0.001$) as did vegetation height ($F = 19.984$, $P < 0.001$). Mean vegetation height was at least four times taller on the control grids than on the cut grids (Table 2) and, as for vegetative cover, this difference was significant in winter, summer and autumn. 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 Methods).

In addition, significant interactions were observed between vegetative cover and season ($F = 3.850$, $P < 0.001$) and vegetation height and season ($F = 3.983$, $P < 0.001$). 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 percent greenness of the vegetation was not significantly different among the grids (two-way ANOVA, $P > 0.05$), but was significantly different between the seasons ($F = 14.680$, $P < 0.001$). 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 2).

Small mammal community

A total of eight species of small mammal was captured on the six grids (Table 3). *Mastomys natalensis* (A. Smith 1834) and *Mus minutoides* A. Smith 1834 were captured on all the grids, whereas *Rabdomys pumilio* (Sparrman 1784) and *Aethomys chrysophilus* (de Winton 1897) were only captured on grid 6.

There were significant differences between the six grids in biomass, species richness, species diversity and evenness (Table 4). In terms of biomass, there were significant differences between the grids ($F = 18.349$, $P < 0.001$) and seasons ($F = 11.826$, $P < 0.001$). The biomass of small mammals was highest on supplemented grid 1. The control grids 5 and 6 had intermediate biomasses while the cut grids 3 and 4 and supplemented grid 2 had the lowest biomasses. Hence the removal of cover appears to have reduced the biomass of small mammals whilst the addition of food on grid 1 appears to have increased biomass. Why biomass did not increase on supplemented grid 2 is discussed below.

In terms of species richness, there were significant differences between grids ($F = 19.688$, $P < 0.001$; Table 4) but not between seasons (two-way ANOVA, $P > 0.05$). The control grids and supplemented grid 1 exhibited high species richness while unsupplemented grids with reduced cover had low species richness. A similar trend was shown by species diversity which differed significantly between grids ($F = 15.637$, $P < 0.001$; Table 4) but not between seasons (two-way ANOVA, $P > 0.05$). Control grids exhibited the highest species diversity while the cut grids in the grazed area (grids 2 and 3) had the lowest species diversity. Evenness scores also differed between grids ($F = 7.564$, $P < 0.001$; Table 4) but not between seasons (two-way ANOVA, $P > 0.05$). Again, evenness scores were highest on the control grids and lowest on the cut grids 2 and 3 in the grazed area.

The effects of supplementary food and vegetative cover on *Mastomys natalensis* will be presented elsewhere (Monadjem & Perrin in preparation; Chapter 8). *Rhabdomys pumilio* and *Aethomys chrysophilus* were only captured on control grid 6, while *Crocidura hirta* Peters 1852 was predominantly caught on the latter grid. Thus for these species it is not possible to assess the effect of vegetative cover or supplementary food on their distributions. *Dendromus mystacalis* Heuglin 1863 was present only between June and September. Before the fire (ie. June to August), *D. mystacalis* was caught on all the grids in the ungrazed area (Fig. 1), but was absent from grids 2 and 3 in the grazed area. In September (after the fire), *D. mystacalis* was caught in the grazed area for the first time. *Steatomys pratensis* Peters 1846 was caught only on the control grids and the manipulated grids in the ungrazed area (Fig. 2). This species was not caught on the grids in the grazed area. *Mus minutoides* was absent between January and March, and was absent from the manipulated grids in the grazed area in winter and spring (Fig. 3). It would thus appear that supplementary food and vegetative cover *per se* are not important in determining the distributions of *D. mystacalis*, *S. pratensis* and *M. minutoides*. Grazing, in contrast, appears to strongly affect the distributions of *D. mystacalis*, *S. pratensis*, and, probably to a lesser extent, *M. minutoides*.

In winter (June to August), *Lemniscomys rosalia* (Thomas 1904) was only captured on the control grids 5 and 6 (Fig. 4). Immediately after the fire, while vegetative cover was low on all the grids, *L. rosalia* was captured in low numbers on all the grids except cut grid 3. By January vegetative cover had increased to former levels, however, the number of *L. rosalia* remained low through to the end of the study. Thus vegetative cover appears to have affected *L. rosalia* greatly, this species exhibiting a preference for the control grids with high cover (before the fire).

DISCUSSION

The results of this study indicate that both supplementary food and vegetative cover appear to influence the structure of communities of small mammals in Swaziland grasslands. The addition of supplementary food increased the biomass of small mammals on grid 1 but not grid 2 (despite the fact that the vegetative cover and vegetation height on both grids had been maintained at the same levels). The reason for the lack of increase in the biomass of small mammals on grid 2 is probably related to the presence of cattle. Grid 2 was situated in a cattle area and hence experienced disturbance from cattle in terms of grazing as well as trampling. Supplementary food was initially placed in 340 ml cans. These cans were trampled and destroyed in July and new cans were installed 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 which may explain the lack of increase in the biomass of the small mammal community on this grid. Alternatively, the cattle were affecting the community of small mammals in other ways. Although not quantified, the cattle were spending a lot of time on grid 2 (possibly due 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 et al. 1982), and the population 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 increased biomass of small mammals on supplemented grid 1 was due mainly to an increase in the numbers of *Mastomys natalensis* (Monadjem & Perrin in preparation; Chapter 5). It has previously been shown that *M. natalensis* populations increase with an increase in food availability (Monadjem & Perrin 1996; Chapter 4 and 7). Species richness was relatively high on grid 1, but species diversity was intermediate (Table 4). This was due to the fact that, although a large number of species were captured on this grid, *M. natalensis* formed the bulk of the small mammals captured.

Both species richness and diversity were lower on the four cut grids. Supplementary food did not appear to affect either species richness or species diversity on the cut grids. However, the cut grids situated in the grazed area exhibited significantly lower species richness and diversity than the cut grids in the ungrazed area. Several studies have reported decreases in species richness or biomass of communities of small mammals with increased grazing pressure (Delany 1964, Grant et al. 1982, Bowland 1989). The usual explanation for this observation has been that grazing affects vegetative cover which in turn affects the small mammal community. Although, in the present study, the species richness and diversity of small mammals was lower on the cut grids in the ungrazed area than on the control grids, these parameters were far lower on the cut grids in the grazed area. This is in spite of the fact that the measured vegetation characteristics did not differ between these grids. Hence, the presence of grazers (in this case cattle) must have been affecting the small mammal community in more ways than just by the removal of vegetation cover. Grazers may be altering other features of the microhabitat, such as soil compaction which may influence the availability of burrows, and hence small mammal diversity.

The fire had a major impact on the small mammal community. Numbers of most species decreased immediately following the fire. This was especially true for *L. rosalia*. Numbers of *L. rosalia* were relatively high before the fire and dropped sharply after the fire. By the end of the study (eight months after the fire) the numbers of *L. rosalia* still had not regained pre-fire levels. Previous studies have shown *L. rosalia* to be able to survive fires and to quickly recolonize burnt areas once grass cover has recovered (Kern 1981, Swanepoel 1981, Bowland & Perrin 1988, Monadjem & Perrin in press; Chapter 10). The reason for *L. rosalia* not having recolonized the area despite the rapid recovery of the vegetation may have been due to the extent of the fire. This particular fire completely burnt a very large area of, at least, a 4 km radius from the study site (and probably much larger). Not a single tuft of grass remained in this area after the fire (personal observation). *Lemniscomys rosalia* selects areas with high vegetative cover (De Graaff 1981, Skinner & Smithers 1990). Thus, all refuges for this species had been completely removed by the fire in this area which may have resulted in the decimation of the local population of *L. rosalia*.

The population of *Dendromus mystacalis* disappeared completely after the fire. Whether the fire was responsible for this is uncertain. During monthly trapping in the 12 months prior to this study in the same area as the present study, *D. mystacalis* was captured only between June and October (Monadjem unpublished data). The reason for the capture for *D. mystacalis* only during winter and spring months may be related to seasonal changes in foraging behaviour. *Dendromus mystacalis* is thought to rarely descend to the ground, preferring instead to climb up among the grass talks (Rosevear 1969, De Graaff 1981, Skinner & Smithers 1990). However, *D. mystacalis* may be forced to forage on the ground in the dry winter and early spring months due to restricted seed and insect availability (Lack 1986, Monadjem unpublished data) in these months. It is commonly stated that *D. mystacalis* prefers tall, rank grasslands (Smithers & Lobao Tello 1976, De Graaff 1981, Skinner & Smithers 1990). However, in the present study this species was commonly captured in the cut grids in the ungrazed area, but not in the grazed area. These observations suggest that *D. mystacalis* does venture away from cover, but is strongly affected by grazing by large mammals.

The ecology of small mammal communities in Africa are still poorly known and studies have rarely progressed beyond the descriptive phase. Carefully designed experimental studies have made significant contributions to the understanding of the ecology of small mammal communities in the northern hemisphere. Such experimental studies should be encouraged in the pursuit of improved understanding of African small mammal communities.

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Table 1.-Summary of experimental treatment of each grid between June 1996 and May 1997.

Grid number	Treatment
Grid 1	reduced cover, supplementary food
Grid 2	reduced cover, supplementary food
Grid 3	reduced cover
Grid 4	reduced cover
Grid 5	control
Grid 6	control

Table 2.-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 grids.

		Treatment		
Vegetation	Season	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

Table 3.- Total number of individuals of small mammal species captured between June 1996 and May 1997 on the six grids at eKundizeni Farm, Swaziland.

	Reduced cover + food		Reduced cover		Control	
Species	Grid 1	Grid 2	Grid 3	Grid 4	Grid 5	Grid 6
Rodentia						
Mastomys natalensis	66	34	18	32	50	47
Lemniscomys rosalia	7	4	0	5	8	11
Mus minutoides	10	6	5	5	7	8
Steatomys pratensis	4	0	0	5	2	7
Dendromus mystacalis	3	3	0	4	6	4
Aethomys chrysophilus	0	0	0	0	0	4
Rhabdomys pumilio	0	0	0	0	0	5
Insectivora						
Crocidura hirta	4	0	1	4	1	15

Table 4.- Mean monthly biomass, species richness, species diversity and evenness of each of the six grids. Each of these estimates is calculated as a mean value for each season: winter (June-August), spring (September-November), summer (December-February), autumn (March-May), and the mean value for the entire study period (June 1996 to May 1997). Row values with different superscripts indicate a significant ($P < 0.05$) difference among grids.

		Reduced cover + food		Reduced cover		Control	
		Grid 1	Grid 2	Grid 3	Grid 4	Grid 5	Grid 6
Biomass	winter	414^{a}	8^{b}	9^{b}	15^{b}	337^{a}	421^{a}
	spring	667^{a}	295^{b}	58^{c}	297^{b}	373^{b}	373^{b}
	summer	836^{a}	63^{d}	187^{d}	372^{c}	713^{a}	514^{b}
	autumn	340^{a}	239^{a}	120^{b}	59^{b}	132^{b}	324^{a}
	mean	564^{a}	151^{bc}	94^{c}	186^{bc}	389^{ab}	408^{a}
Richness	winter	3.3^{b}	0.3^{d}	0.3^{d}	1.3^{c}	3.0^{b}	7.0^{a}
	spring	3.3^{a}	2.0^{b}	0.7^{c}	2.0^{b}	2.0^{b}	4.0^{a}
	summer	2.7^{a}	0.7^{b}	1.0^{b}	3.0^{a}	1.7^{b}	3.3^{a}
	autumn	2.0^{b}	2.0^{b}	1.7^{b}	2.0^{b}	3.3^{a}	3.0^{a}
	mean	2.8^{b}	1.3^{c}	0.9^{c}	$2.1b^{c}$	2.5^{b}	4.3^{a}
Diversity	winter	0.23^{c}	0^{d}	0^{d}	0.07^{d}	0.34^{b}	0.65^{a}
	spring	0.13^{c}	0.12^{c}	0^{d}	0.20^{b}	0.13^{c}	0.41^{a}
	summer	0.16^{b}	0.06^{b}	0.05^{b}	0.29^{a}	0.07^{b}	0.30^{a}
	autumn	0.19^{b}	0.18^{b}	0.06^{c}	0.20^{b}	0.36^{a}	0.37^{a}
	mean	0.18^{bc}	0.09^{bc}	0.03^{c}	0.19^{bc}	0.23^{b}	0.43^{a}
Evenness	winter	0.49^{b}	0^{c}	0^{c}	0.22^{c}	0.75^{a}	0.77^{a}
	spring	0.26^{b}	0.29^{b}	0^{c}	0.49^{ab}	0.38^{b}	0.71^{a}
	summer	0.39^{ab}	0.18^{c}	0.15^{c}	0.62^{a}	0.22^{bc}	0.58^{a}
	autumn	0.50^{b}	0.49^{b}	0.20^{c}	0.54^{b}	0.69^{a}	0.77^{a}
	mean	0.41^{ab}	0.24^{bc}	0.09^{c}	0.47^{ab}	0.51^{ab}	0.71^{a}

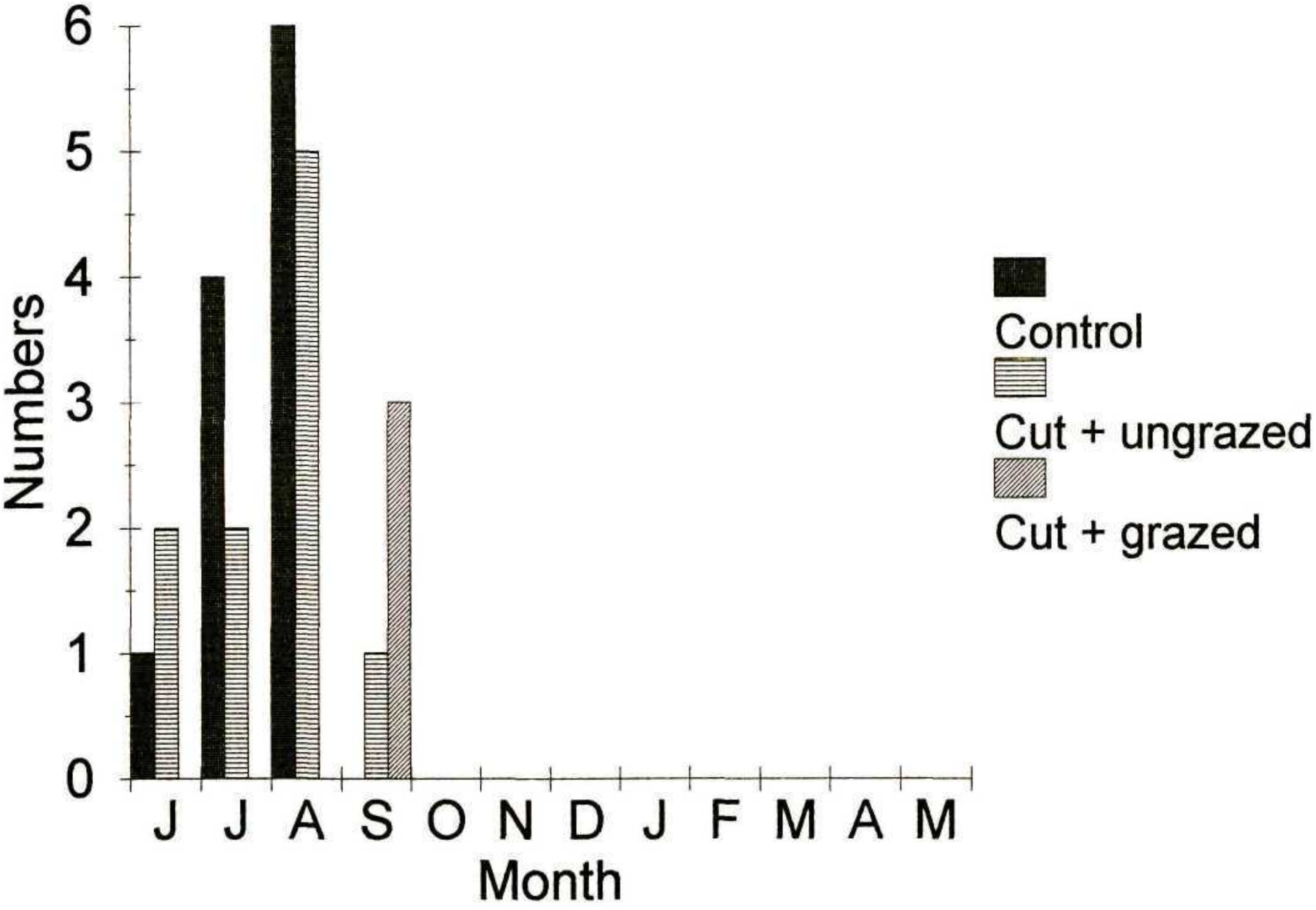

Fig. 1- The total number of *Dendromus mystacalis* captured on the control grids (5 and 6), cut grids (1 and 4) in the ungrazed area, and cut grids (2 and 3) in the grazed area between June 1996 and May 1997.

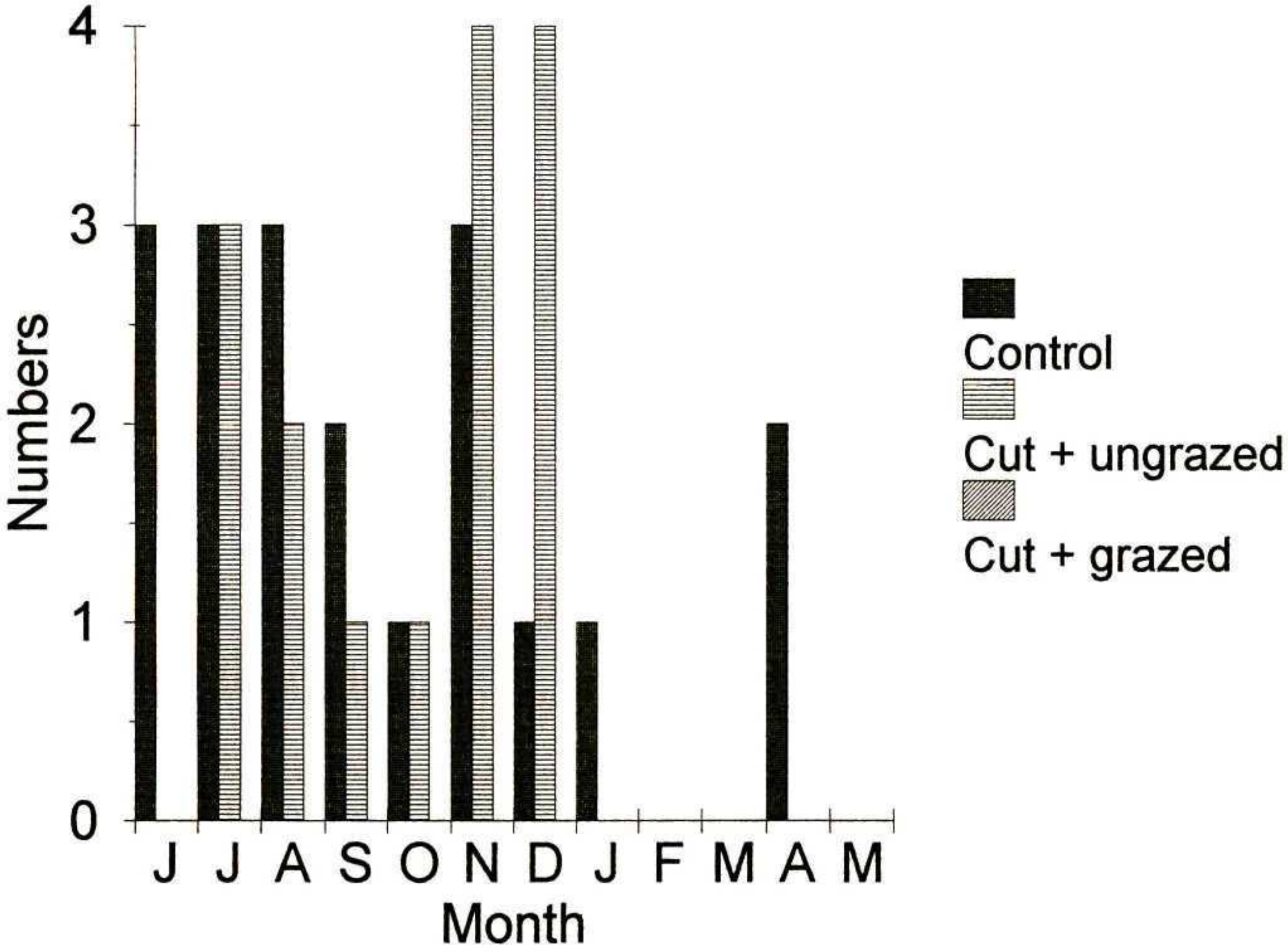

Fig. 2- The total number of *Steatomys pratensis* captured on the control grids (5 and 6), cut grids (1 and 4) in the ungrazed area, and cut grids (2 and 3) in the grazed area between June 1996 and May 1997.

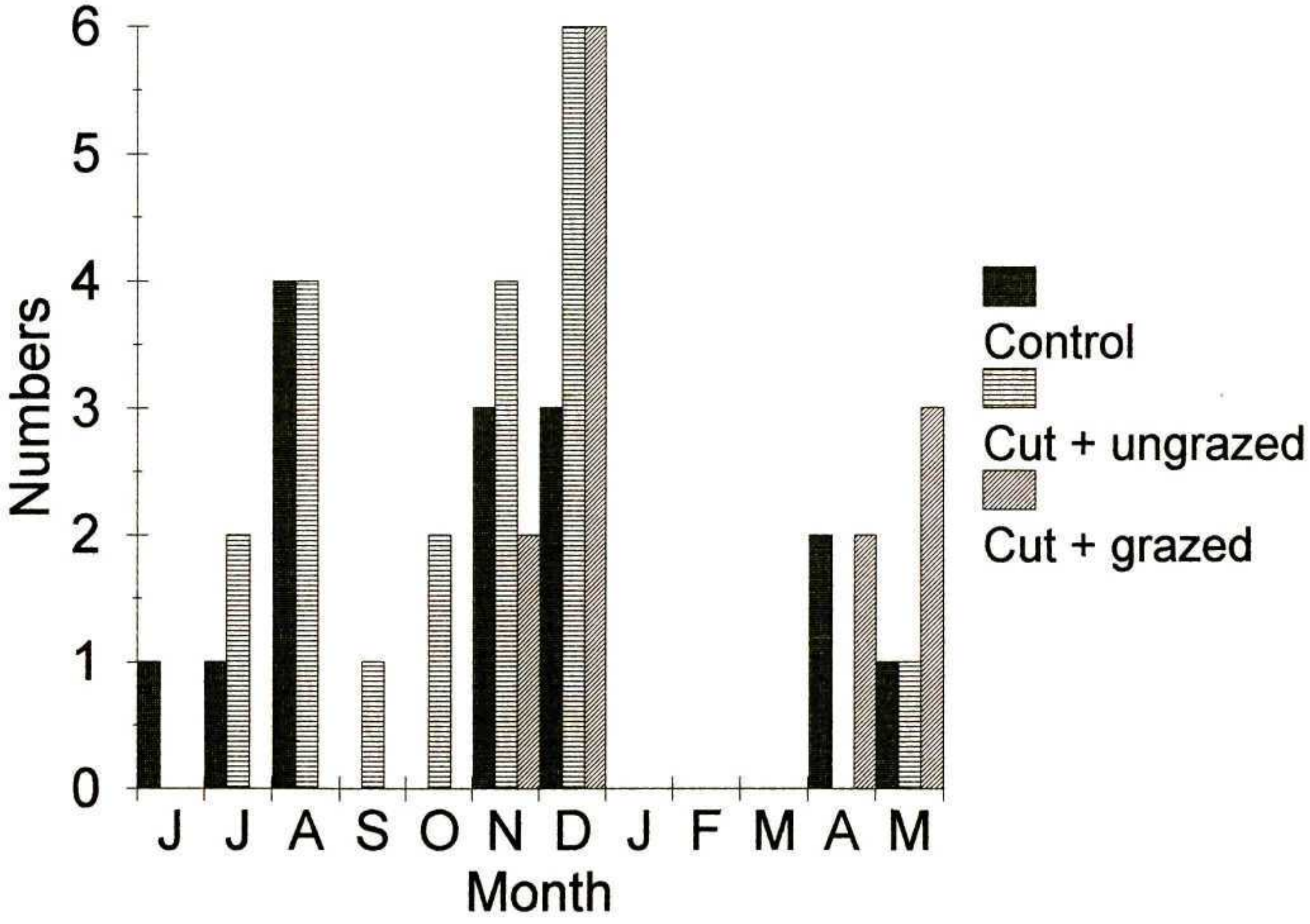

Fig. 3- The total number of *Mus minutoides* captured on the control grids (5 and 6), cut grids (1 and 4) in the ungrazed area, and cut grids (2 and 3) in the grazed area between June 1996 and May 1997.

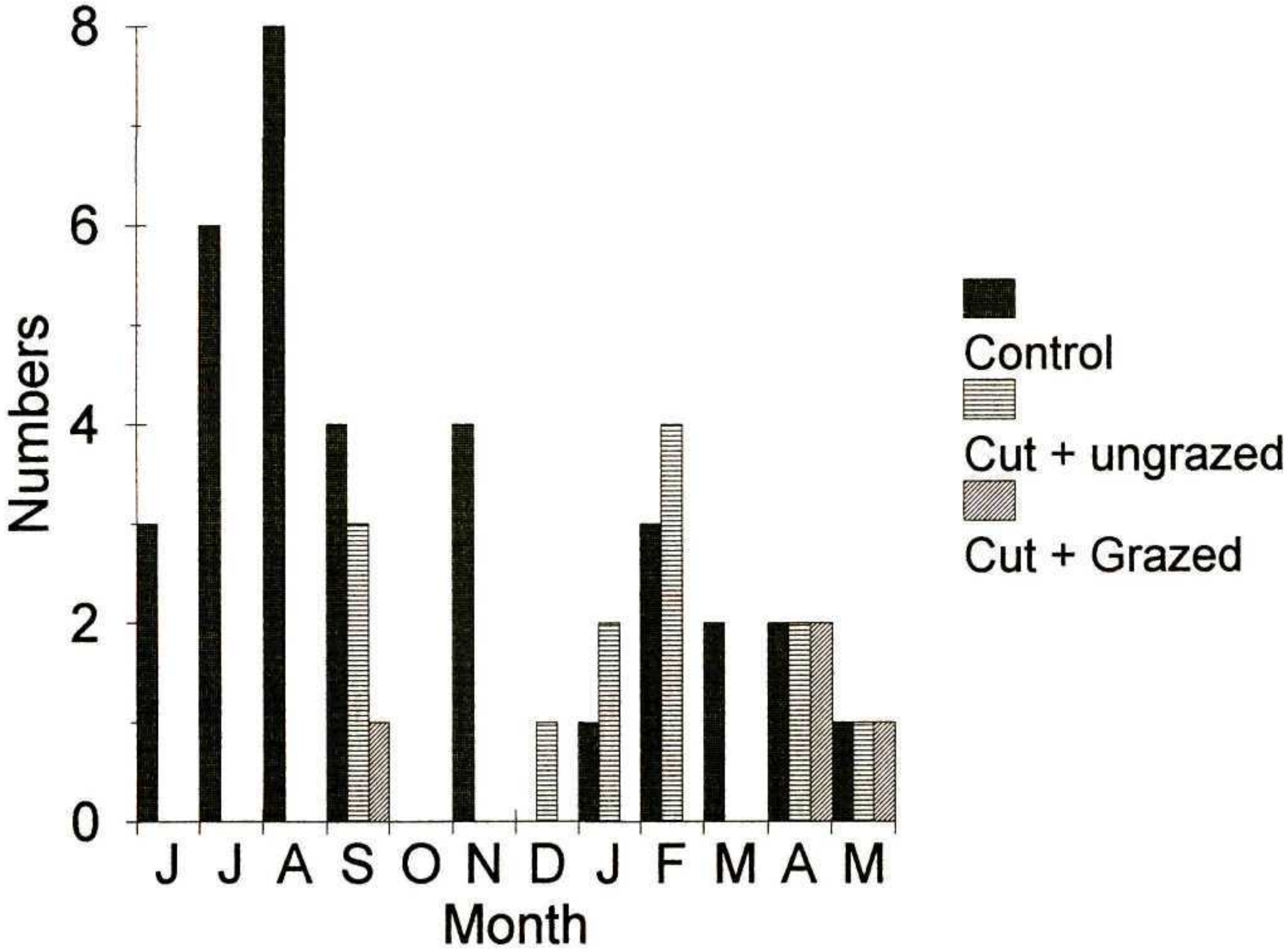

Fig. 4- The total number of *Lemniscomys rosalia* captured on the control grids (5 and 6), cut grids (1 and 4) in the ungrazed area, and cut grids (2 and 3) in the grazed area between June 1996 and May 1997.

CHAPTER 7*

THE EFFECT OF FOOD SUPPLEMENTATION ON *MASTOMYS NATALENSIS* (MURIDAE: RODENTIA) IN A SWAZILAND GRASSLAND

*Monadjem, A. & Perrin, M.R. Submitted. *Transactions of the Royal Society of South Africa*

SUMMARY

The effects of food supplementation on a *Mastomys natalensis* population were experimentally studied 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. Mice were trapped monthly over a twelve month period. Food supplemented grids supported more than twice the number of mice than the control grid. This increase was a consequence of high rates of immigration onto the supplemented grids. Food supplementation also extended the breeding season of the females by at least two months, but not of the males. Late in the dry season (August - October) the mean mass of mice was higher on the supplemented grids. Monthly survival rates were higher on the supplemented grids immediately after supplementation (July - August), and during mid-summer (December - February). The presence of extra food, however, did not prevent the spring (October -November) decline.

INTRODUCTION

Food supplementation studies have shown food to be a limiting factor of rodent populations. In the majority of studies food addition increased rodent population density (Taitt & Krebs, 1981; Flowerdew, 1972; Zubaid & Gorman, 1993; Doonan & Slade, 1995). Furthermore, manipulated increases in food supply have resulted in: 1) extension of the breeding season (Hansen & Batzli, 1979; Hubert *et al.,* 1981; Taitt, 1981; Zubaid & Gorman, 1993), 2) increases in reproductive intensity (Watts, 1970; Taitt & Krebs, 1981; Saitoh, 1989), 3) decreases in home range area (Taitt, 1981), and 4) increases in growth rate and body weight (Fordham, 1971; Taitt, 1981; Leirs *et al*., 1990; Neal & Alibhai, 1991).

Mastomys natalensis (multimammate mouse: Muridae: Rodentia) is widespread in southern Africa and tends to reach highest numbers in disturbed habitats (Meester, Lloyd & Rowe-Rowe, 1979; de Graaff, 1981). The reproductive potential of *M. natalensis* is high (Skinner & Smithers, 1990) and frequent demographic outbreaks occur (Leirs & Verheyen, 1995). Increases in density of *M. natalensis* have been linked to rainfall (Neal, 1977; Bronner, Rautenbach & Meester, 1988; Leirs *et al*., 1989). Despite food manipulation experiments in Senegal (Hubert *et al*., 1981), Uganda (Taylor & Green, 1979) and Tanzania (Leirs *et al*., 1990), the question of whether food supply is a limiting factor in *Mastomys* populations remains inconclusive.

The present study was designed to test the effect of food supplementation on five life-history parameters of *M. natalensis*: population density; duration and intensity of the breeding season; mean weight of adult males; mean monthly survival rates; and recruitment.

METHODS

Study area

Three permanently marked grids (100 m × 100 m) were established in an unutilized 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 Metereological 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 three grids, one control and two experimental, were between 70 m and 100 m apart from each other. The vegetation was very similar on the three grids. *Hyparrhenia hirta* was the dominant grass species on all grids. The only other common grass species was *Hyperthelia dissoluta* which was abundant on the control grid and present on grid 1. No trees were present on or near any of the three grids, while a few *Lippia javanica* shrubs (up to 1.5 m tall) occurred irregularly on each grid. 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. This estimate presented few problems since the grass was generally thick and a "canopy" was usually obvious. 4) Finally, the percentage 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, 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.

An uncontrolled 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 (grids 1 and 3). It also burnt to within 15 m of the control grid. After the fire, habitat characteristics were recorded separately for the burnt and unburnt sections of grids 1 and 3 (ie. five quadrats were placed in the burnt and five in the unburnt sections per grid).

Rodent trapping

Rodents were trapped monthly on the 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 days 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. Juveniles 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. 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 grids were tested using a one-way analysis of variance (ANOVA). Where heteroscedasticity was present, data were logarithmically transformed to adjust nonconstant variances (Zar, 1984). Data not normally distributed were tested using the nonparametric Kruskal-Wallis one-way analysis of variance (Zar, 1984).

Supplementary feeding

The control grid received no supplementary food, while the two experimental grids received additional food in the form of equal amounts of rolled oats and rabbit pellets. Eight kilograms of food was added monthly to the first experimental grid (grid 1) from July 1995 (immediately after sampling the rodent population) until May 1996, and also to the second experimental grid (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. 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 (ie. 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 grids are shown in Table 1. 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 percent 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 growths of grass, however, were completely green. By December there was little visual difference between the burnt and unburnt areas.

Trapping

At the beginning of the study in June - July (before food addition), the numbers of *M. natalensis* were similar on the control grid and experimental grid 1; the second experimental grid (grid 3) had lower numbers of *M. natalensis* during this period (Figure 2). However, with the commencement of feeding the numbers of *M. natalensis* on grids 1 and 3 rose to approximately five times that on the control, and remained higher for the duration of the study. The numbers of *M. natalensis* on grids 1 and 3 were significantly higher than those on the control both in the late dry season from August to November (ANOVA; F=6.91, *d.f.*=2,9, *P*<0.05), and over the whole year from August to May (ANOVA; F=5.16, *d.f.*=2,27, *P*<0.05). *Mastomys natalensis* thus showed a clear increase in population density after food was added. Although food supplementation did increase the population of *M. natalensis*, it did not prevent a numerical decline beginning in spring. Numbers on grids 1 and 3 decreased by a factor of two in November and remained lower until the end of the study (Figure 2). The numbers of *M. natalensis* on the two experimental grids were very similar from August (after the initiation of supplementary feeding) until April. This is despite the fact that from October grid 3 received half the amount of food supplied to grid 1. It appears that 4 kg/ha/month of supplementary food was sufficient to significantly raise population numbers of *M. natalensis*.

The initial late winter increase (August to September) was due to immigration from neighbouring areas, since no juveniles entered the population until January. The number of immigrants caught on grids 1 and 3 was more than three times the yearly average for the month immediately following food supplementation (Figure 3). Furthermore, after food supplementation a larger monthly number of immigrants was caught on grids 1 and 3 than on the control; this difference was significant (ANOVA; F=4.67, *d.f.*=2,27, $P<0.05$).

Male *M. natalensis* initiated breeding one month earlier than females (Figure 4). Males on all grids had scrotal testes between September and April-May. Food supplementation apparently neither advanced nor extended the breeding season of males. Females had perforate vaginae between October and May on grids 1 and 3, and between October and March, on the control. "Peak" breeding (months in which more than 50% of the females were perforate) occurred between November and April for grids 1 and 3, and between December and March for the control. Thus, the breeding season of females was extended by at least two months on the supplemented grids. The proportion of individuals in reproductive condition for the different seasons is shown in Table 2. A larger proportion of females were perforate on grids 1 and 3 than on the control during spring (September to November), summer (December to February) and autumn (March to May). The latter difference was significant (χ^2 test, $P<0.1$). Similarly, a greater proportion of females were lactating on the supplemented grids than on the control in summer and autumn. The small sample sizes, however, precluded statistical analysis.

Juveniles were caught between January and May on grids 1 and 3, and between January and March on the control (Figure 3). Although the small sample size precluded statistical analysis, juveniles were caught over two additional months in the supplemented grids, a trend which mirrors that of the female breeding season.

Only the weights of adult male *M. natalensis* were compared between the grids since pregnant females would have biased the mean weights of females, and pregnancy was not easily detected in this study. Furthermore, the first adult-sized female on the control was only caught in November, which marked the beginning of the female breeding season. Prior to food supplementation there was no difference between the mean body weight of adult males on the grids. For three months after food addition, between August and October, the mean body weight of adult males was significantly greater on grids 1 and 3 than on the control (Kruskal-Wallis; H=6.489, $P<0.05$; Table 3). There was, however, no difference in mean body weight during summer or autumn.

Monthly survival rates (calculated as the proportion of mice that were captured at time t that were subsequently recaptured at time t+1) were similar on the grids (Table 4). Survival rates were, however, significantly higher on the supplemented grids in August (χ^2 =7.948, $P<0.05$) and in January-February (χ^2 =5.310, $P<0.1$). The pattern of change of monthly survival rates over the period of study was similar for the two supplemented grids. For both grids monthly survival rates were high (above 0.5) between July and December-January. Survival rates dropped after February, especially so on grid 1. The pattern of monthly survival rates was not so consistent on the control. Survival rates were very high (1.00) between July and October, except for immediately after the initiation of food supplementation when the survival rate dropped to 0.28. The survival rate dropped sharply in November and increased again in December (Table 4). Monthly survival rates were generally low (below 0.4) after December.

Effects of the fire

The most noticeable effect of the fire was to slightly decrease *M. natalensis* numbers on grids 1 and 3 and to greatly increase numbers on the control immediately after the fire (Fig. 2). Numbers on the control doubled during October resulting from increased immigration (14 immigrants, compared to 3 in September and 1 in November), probably from the adjacent burnt area. By November numbers on the control had dropped to the pre-fire level. Despite the temporary numerical increase in October on the control grid, the numbers of *M. natalensis* were significantly higher on grids 1 and 3 (see above for the statistics). On both experimental grids the numbers of *M. natalensis* were lower on the burnt section than the unburnt section in the two months subsequent to the fire ($P<0.05$, see Table 5 for χ^2 values). By December, however, numbers were similar on burnt and unburnt sections. There was no difference in number of mice caught on the burnt and unburnt sections of grids 1 and 3 between December and May ($P>0.05$ for both tests; see Table 5). Hence, the fire had only a short-term effect on the numbers of *M. natalensis* present on the three grids.

The fire did not advance the onset of breeding of mice on grids 1 and 3 when compared with mice on the control (Figure 4).

DISCUSSION

The addition of food resulted in an increased number of mice on the supplemented grids. This response has been experimentally induced in: *Apodemus sylvaticus* in Scotland (Zubaid &

Gorman, 1993) and England (Flowerdew, 1972); *Sigmodon hispidus* in Kansas, U.S.A. (Doonan & Slade, 1995); *Peromyscus maniculatus* and *Microtus townsendii* in Canada (Taitt, 1981; Taitt & Krebs, 1981); and *Clethrionomys rufocanus* in Japan (Saitoh, 1989). However, Leirs & Verheyen (1995) working in Tanzania did not observe an increase in *M. natalensis* numbers following a 15 kg maize supplement per hectare per week. The latter study, however, was conducted on fallow maize fields which supported a much higher number of *M. natalensis* than the present study, peaking at well over 400 mice per hectare on the control grid (the maximum MNA figure for the control grid in this study was 28 mice). Factors other than food may have been limiting the Tanzania population, such as a shortage of burrows or social behaviour.

The mean body mass of *Mastomys natalensis* appeared to have been increased on grids 1 and 3 in the late dry season only. In Tanzania, Leirs *et al.* (1990) showed that *M. natalensis* were slightly heavier on the food supplemented grid than those on the control. Increases in mass of mice with food supplementation have also been reported for *P. maniculatus* (Fordham, 1971; Taitt, 1981), *M. townsendii* (Taitt & Krebs, 1981), *A. sylvaticus* (Flowerdew 1972), and *Tatera leucogaster* (Neal & Alibhai, 1991). Why mice were heavier only during the late dry season is not known. Perhaps the heavy rains of 1995-1996 resulted in a concomitant increase in the food supply throughout the study area, thus allowing mice on the control to rapidly gain weight and reach the same mass as those on the supplemented grids.

Food supplementation also appeared to have extended the breeding season of female *M. natalensis*, and increased the intensity of autumnal breeding. Several of the workers mentioned above have made similar observations (Taitt, 1981; Taitt & Krebs, 1981; Saitoh, 1989; Zubaid

& Gorman, 1993). Leirs *et al.* (1994) were not able to extend the breeding season of *M. natalensis* in Tanzania, despite the addition of large amounts of maize. Hubert *et al.* (1981), however, were able to extend the breeding season of *Mastomys erythroleucus* in Senegal by adding extra food, but only if the rainy season was also extended. In this study the breeding season of males was not extended. This may be caused by the lower investment that males make to individual reproductive events; it is energetically cheaper to produce sperm, than it is to bear offspring. Females need to develop reserves before they are able to reproduce (Field, 1975; Fleming, 1979). Adult males on the supplemented grids had greater mean body mass in the late dry season than those on the control. This may also have applied to the supplemented females, which may have been in better condition at the onset of the breeding season (no adult-sized females were caught on the control between August and October 1995, although they were present on the supplemented grids in small numbers) .

Juveniles were captured over a longer period on the supplemented grids than on the control grid supporting the observation that supplemented females enjoyed an extended breeding season. What effects the fire may have had on the onset of breeding is difficult to gauge. The fire resulted in a flush of green vegetation on the burnt sections of grids 1 and 3, which was absent on the control. 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 *et al.*, 1975; Neal & Alibhai 1991) including *Mastomys coucha* (Linn, 1991; Leirs & Verheyen, 1995). However, the fire burnt to within 15 m on the one side of the control and thus mice on the control would have had access to the green flush as well. Furthermore, the fire-induced green flush coincided with the appearance of green vegetation in the unburnt sections of grids 1 and 3 and on the control. Thus green vegetation would have become available on all three grids at about the same time.

Food supplementation appeared not to significantly affect the monthly survival rates of *M. natalensis* except in August immediately after feeding had commenced. The monthly survival rate on the control dropped sharply in August, and may have been induced by a shortage of food since survival rates remained high on the supplemented grids. The high monthly survival rate on the control in September-October was probably an artifact: the small number of mice that survived the "crunch" in August were able to survive through September and October. Food supplementation, however, was not able to prevent the spring-summer decline. *Mastomys natalensis* under natural conditions do not usually survive more than twelve months (Leirs & Verheyen, 1995). *Mastomys coucha* kept in the laboratory under permanently good conditions did survive a full year, but began seriously loosing body condition after eight months (Leirs & Verheyen, 1995). The spring-summer decline is probably a result of a die-off of mice born nine to ten months earlier, and which are at the end of their natural lives anyway. Hence food supplementation is unlikely to avert this seasonal mass mortality.

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

	Grid 1						Control			Grid 3					
	Unburnt			Burnt						Unburnt			Burnt		
Month	Cover index	Height	Green (%)	Cover index	Height	Green (%)	Cover index	Height	Green (%)	Cover index	Height	Green (%)	Cover index	Height	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

Table 2. Proportion of adult male and female *Mastomys natalensis* in breeding condition on the supplemented and control grids between June 1995 and May 1996 (winter: June-August; spring: September-November; summer: December-February; autumn: March-May). The values in brackets indicate the sample sizes. Differences between grids were compared using chi-square. Due to small sample sizes, differences between number of females lactating on the grids could not be tested.

	Winter 1995	Spring 1995	Summer 1995-1996	Autumn 1996
Males				
Grid 1	0 (53)	0.63 (56)	0.95 (21)	0.29 (21)
Grid 3	0 (41)	0.70 (54)	0.84 (25)	0.57 (14)
Control	0 (22)	0.72 (25)	0.89 (9)	0.31 (13)
χ^2 value	-	0.335	0.160	2.050
Females (perforate vaginae)				
Grid 1	0 (39)	0.18 (44)	1.00 (31)	0.52 (21)
Grid 3	0 (32)	0.09 (45)	0.91 (22)	0.80 (10)
Control	0 (20)	0.08 (15)	0.75 (12)	0.27 (11)
χ^2 value	-	2.020	0.588	2.777*
Females (lactating)				
Grid 1	0 (39)	0 (44)	0.26 (31)	0.24 (21)
Grid 3	0 (32)	0 (45)	0.18 (22)	0.30 (10)
Control	0 (20)	0 (15)	0.17 (12)	0.09 (11)

*$P<0.1$

Table 3. Monthly mean weight of adult male *Mastomys natalensis* between June 1995 and May 1996. The values in brackets indicate the sample sizes. Differences between grids were compared using the Kruskal-Wallis one-way analysis of variance. The vertical lines indicate the seasons over which each test was performed (June-July: before food supplementation; August-October: dry season following supplementation; November-February: wet season; March-May: early dry season).

Month	Mean weight of adult male *M. natalensis* (g)			Kruskal-Wallis (H) value
	Grid 1	Grid 3	Control	
Jun.	43.3 (9)	41.3 (4)	37.0 (6)	2.000
Jul.	36.2 (6)	37.5 (2)	33.0 (4)	
Aug.	39.2 (16)	36.8 (16)	34.0 (1)	6.489*
Sep.	39.9 (16)	38.3 (22)	38.0 (2)	
Oct.	42.2 (17)	38.9 (17)	35.7 (9)	
Nov.	47.9 (7)	44.8 (11)	45.0 (5)	0.921
Dec.	58.9 (7)	58.3 (6)	50.3 (3)	
Jan.	58.0 (4)	49.0 (3)	59.0 (3)	
Feb.	58.3 (4)	56.6 (5)	-	
Mar.	46.7 (3)	53.0 (2)	46.0 (2)	0.800
Apr.	35.0 (1)	47.0 (4)	55.0 (2)	
May	46.4 (7)	45.0 (2)	40.0 (1)	

*$P<0.05$

Table 4. Mean monthly survival rates of adult *Mastomys natalensis* between June 1995 and May 1996. The values in brackets indicate sample sizes. Differences between grids were compared using chi-square. Where present, the vertical lines indicate months which have been combined (due to small sample sizes) for statistical analysis.

	Mean monthly survival			
Month	Grid 1	Grid 3	Control	χ^2 value
Jul.	1.00 (22)	0.88 (9)	1.00 (14)	0.091
Aug.	0.75 (24)	1.00 (11)	0.28 (25)	7.948**
Sep.	0.67 (52)	0.78 (55)	1.00 (8)	4.422
Oct.	0.67 (49)	0.66 (56)	1.00 (14)	1.951
Nov.	0.47 (43)	0.58 (40)	0.32 (28)	2.677
Dec.	0.64 (25)	0.77 (26)	0.90 (10)	0.716
Jan.	0.64 (22)	0.22 (23)	0.22 (9)	5.310*
Feb.	0.50 (20)	0.63 (19)	0.09 (11)	
Mar.	0.25 (24)	0.44 (16)	0.67 (3)	1.061
Apr.	0.33 (10)	0.50 (10)	0.25 (8)	
May	0.30 (22)	0.10 (10)	0.33 (6)	

*$P<0.1$

**$P<0.05$

Table 5. Numbers of *Mastomys natalensis* caught in the burnt and unburnt halves of experimental grids 1 and 3.

	Numbers caught					
	Grid 1			Grid 3		
	Unburnt	Burnt	χ^2	Unburnt	Burnt	χ^2
Oct. 1995-Nov. 1995	41	16	10.960*	39	23	4.129*
Dec. 1995-May 1996	52	56	0.148	37	45	0.78

*$P<0.05$

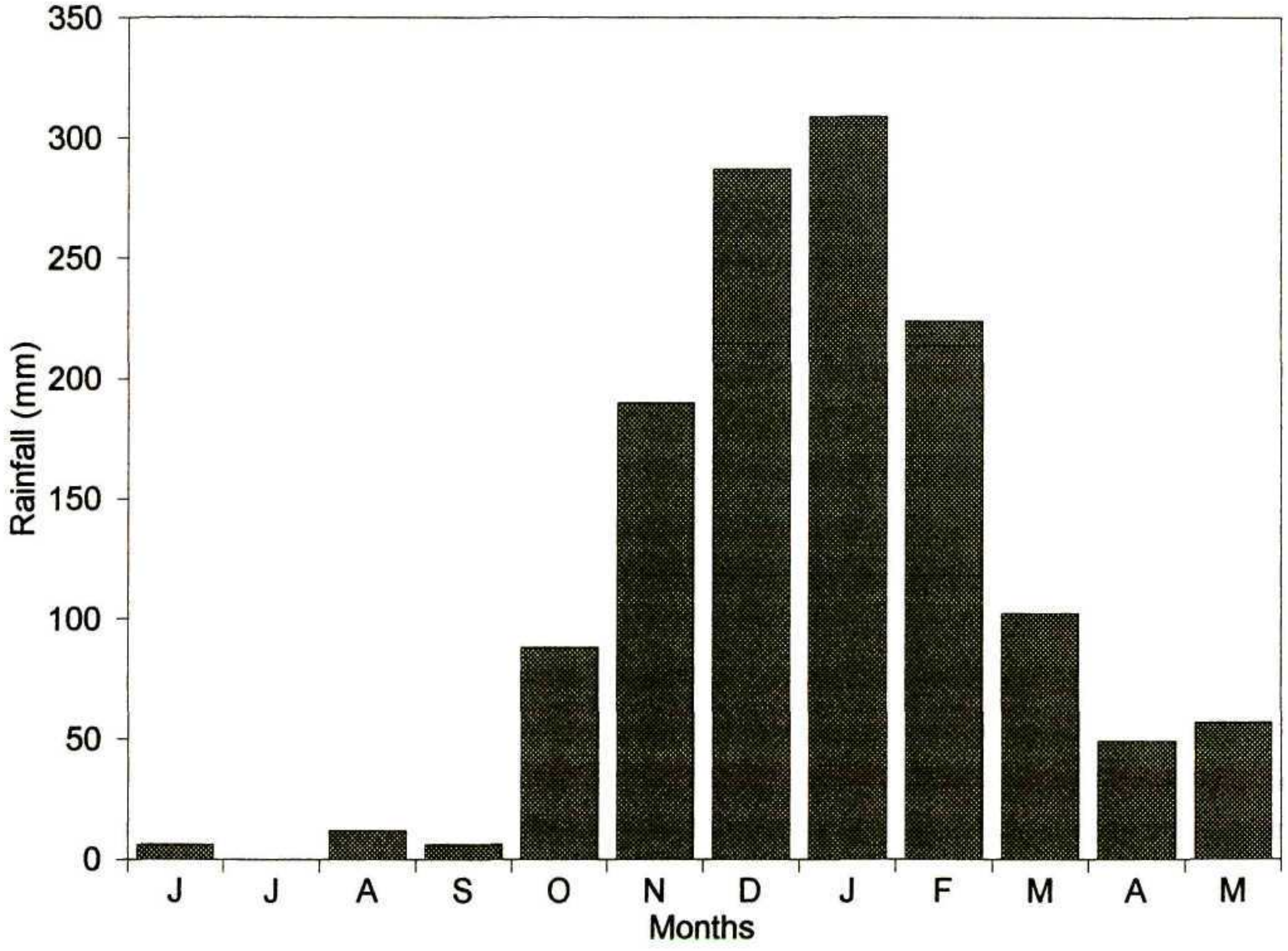

Figure 1. Total monthly rainfall at eKundizeni Farm, Swaziland from June 1995 to May 1996.

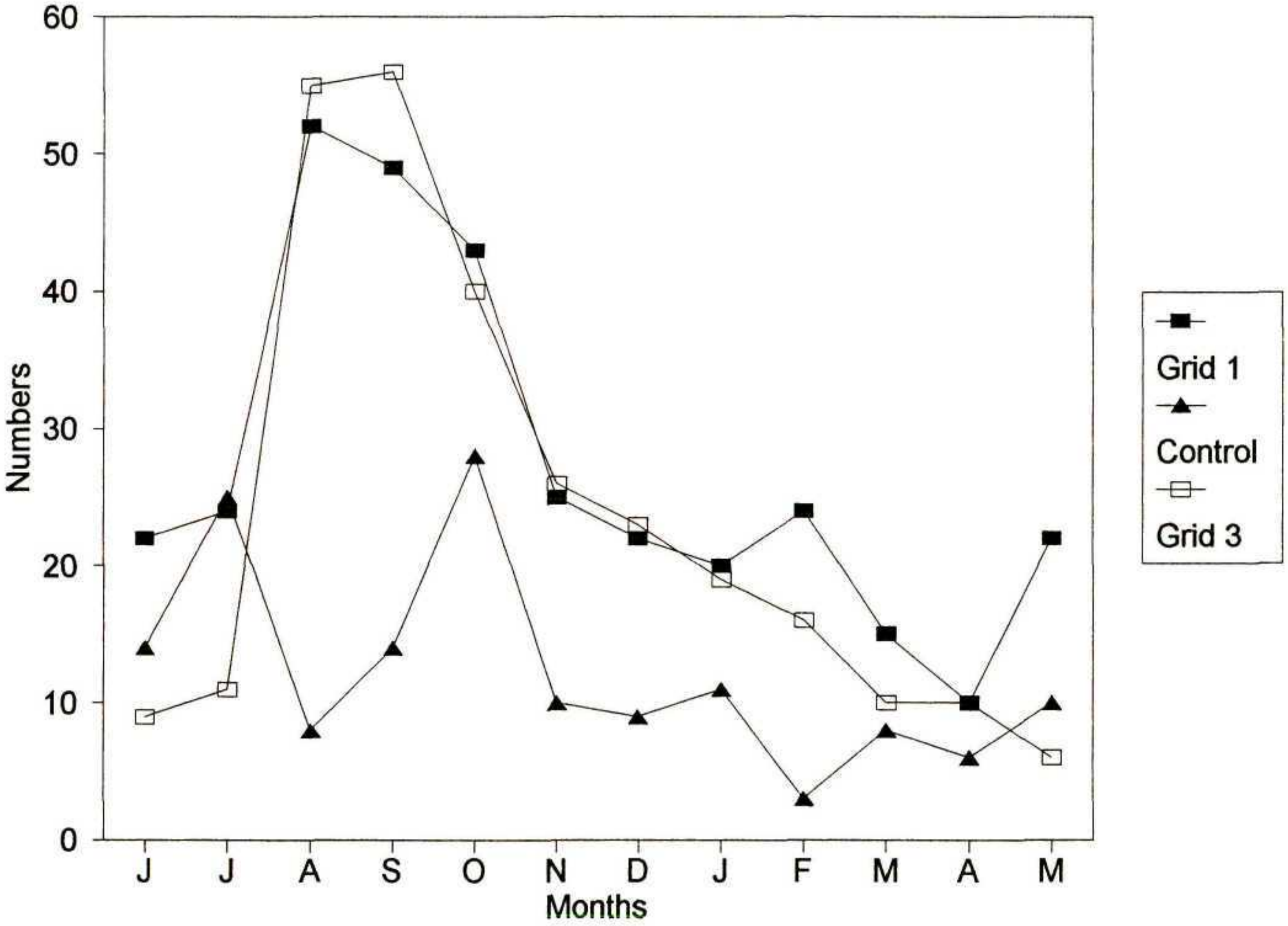

Figure 2. Minimum number of *Mastomys natalensis* alive on supplemented grids 1 and 3, and the control between June 1995 and May 1996.

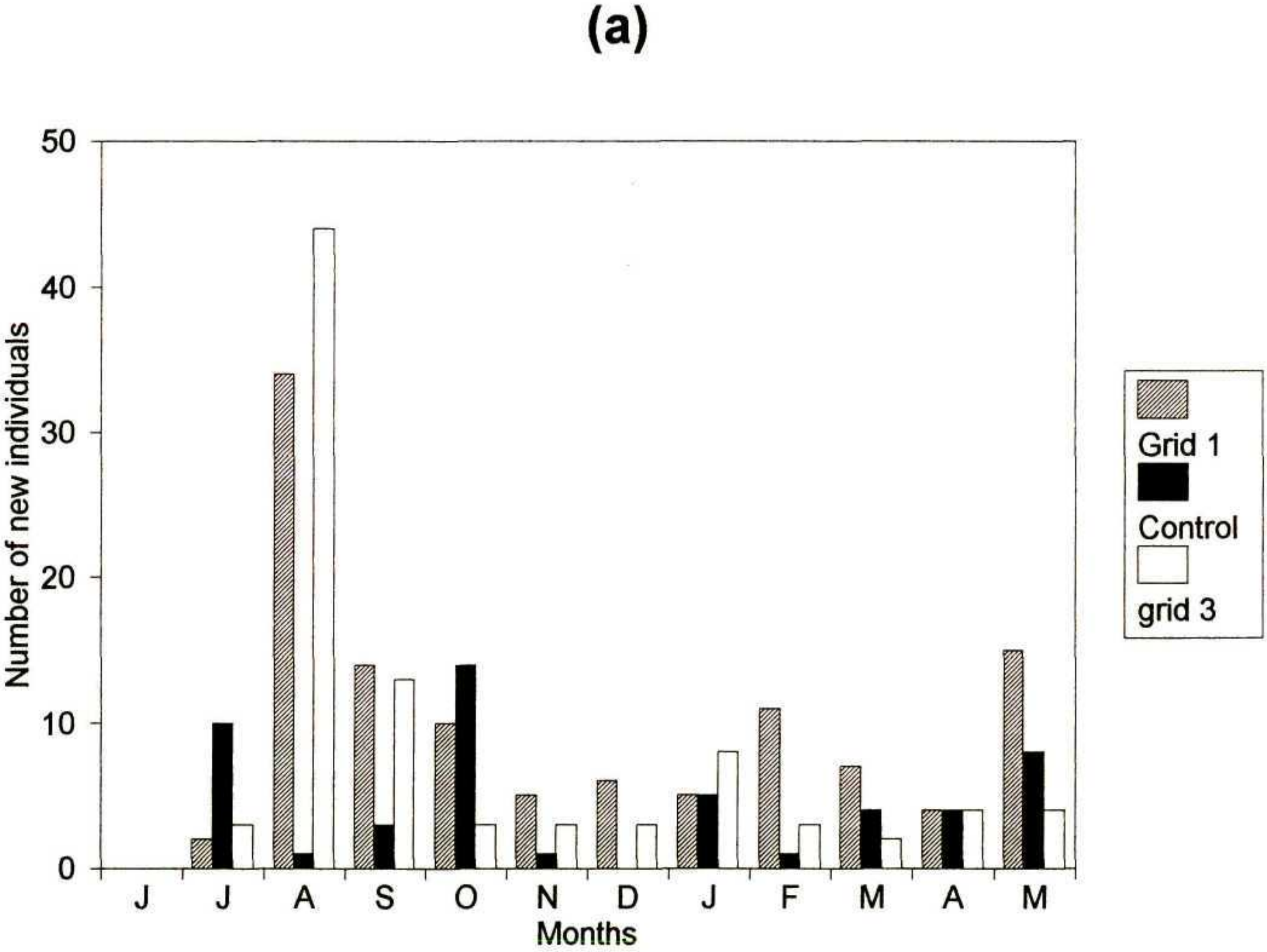

Figure 3. The number of: (a) immigrants, and (b) juveniles, trapped on the three grids between June 1995 and May 1996.

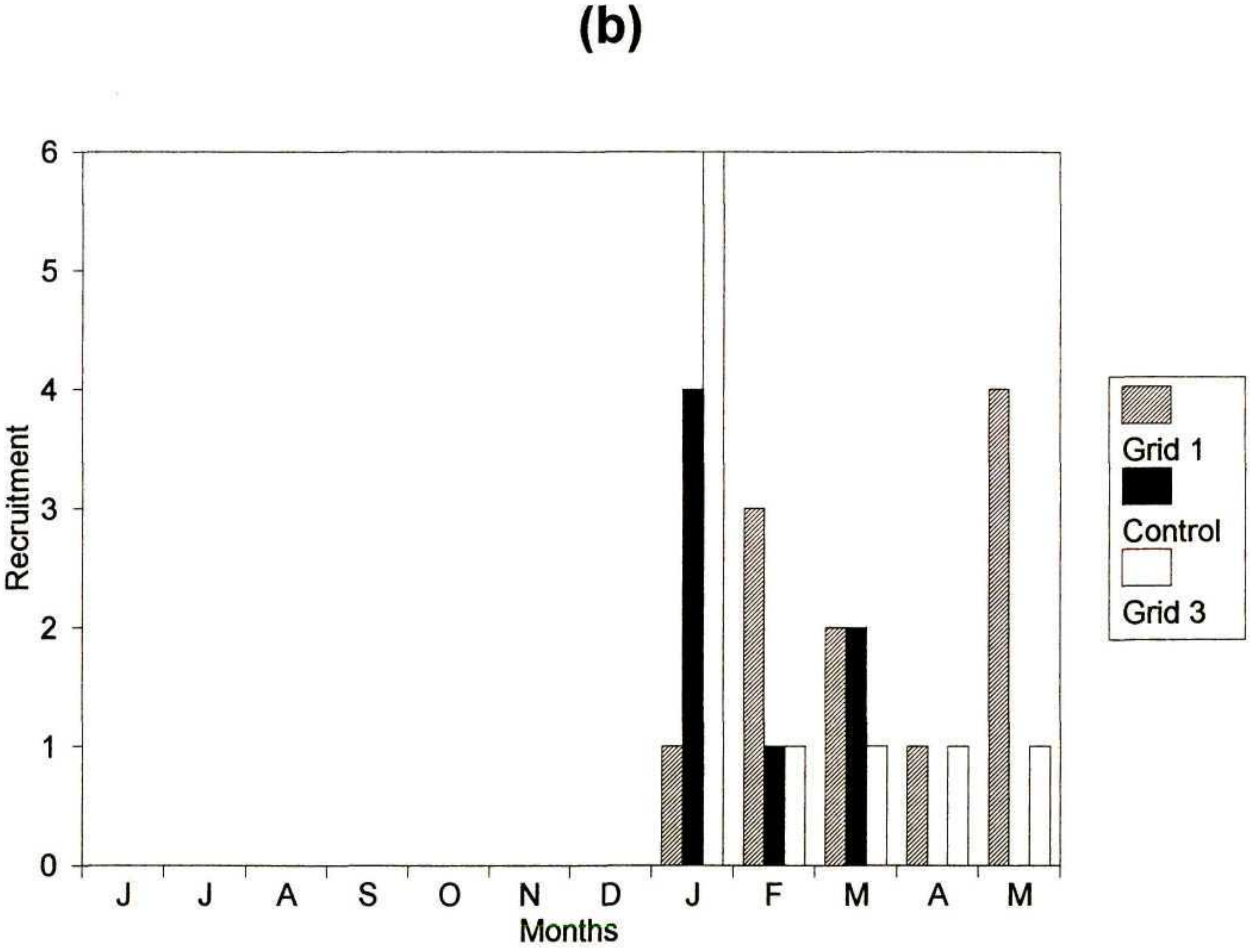

Figure 3. The number of: (a) immigrants, and (b) juveniles, trapped on the three grids between June 1995 and May 1996.

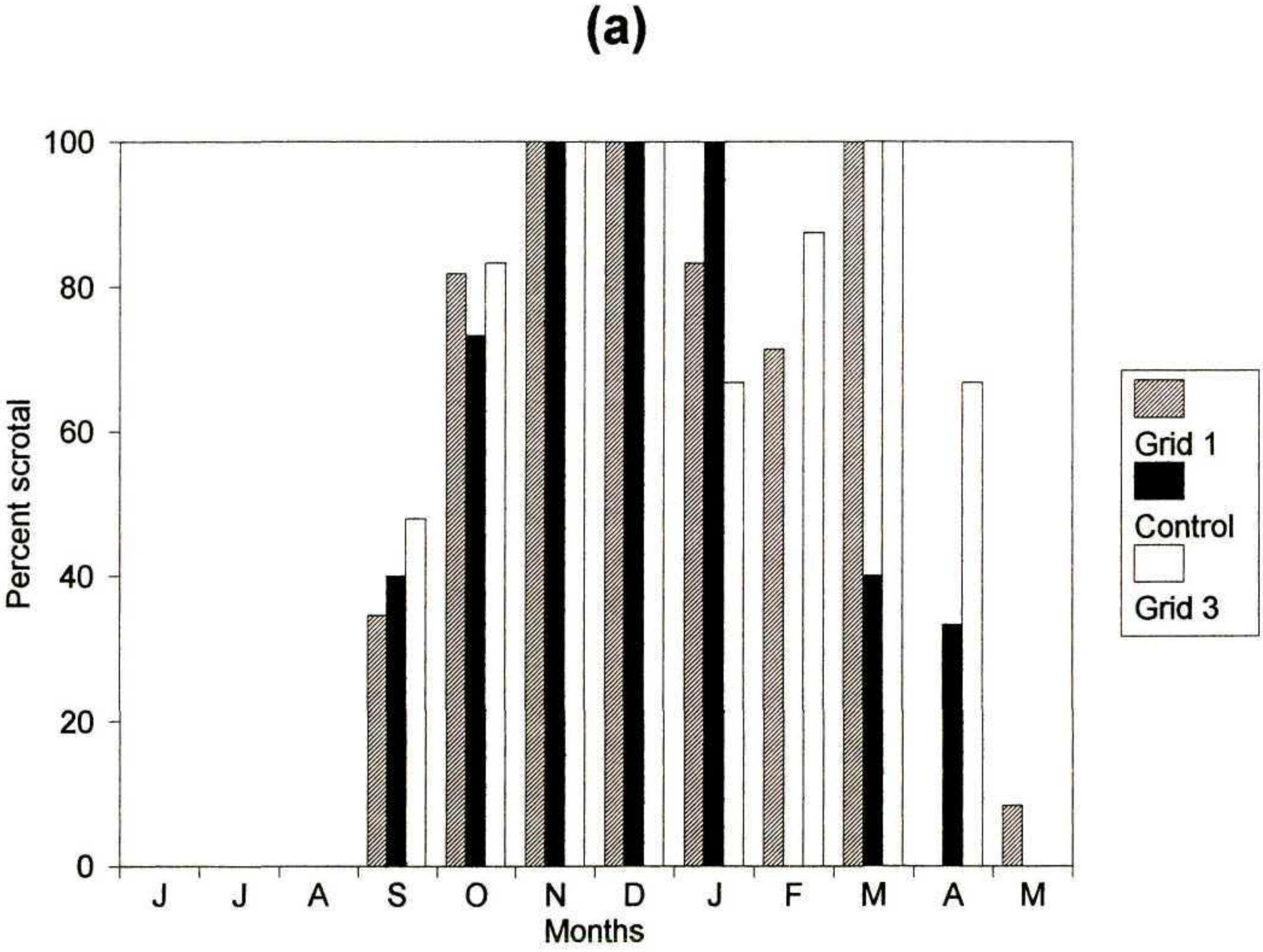

Figure 4. The proportions of: (a) adult males with scrotal testes, and (b) females with perforate vaginae, trapped between June 1995 and May 1996 on the three grids.

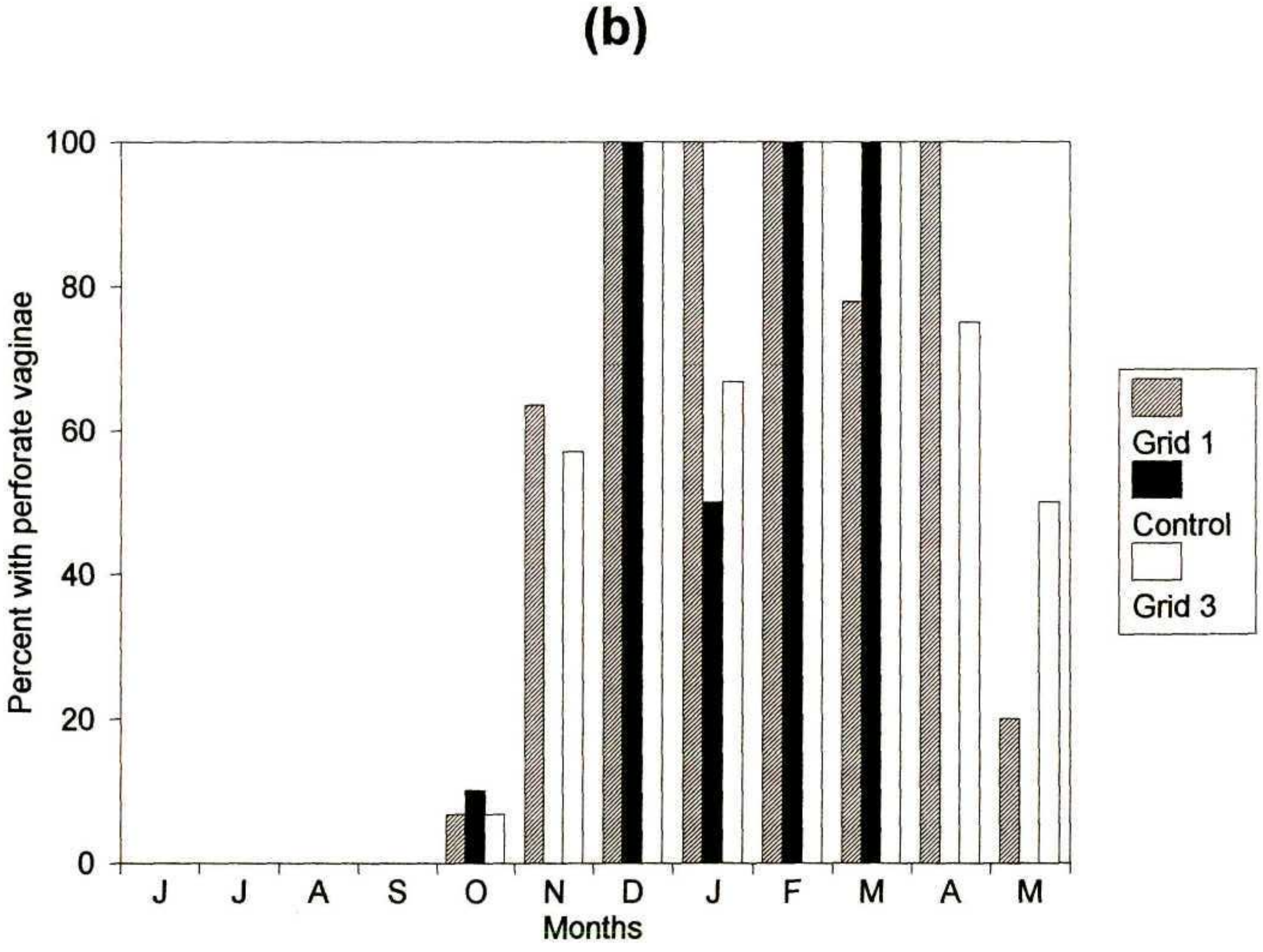

Figure 4. The proportions of: (a) adult males with scrotal testes, and (b) females with perforate vaginae, trapped between June 1995 and May 1996 on the three grids.

CHAPTER 8*

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 grids. 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 that on the control. In contrast, despite the reduced cover on the food supplemented grids, the population on at least one of the supplemented grids exhibited a higher number and proportion of adult and resident mice than that on the control. Mastomys natalensis appears to select patches with greater vegetative cover which it will abandon in the presence of an abundant food source.

Key words: Mastomys natalensis, multimammate mouse, vegetative cover, supplemental food, population dynamics, habitat

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 and Merriam, 1985; Canova et al., 1994; Peles and Barrett, 1996). Habitat selection studies of small mammals in Africa have mainly been of a correlative nature (Happold, 1975; Bond et al., 1980; Rowe-Rowe and Meester, 1982; Martin and 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 and 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 and Krebs, 1983; Edge et al., 1995; Peles and Barrett, 1996) and in the hispid cotton rat Sigmodon hispidus (Eshelman and 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 and Krebs, 1983; Kotler et al., 1989). Furthermore, supplementary feeding induced the cotton rats to occupy open patches which, without the food, were avoided.

Mastomys natalensis, the multimammate mouse, is a very common and widespread species of murid rodent occurring in SubSaharan Africa (Leirs and Verheyen, 1995). Mastomys natalensis is a pioneer species which rapidly colonizes disturbed habitats (Meester et al., 1979); it is capable of surviving in a wide range of habitats (De Graaff, 1981; Skinner and Smithers, 1990), but is most successful, in terms of population density and reproductive output, in disturbed habitats such as fallow fields (Telford, 1989; Leirs and Verheyen, 1995). The abundance of M. natalensis has been positively correlated with vegetative cover in a number of studies (Martin and Dickinson, 1985; Chidumayo, 1980, 1984; Leirs and Verheyen, 1995; Leirs et al., 1996; Monadjem, 1997a). In other studies, however, vegetative cover apparently did not affect the distribution and abundance of M. natalensis (Neal, 1970; Taylor and Green, 1976; Cheeseman and Delany, 1979). The experimental addition of supplementary food has resulted in an increase in the numbers, reproduction, and mass of M. natalensis (Hubert et al., 1981; Leirs and Verheyen, 1995; Monadjem and Perrin, 1996; Monadjem and Perrin, in preparation; Chapters 4 and 7).

The present study was designed to experimentally test 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 (70m × 70m) 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. 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.

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) 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.

An uncontrolled fire swept through the study area on September 13, 1996 and completely burnt the vegetation on all of the grids.

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 1and 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. The feeding stations were checked twice monthly during which time all the cans were cleaned and refilled. Due 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.

A summary of the experimental treatments appears in Table 1.

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 days 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 color. Juveniles had soft, grey fur, while in adults the color 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 and Perrin, in preparation; Chapter 7). 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).

Statistical analyses.-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. 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, $F = 27.599$, $P < 0.001$; height, $F = 31.654$, $P < 0.001$). Mean percent vegetative cover was approximately twice as high on the control grids than on the manipulated grids, and this difference was significant in winter, summer and autumn, but not spring (Table 2). Vegetative cover differed significantly among seasons ($F = 74.465$, $P < 0.001$) as did vegetation height ($F = 19.984$, $P < 0.001$). Mean vegetation height was at least four times taller on the control grids than on the cut grids (Table 2), and as for vegetative cover, this difference was significant in winter, summer and autumn. 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 ($F = 3.850$, $P < 0.001$) and vegetation height and season ($F = 3.983$, $P < 0.001$). 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 percent greenness of the vegetation was not significantly different among the grids (two-way ANOVA, $P > 0.05$), but was significantly different between the seasons ($F = 14.680$, $P < 0.001$). 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 2).

Population dynamics.-A total of 223 M. natalensis were live-trapped 640 times between June 1996 and May 1997.

Where differences between replicates of the same treatment are not significant (Tukey test, $P > 0.05$), the mean of the replicates is 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 Fig. 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 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 ($F = 25.869$, $P < 0.001$) and in the different seasons ($F = 9.620$, $P < 0.001$). The interaction between the different grids and seasons was also significant ($F = 3.148$, $P < 0.05$). Grid 1 supported a higher number of M. natalensis than the other grids in all seasons except autumn (Table 3). 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 ($F = 3.951$, $P < 0.05$). Grid 1 had significantly higher numbers of immigrants than other grids in winter, spring and summer, but not in autumn (Table 3).

The number of resident M. natalensis also varied between the grids ($F = 32.271$, $P < 0.001$).

The largest number of residents were observed on grid 1 in all seasons (Table 3). The control grids had 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 ($F = 10.441$, $P < 0.001$), 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. The proportion of resident M. natalensis was very low on grid 2 except in spring (Table 3).

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 ($F = 8.971$, $P < 0.05$). 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 ($F = 16.935$, $P < 0.001$). Breeding commenced later in females (November) than in males (September).

The proportion of adult M. natalensis was significantly different among the grids ($F = 2.923$, $P = 0.05$). The proportion of adults was significantly higher on grid 1 and the control grids in winter (Table 3). 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 *M. 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 and trampling. Supplementary food was initially placed in 340 ml cans. These cans were trampled and destroyed in July and new cans were installed 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 drop 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 due to the fact that, as a result of being mowed, a fresh growth of grass was usually available on this grid). Cattle and wild ungulates can influence the structure and productivity of small mammal communities (Grant et al., 1982), and the population of individual species (Bowland and 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 (eg. Leirs and Verheyen, 1995; Monadjem, 1997a), and showing no preference for either high or low cover (eg. Taylor and 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 and Verheyen, 1995) relying heavily on seeds (Taylor and Green, 1976; Swanepoel, 1980; Monadjem, 1997b) and insects (Field, 1975; see Chapter 2). With a lack of information on the subject, there is no a priori reason to expect open areas to harbour more seeds or arthropods, although it has been shown that open patches support a lower abundance of orthopterans than more densely vegetated areas (Prendini et al., 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 and 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 has been observed elsewhere in Africa (Neal, 1970; Cheeseman and Delany, 1979; Martin and Dickinson, 1985; Rowe-Rowe, 1995), although some studies have reported no change (Bowland and 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 and Perrin, 1996; Monadjem and Perrin, in preparation; Chapters 4 and 7). 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 April 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 and Perrin, in preparation; Chapter 7). 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 elsewhere (Leirs and 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 before (Leirs and Verheyen, 1995; Monadjem and Perrin, in preparation; Chapter 7). 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 and Perrin, in preparation; Chapter 7). This may have been due to the fact that the breeding season in the present study was preceded by an extra-ordinarily wet summer (October 1995 to April 1996). Food, in the way of grass seeds and arthropods, may have thus 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 and Happold, 1986). Predation has a significant impact on vole demography (Lin and Batzli, 1995), and it has even been suggested that predation may influence whether the populations will exhibit cyclic fluctuations or not (Hansson and 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 et al., 1983; Bowland and 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?

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TABLE 1.-Summary of experimental treatment of each grid between June 1996 and May 1997.

Grid number	Treatment
Grid 1	reduced cover, supplementary food
Grid 2	reduced cover, supplementary food
Grid 3	reduced cover
Grid 4	reduced cover
Grid 5	control
Grid 6	control

TABLE 2.-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.

		Treatment		
Vegetation	Season	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

TABLE 3.-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.

		Treatment			
				Reduced cover + food	
	Season	Control	Reduced 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^{ab}
	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	winter	1.8 ± 0.5^{a}	0.5 ± 0.3^{a}	11.0 ± 1.0^{b}	0.5 ± 0.5^{a}
(numbers)	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}	6.3 ± 2.0^{b}	0.7 ± 0.7^{c}
	autumn	2.8 ± 0.8	1.3 ± 0.8	2.0 ± 0	4.0 ± 0
Residents	winter	1.8 ± 0.5^{ab}	0^{a}	3.5 ± 3.5^{b}	0^{a}
(numbers)	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	winter	0.51 ± 0.13^{a}	0^{b}	0.21 ± 0.21^{b}	0^{b}
(proportion)	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	winter	0.76 ± 0.10^{a}	0^{b}	0.60 ± 0.07^{a}	0^{b}
(proportion)	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}

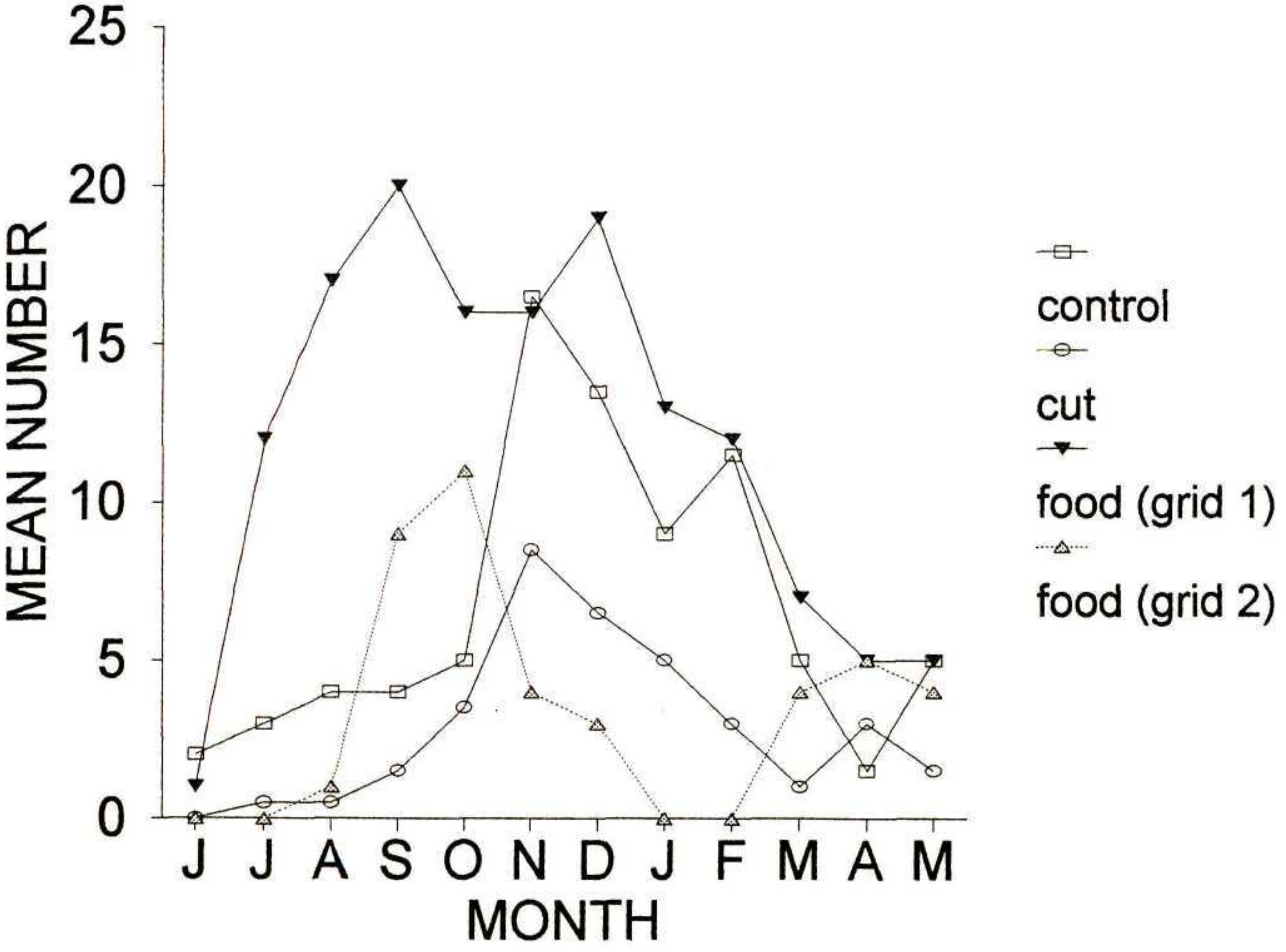

Fig. 1.-Mean monthly number of Mastomys natalensis in control, reduced cover and two reduced cover with supplementary food treatments between June 1996 and May 1997.

CHAPTER 9*

THE EFFECT OF SUPPLEMENTARY FOOD ON THE HOME RANGE OF THE MULTIMAMMATE MOUSE MASTOMYS NATALENSIS

*Monadjem, A. & Perrin, M.R. Slightly modified version accepted. *South African Journal of Wildlife Research*

The effect of supplementary food on the home range area of multimammate mice Mastomys natalensis was investigated. A population of M. natalensis was live-trapped on two experimental grids (food added) and a control grid (no food added) for a twelve month period. Home range area was estimated using the minimum convex polygon and the harmonic mean methods. Home range estimates from these two methods were highly correlated ($p < 0.001$). The mean distance between successive captures was also calculated and was correlated with the home range estimates ($p < 0.001$). Mice on the experimental grids had smaller home ranges and shorter mean distance between captures than mice on the control grid. The home range estimates obtained in this study compare well with those from Tanzania.

The multimammate mouse Mastomys natalensis is a widespread African murid rodent which, due to its ability to reach plague proportions, is of great economic importance (Leirs & Verheyen 1995). Despite its economic importance, much remains unknown or unclear about the biology of this species. To our knowledge, only three published articles exist that deal with movements of M. natalensis (Sheppe 1972; Leirs & Verheyen 1995; Leirs, Verheyen &

Verhagen 1996). Sheppe (1972) showed that M. natalensis undertook seasonal movements on and off a Zambian floodplain to avoid flood waters. In the other two studies conducted in Tanzania, the home range of M. natalensis was calculated by capture-mark-release and by radio-telemetry (Leirs & Verheyen 1995; Leirs et al. 1996).

Numerous studies on rodents have shown that the addition of supplementary food results in a decrease in the home range of the individuals receiving the food (Bendell 1959; Andrzejewski & Mazurkiewicz 1976; Mares, Watson & Lacher 1976; Taitt 1981; Zubaid & Gorman 1993), indicating that the act of foraging for food is a major determinant of the size of home range in these species.

The objective of this study was to investigate the effect that the addition of supplementary food has on the home range of Mastomys natalensis, and to compare the home range estimates obtained in this study with those reported for Tanzania.

Three permanently marked grids (100m × 100m) were established, in May 1995, on an unutilized natural grassland site in the Swaziland Middleveld, near Matsapha (26°33'S 31°16'E). One grid served as the control, while 8 kg of food, consisting of equal amounts of rolled oats and rabbit pellets, were added monthly to each experimental grid (grids 1 and 3) from July (immediately after the July sampling period) until May 1996. Rodents were trapped monthly on all three grids from June until May. One hundred Elliot and Sherman live-traps were set 10 m apart on each grid on three consecutive nights per month. Each trapped rodent was uniquely toe-clipped, sexed, weighed and its reproductive condition was assessed. A detailed account of the study area and methods will be published elsewhere (Monadjem & Perrin in preparation; Chapter 7).

Home range has been defined as the area where an individual normally moves during its normal daily activities of gathering food, mating and caring for offspring (Burt 1943) and numerous methods have been developed to quantify this (Hayne 1949; Ackerman, Leban, Samuel & Garton 1990). We estimated home range by the minimum convex polygon method and the harmonic mean method using the programme HOME RANGE (Ackerman et al. 1990). The bivariate normal ellipse and weighted bivariate normal ellipse methods were not appropriate since more than half of the locations did not fit a bivariate normal distribution, which is an assumption of both methods (Ackerman et al. 1990). We also calculated the mean distance between successive captures. Only mice that had been captured five times or more were included in the analyses. A total of 76 mice (35 from grid 1, 31 from grid 3, and 10 from the control) were included.

The estimates of home range based on the minimum convex polygon and harmonic mean methods are presented in Table 1, as are the mean distance between captures. The home range estimates based on the convex polygon method were smaller than those based on the harmonic mean method. However, the estimates from these two methods were closely correlated ($r_{76} = 0.84$, $p < 0.001$). Furthermore, the mean distance between captures was also correlated with the estimates from both convex polygon ($r_{76} = 0.63$, $p < 0.001$) and harmonic mean ($r_{76} = 0.45$, $p < 0.001$) methods. This finding suggests that the mean distance between successive captures may be used as an indicator of home range size for M. natalensis. There were no significant differences between the sexes for either the home range estimates nor for the mean distance between captures ($p > 0.05$).

The home range estimates reported here are similar to those reported by Leirs & Verheyen

(1995). Using the minimum convex polygon method, Leirs & Verheyen (1995) estimated the home range of 217 male M. natalensis to be 598 m^2 and that of 221 females to be 590 m^2. Results from radio-telemetry, however, indicated a home range approximately twice as large (Leirs et al. 1996), suggesting that home range estimates based on trapping data are underestimates. This, however, may not be the case as the reason for the larger estimates from telemetry data is due to the inclusion of long-distance excursions of short duration (Leirs et al. 1996) which may not be part of the home range (i.e. these excursions may be exploratory in nature, and not related to daily activities).

There appeared to be differences in home range size and mean distance between captures between the three grids (Table 2). The mean distance between captures was greater on the control grid than the experimental grids, while the home range of M. natalensis was smaller on the experimental grids than on the control, although none of these differences were statistically significant (two-way ANOVA, $p > 0.05$ for all three estimates). However, since the calculated mean values were very similar for the experimental grids, and since the estimates on the control were consistently higher (mean distance between captures) or lower (home range estimates), it is suggested that these differences are in fact biologically significant. Statistical significance may have been attained with larger sample sizes. Thus, it would appear that M. natalensis individuals travel shorter distances and cover smaller home ranges when food availability is high.

These data also have a bearing on territoriality in M. natalensis. Although home ranges are not the same as territories (Burt 1943), in territorial species one would expect little, if any, overlap between home ranges of neighbouring individuals. Although a spatial analysis is not presented here, the data presented here suggest that there is not great overlap between the home ranges of neighbouring *M. natalensis* in this study. For example, the mean home range (using the convex polygon method) of males from grid 1 was 600 m^2 and females was 659 m^2 suggesting that 17 male and 15 female *M. natalensis* would be able to survive on a 1 hectare grid without overlapping home ranges. Over the study period of 12 months, the numbers of *M. natalensis* caught per month rarely exceeded these figures (Monadjem & Perrin 1996; Monadjem & Perrin in preparation; Chapters 4 and 7), and never by more than two fold. These observations are in contrast to the findings of Leirs & Verheyen (1995) who provide strong evidence that *M. natalensis* does not exhibit territoriality. These seemingly contradictory findings may be explained by the fact that the numbers of *M. natalensis* on our study site was an order of magnitude lower than that on Leirs & Verheyen's (1995) site (the latter site was situated in fallow fields while ours was in natural grassland). It is possible that *M. natalensis* maintain non-overlapping home ranges at lower densities, with increasing overlap at increasing densities.

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Table 1 Home range estimates of Mastomys natalensis based on minimum convex polygon and harmonic mean methods. Also included are the mean distances between successive captures (MDSC). Data from all three grids have been included here. All values are mean ± standard error

	n	Convex polygon (m^2)	Harmonic mean (m^2)	MDSC (m)
Male	40	652.5 ± 82.6	818.7 ± 102.9	21.6 ± 1.4
Female	36	718.1 ± 88.2	911.9 ± 123.3	20.8 ± 1.3
Combined	76	683.6 ± 59.9	862.9 ± 79.3	21.2 ± 1.0

Table 2 Comparison of home range estimates of Mastomys natalensis, based on minimum convex polygon and harmonic mean methods, between two supplementary grids and the control. Also included are the mean distances between successive captures (MDSC). All values are mean ± standard error

	n	Convex polygon (m^2)	Harmonic mean (m^2)	MDSC (m)
Control				
male	6	900.0 ± 171.8	960.0 ± 139.9	27.6 ± 4.9
female	4	837.5 ± 352.0	937.3 ± 469.0	24.8 ± 3.0
Grid 1				
male	18	600.0 ± 135.8	831.0 ± 182.1	19.9 ± 1.7
female	17	658.8 ± 127.6	896.4 ± 185.5	20.9 ± 2.2
Grid 3				
male	16	618.8 ± 122.5	751.9 ± 148.1	21.3 ± 2.3
female	15	753.3 ± 133.8	922.8 ± 173.3	19.7 ± 1.7

CHAPTER 10*

POPULATION DYNAMICS OF *LEMNISCOMYS ROSALIA* (MURIDAE: RODENTIA) IN A SWAZILAND GRASSLAND: EFFECTS OF FOOD AND FIRE

*Monadjem, A. & Perrin, M.R. Accepted. *South African Journal of Zoology*

The effects of food supplementation on a population of *Lemniscomys rosalia* was experimentally studied 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 twelve 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.

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 *et al.* 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; Chapter 4). 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 Metereological 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" (ie. 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 percent 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.

Four seasons were recognized as follows: winter, June to August; spring, September to November; summer, December to February; and autumn, March to May.

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 (ie. 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 vaginae. 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 were 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 nonconstant 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 (ie. 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 percent cover, percent green grass and grass height between the grids and seasons (percent cover: F = 9.520, *d.f.* = 14,39, $p < 0.05$; percent 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 percent of the grass that was green peaked between December and March. After the fire (September), the burnt sections of grids 1 and 3 had loss 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, percent 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 *Crocidura hirta* (13 individuals).

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 body adult weight of *L. rosalia* was investigated by a two-way analysis of variance, and varied by sex and season. Males were significantly heavier than females (F = 28.984, *d.f.* = 1,160, $p < 0.05$), although males were heavier than females only outside the breeding season (Table 2). 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 due 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 heavier class representing the individuals born the previous summer (or before then) and the lighter 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. 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 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 percent of all *L. rosalia* survived one month, while sixteen percent 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 between 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, d.f. = 2,47, $p > 0.05$; Table 3). Mean distance between captures did not differ before and after food supplementation (F = 2.738, d.f. = 2,47, $p > 0.05$). 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 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 due to 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. Rodent home ranges often decrease in the presence of supplementary food (Taitt 1981; Boutin 1990; Sullivan 1990), presumably due 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; Chapter 4). 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 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 retrapped in unburnt areas in the month after the fire, while in the unburnt areas eight out of fourteen mice were retrapped over the same period. Thus, *L. rosalia* is able to escape the direct effects of fire, but does not remain in burnt areas. Due 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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Table 1 Vegetation characteristics of the experimental grids 1 and 3 and the control grid

	Grid 1						Control			Grid 3					
	Unburnt			Burnt						Unburnt			Burnt		
Month	Cover (%)	Height (cm)	Green (%)	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

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)

	Mean adult weight of *Lemniscomys rosalia* (g)	
Season	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

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

	Mean distance between captures (m)		
Period	Grid 1	Control	Grid 3
Jun.1995-Jul. 1995 (before supplementation)	27.4 ± 4.2 (7)	25.2 ± 5.1 (7)	18.3 ± 3.1 (3)
Aug. 1995-May 1996 (after supplementation)	26.4 ± 2.1 (13)	25.5 ± 3.1 (9)	34.9 ± 3.3 (11)

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

	Numbers caught					
	Grid 1			Grid 3		
	Unburnt	Burnt	χ^2	Unburnt	Burnt	χ^2
Jun. 1995-Sep. 1995*	17	24	1.195	7	16	3.522
Oct. 1995-Dec. 1995	28	6	14.236**	18	0.00	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.
**$P < 0.05$

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

	Percent survival								
Area	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)	-	-

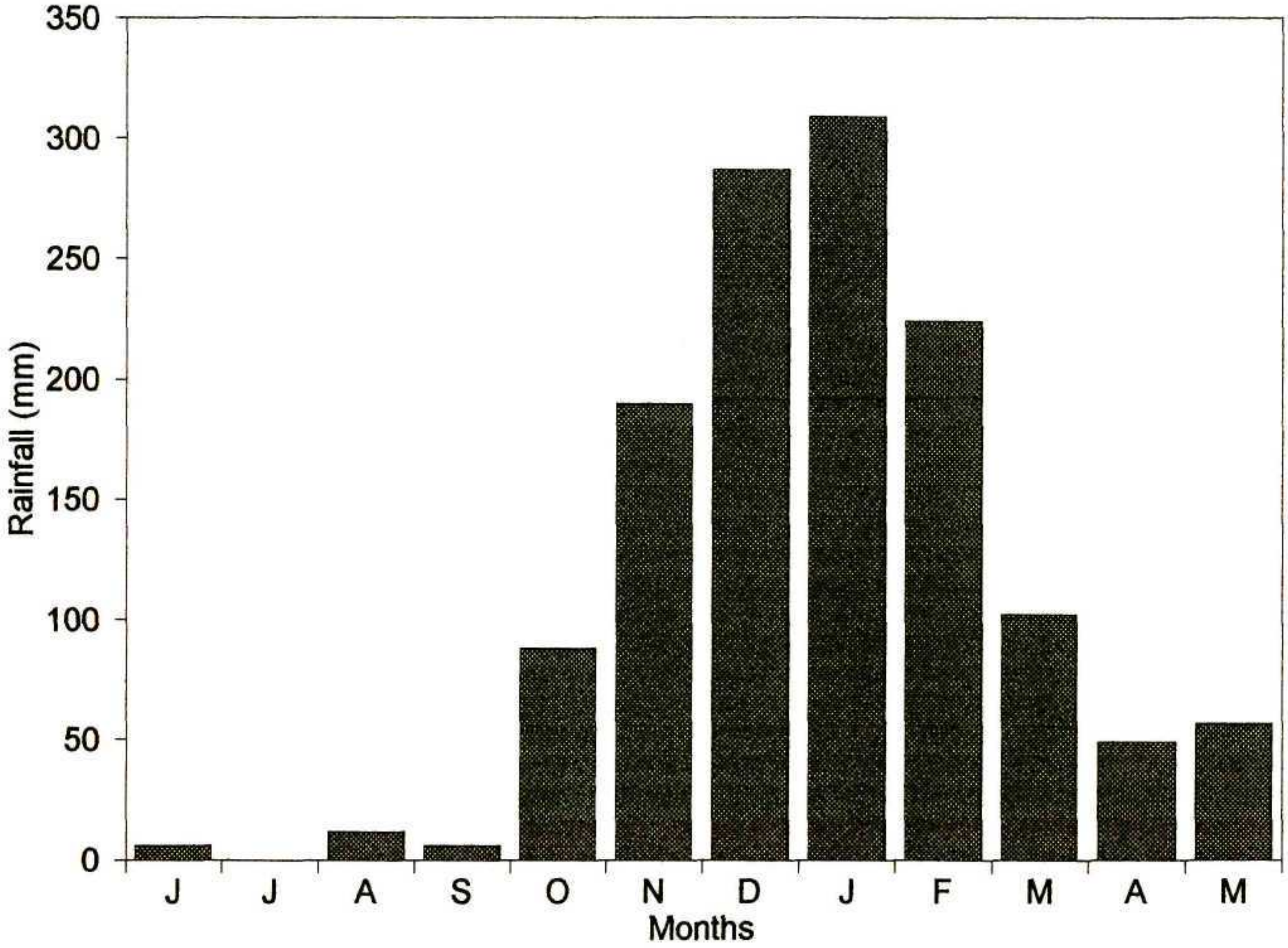

Figure 1 Total monthly rainfall at eKundizeni Farm, Swaziland from June 1995 to May 1996. Total rainfall for this period was 1329 mm.

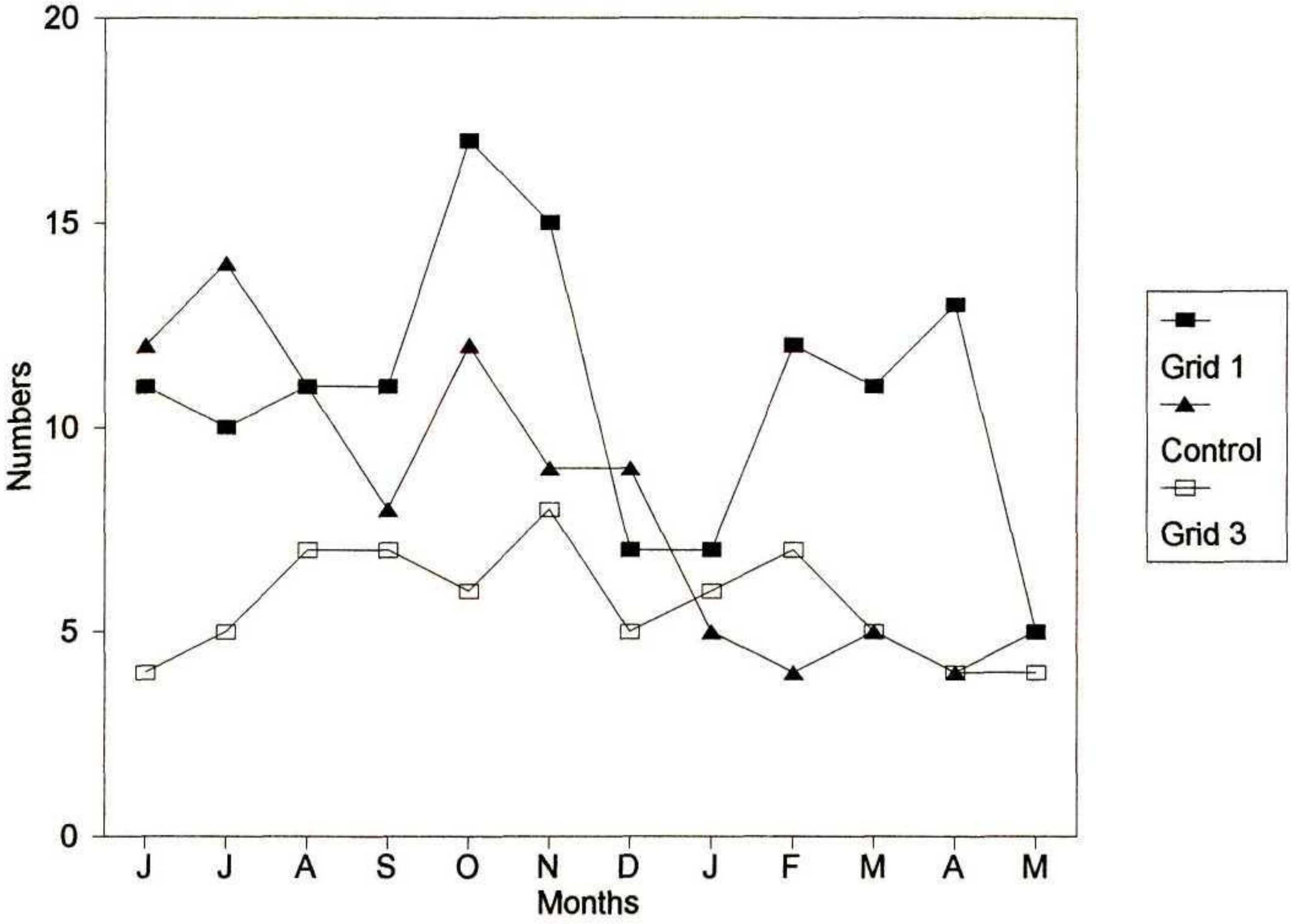

Figure 2 Minimum number of *Lemniscomys rosalia* alive on supplemented grids 1 and 3, and the control between June 1995 and May 1996.

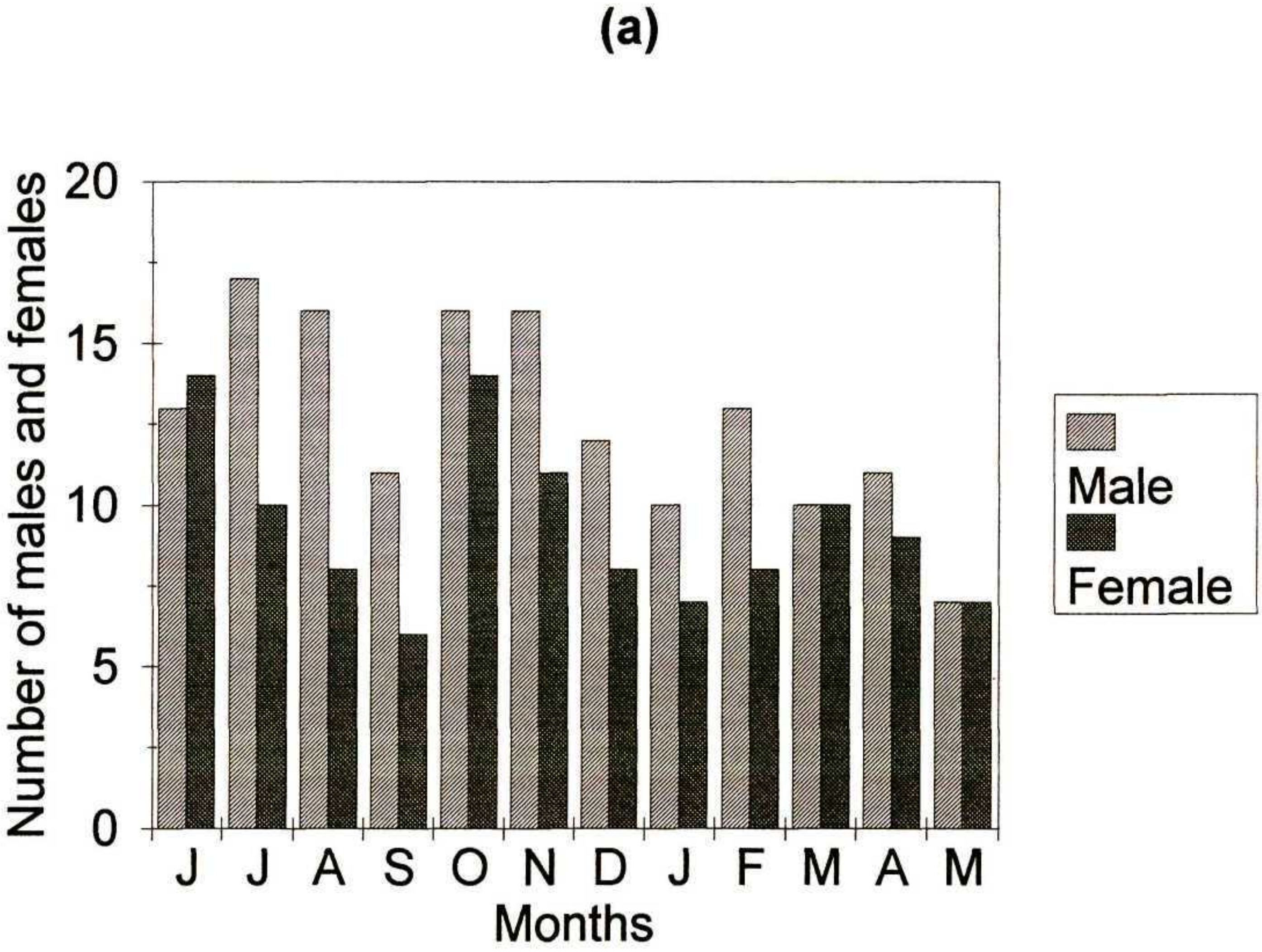

Figure 3 The number of: (a) males and females, (b) immigrants, and (c) juveniles, trapped on the three grids between June 1995 and May 1996.

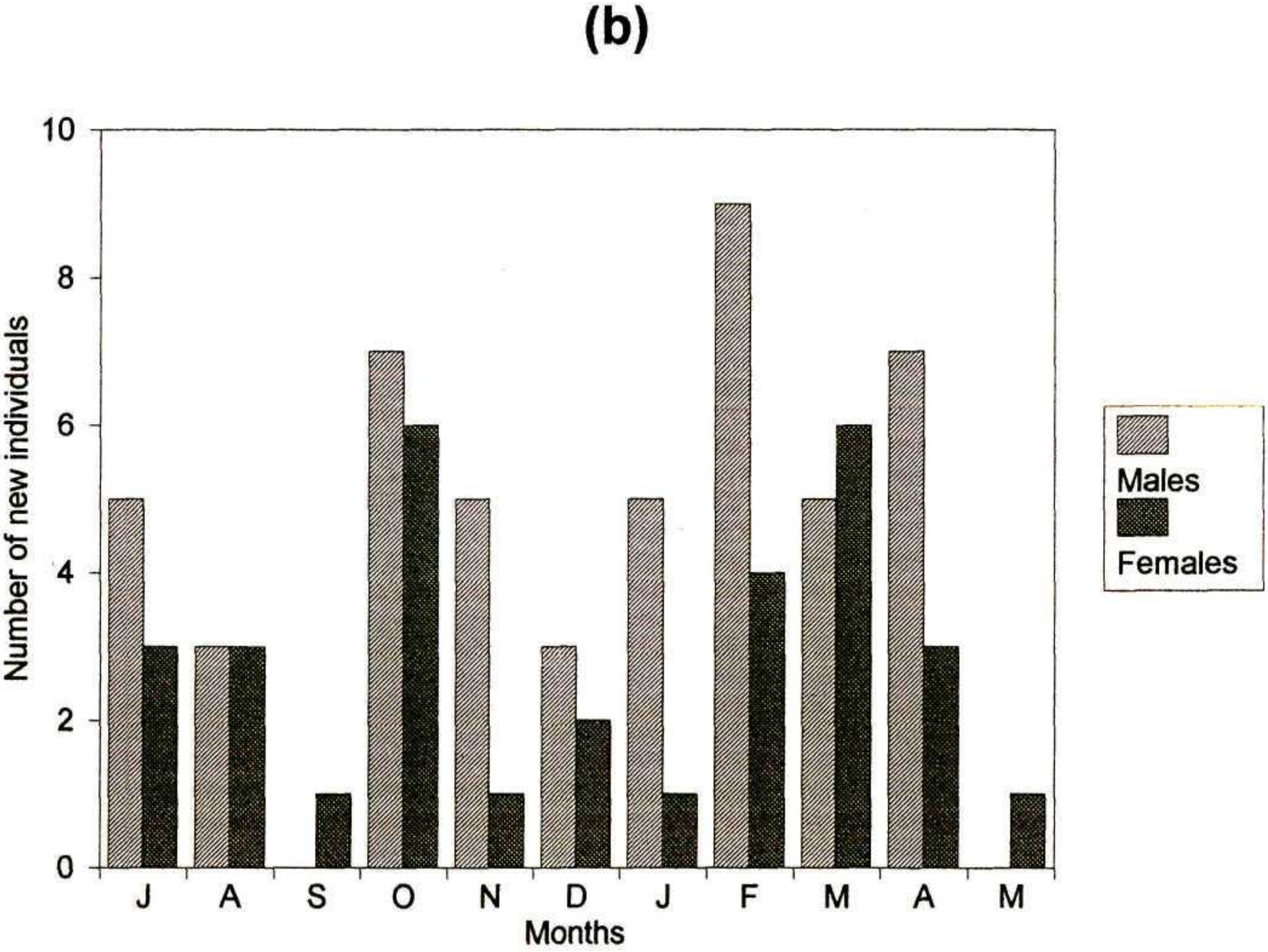

Figure 3 The number of: (a) males and females, (b) immigrants, and (c) juveniles, trapped on the three grids between June 1995 and May 1996.

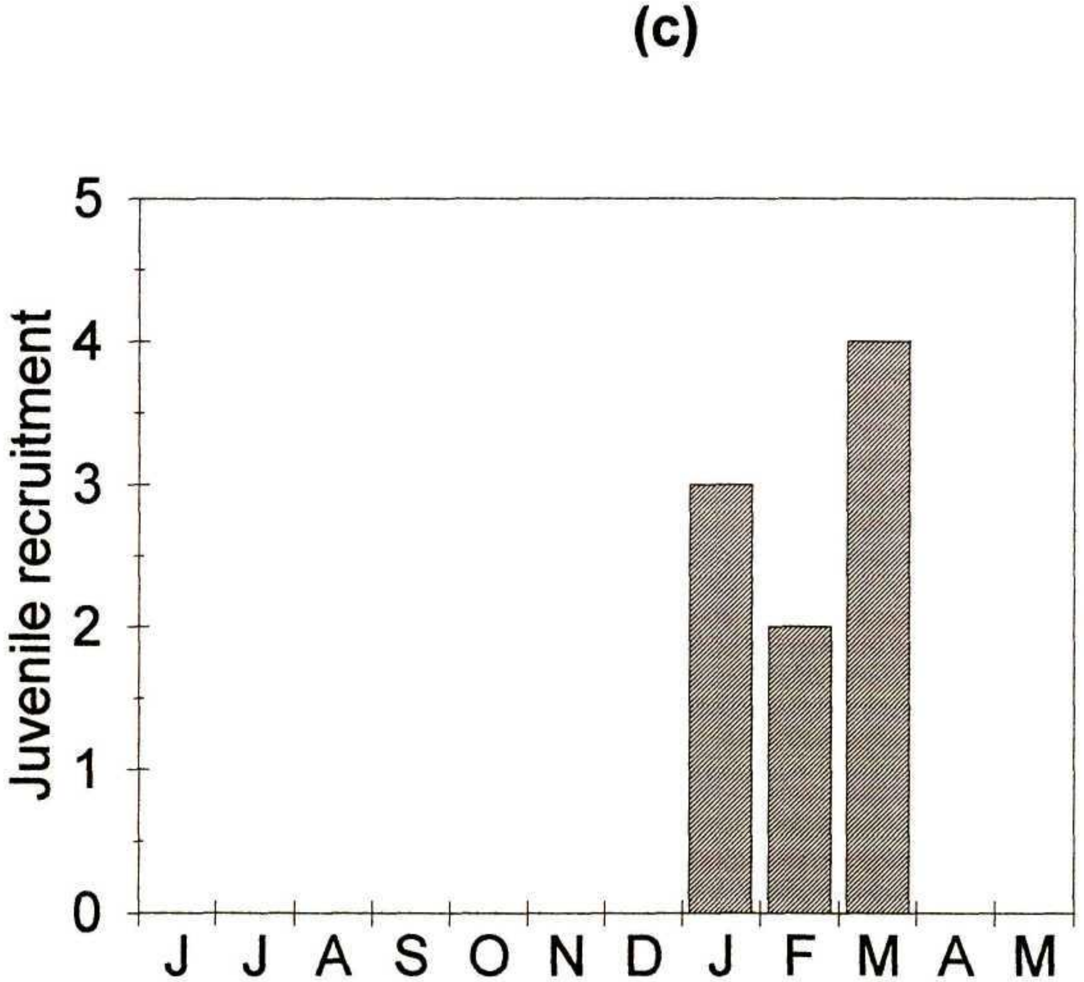

Figure 3 The number of: (a) males and females, (b) immigrants, and (c) juveniles, trapped on the three grids between June 1995 and May 1996.

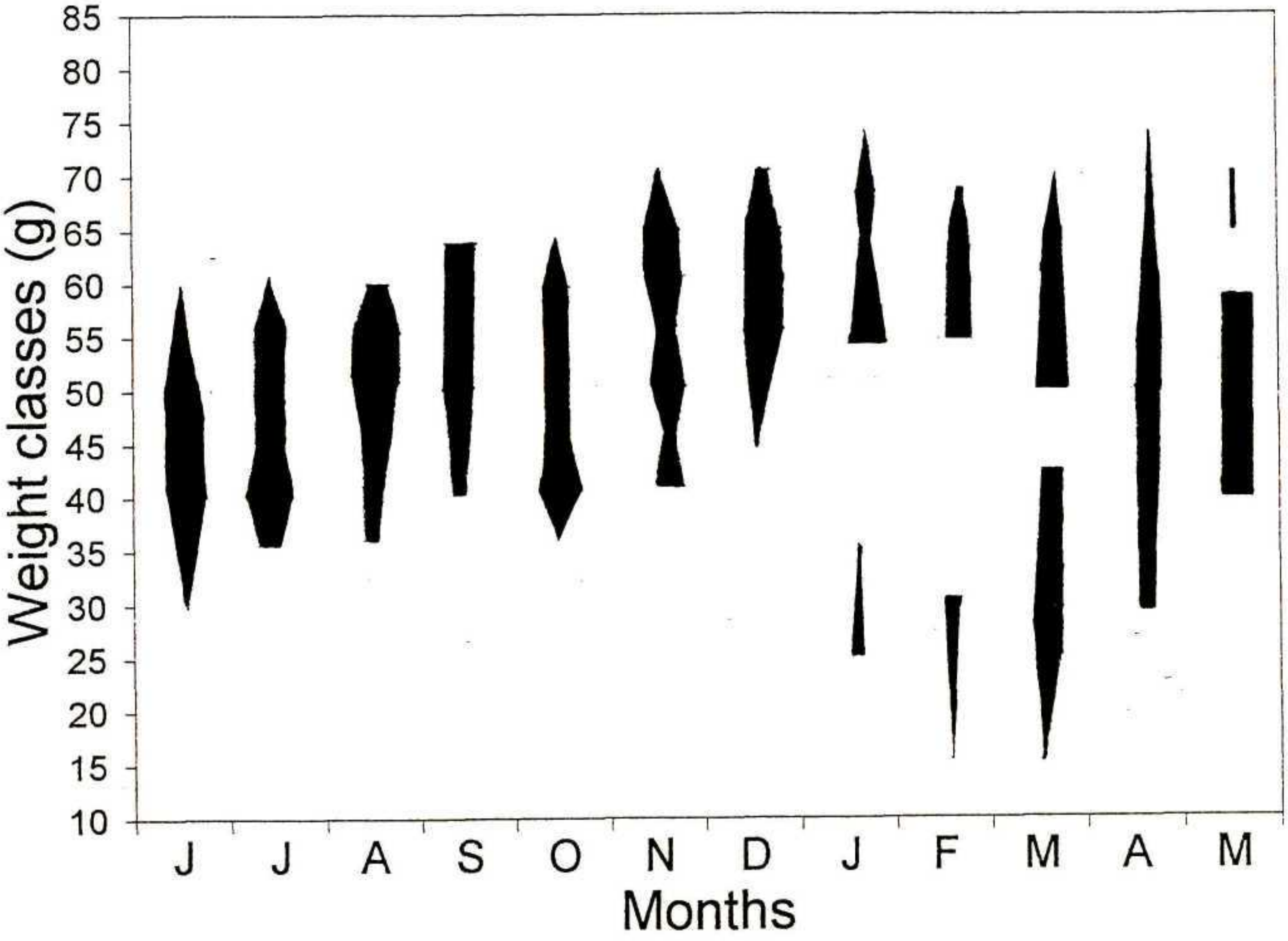

Figure 4 The monthly age structure of *Lemniscomys rosalia* captured between June 1995 and May 1996.

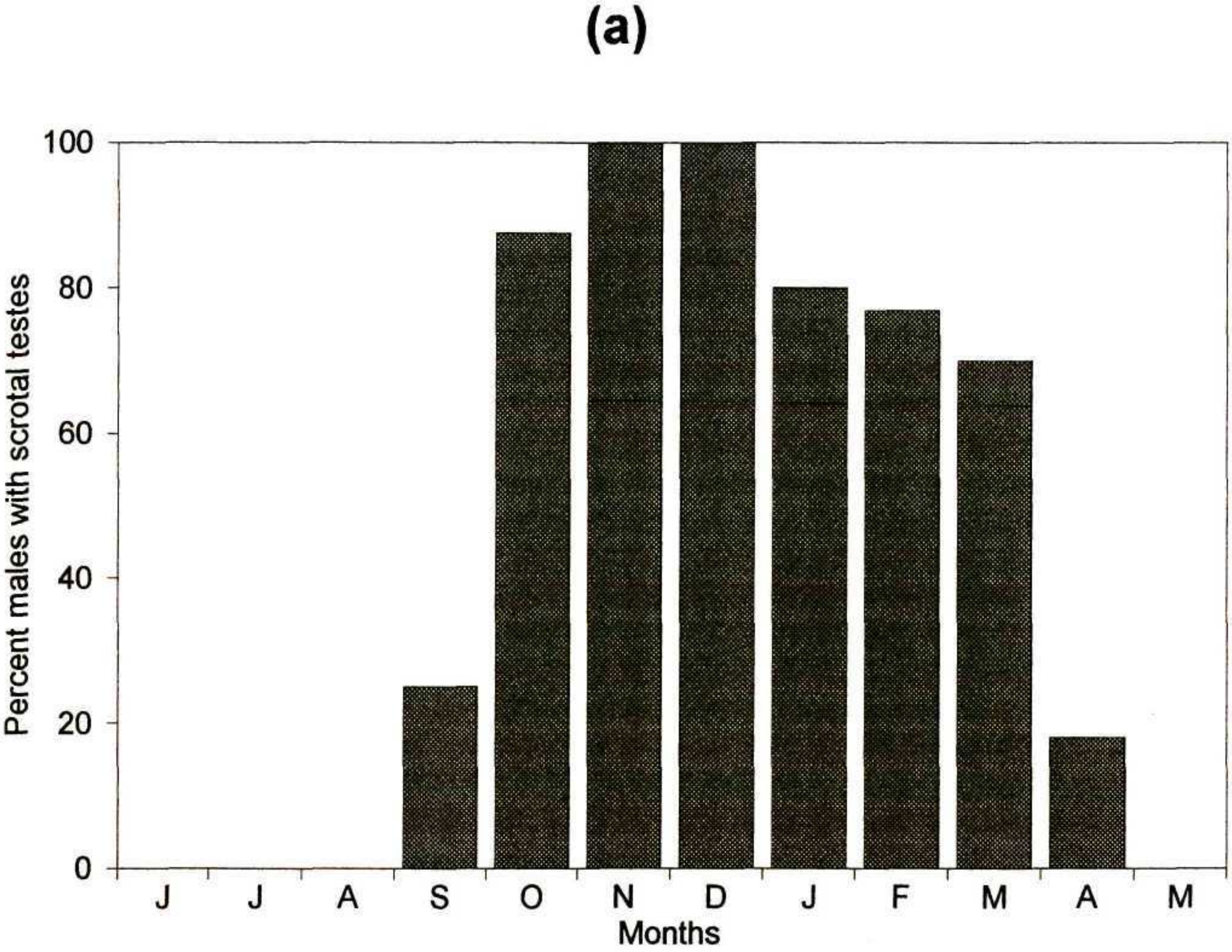

Figure 5 The proportions of: (a) adult males with scrotal testes, and (b) adult females with perforate vaginae, trapped between June 1995 and May 1996 on the three grids.

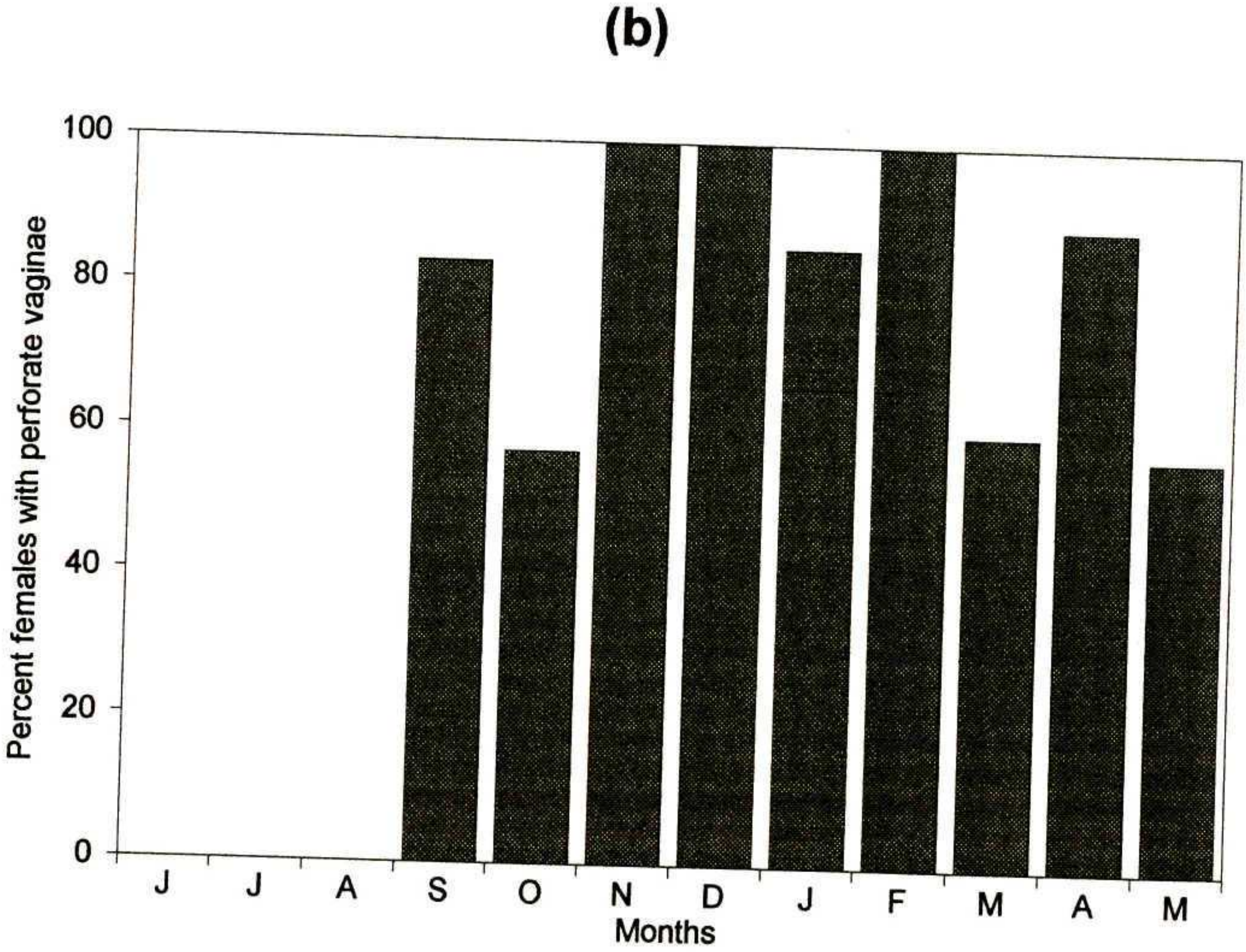

Figure 5 The proportions of: (a) adult males with scrotal testes, and (b) adult females with perforate vaginae, trapped between June 1995 and May 1996 on the three grids.

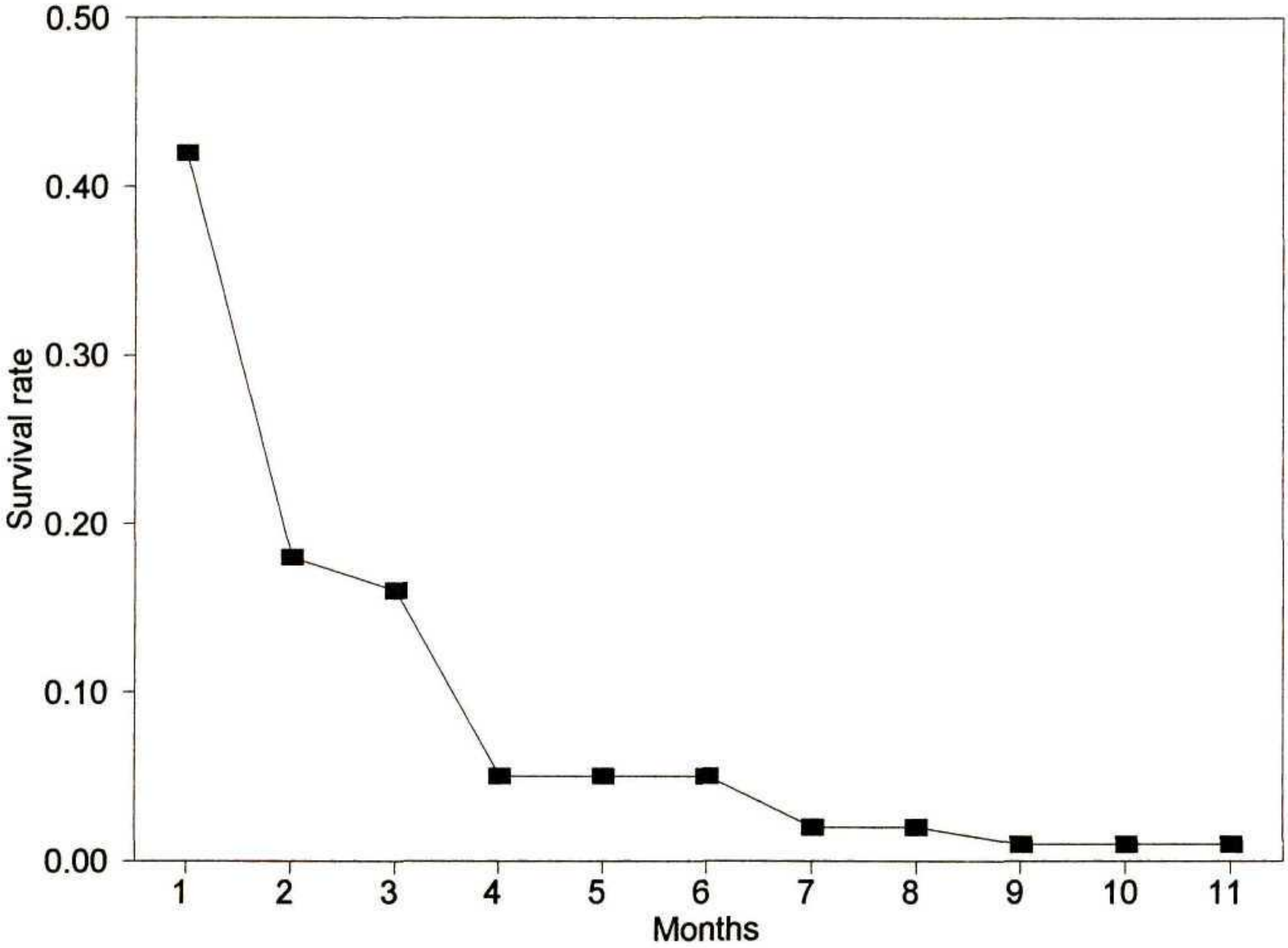

Figure 6 Survival rates of *Lemniscomys rosalia* on the three grids over an eleven month period.

CHAPTER 11*

POPULATION DYNAMICS OF *MUS MINUTOIDES* AND *STEATOMYS PRATENSIS* (MURIDAE: RODENTIA) IN A SUBTROPICAL GRASSLAND IN SWAZILAND

*Monadjem, A. Slightly modified version accepted. *African Journal of Ecology*

Summary

The population dynamics of *Mus minutoides* and *Steatomys pratensis* are virtually unknown. These two species were live-trapped over a twelve month period in a subtropical grassland in Swaziland. Numbers of *M. minutoides* were relatively high in winter, declined in spring and the population disappeared in summer and autumn. In contrast, numbers of *S. pratensis* increased gradually from winter to summer and reached a peak in autumn. There were no differences between the mean weights of male and female *M. minutoides* and *S. pratensis.* There were, however, seasonal differences in the mean weight of male *S. pratensis,* with highest weights recorded in summer. Individuals of both species came into breeding condition in spring (October-November). Reproduction had ceased by the end of autumn (April-May). Monthly survival rates of *M. minutoides* were highest in winter, but did not vary seasonally in *S. pratensis*. Burning had a pronounced effect on the distribution of *S. pratensis*. *Steatomys pratensis* individuals selected recently burnt but revegetated areas over unburnt areas. The effect of burning on the *M. minutoides* population is difficult to assess as this species disappeared shortly after the fire.

Key words: *Mus minutoides*, *Steatomys pratensis*, population dynamics, reproduction, Swaziland

Introduction

Mus minutoides A. Smith and *Steatomys pratensis* Peters are common murid rodents occurring widely in southern and east Africa (Skinner & Smithers, 1990). The thermal biologies of these two species are well known (Richardson & Perrin, 1992; Ellison, 1995; Webb & Skinner, 1995; Downs & Perrin, 1996); however, they have received little attention from ecologists, and very little is known about their population and breeding biologies under natural conditions.

Mus minutoides is the smallest southern African rodent (De Graaff, 1981) with a mass of 6-8 g. The breeding biology of *M. minutoides* has been studied in captivity (Willan & Meester, 1978), but only anecdotal information is available on its breeding cycle in the wild (Delany, 1986; Skinner & Smithers, 1990). Information on the population dynamics of *M. minutoides* comes from a few general small mammal studies, in which very small numbers of *M. minutoides* were caught (Cheeseman & Delany, 1979; Kern, 1981; Sheppe & Haas, 1981). In northern Botswana *M. minutoides* appears to breed seasonally (Sheppe & Haas, 1981), although in KwaZulu-Natal (South Africa) it has also been suggested that it breeds throughout the year (Rowe-Rowe & Meester, 1982a).

Adult *S. pratensis* weigh approximately 26-40 g (De Graaff, 1981). *Steatomys pratensis* excavate their own burrows (De Graaff & Nel, 1992), display torpor in cold conditions

(Richardson & Perrin, 1992; Ellison, 1995) and survive up to 3 years in captivity (Hanney, 1965). In captivity *S. pratensis* is a seasonal breeder (Richardson & Perrin, 1992).

Mus minutoides is widespread and common in Swaziland (Monadjem, 1997a). A study of *M. minutoides* in Swaziland's eastern lowveld savanna showed its population to be relatively high and seasonally stable (Monadjem, in press a). *Steatomys pratensis*, in contrast, has a more restricted distribution in Swaziland (Monadjem, 1997a,b). This study was initiated to ascertain the effects of supplementary food on small mammal populations (Monadjem & Perrin, 1996; Chapter 4). During the course of this study, relatively large numbers of *M. minutoides* and *S. Pratensis* were captured. This paper was published mainly due to the paucity of information available on the population dynamics of these two species.

Study area and methods

Study area

Three permanently marked grids (100 m × 100 m) were established in an unutilized 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 three grids, 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 grids. *Hyparrhenia hirta* (L.) was the dominant grass species on all grids. The only other common grass species was *Hyperthelia dissoluta* (Nees) which was abundant on the control grid and present on grid 1. No trees were present on or near any of the three grids, while a very few *Lippia javanica* (Burm.f.) shrubs (up to 1.5 m tall) occurred irregularly on each grid. 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. This estimate presented few problems since the grass was generally thick and a "canopy" was usually obvious. 4) Finally, the percent 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 (ie. 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 days 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 vaginae.

The number of individuals on each grid were estimated using the minimum number known alive method (MNA: Krebs, 1966). Differences between the three grids were tested using analysis of variance ANOVA (Zar, 1984). Home ranges were estimated by the mean distance between successive captures method (Davis 1953). Only those individuals that were caught four or more times in non-peripheral traps were included in the latter analysis. Unless specified, all means are presented ± standard deviations. Where data are presented by season, the following four seasons were distinguished: winter, June to August; spring, September to November; summer, December to February; and autumn, March to May.

Supplementary feeding

The control grid 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 grid (grid 1) from July (immediately after sampling the rodent population) until May, and also to the second experimental grid (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. 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 (ie. grid 1 received 4 kg of supplementary food twice a month, totaling 8 kg of food per month).

Results

Rain and habitat variables

Recorded monthly rainfall during this study is shown in Fig. 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. 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 percent 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 growths of grass, however, were completely green. By December there was little visual difference between the burnt and unburnt areas.

During this study 75 *M. minutoides* and 43 *S. pratensis* were captured 155 and 115 times, respectively. Other rodent species caught in the study area were *Mastomys natalensis* (Smith) (310 individuals), *Lemniscomys rosalia* (Thomas) (108 individuals), *Dendromus mystacalis* (Heuglin) (12 individuals), *Aethomys chrysophilus* (de Winton) (8 individuals), *Otomys angoniensis* Thomas (1 individual), and the insectivore *Crocidura hirta* Peters (13 individuals).

Effect of supplementary food

No significant differences were observed between the populations of *M. minutoides* on the three grids and thus data were combined for all grids for subsequent analyses. The results for *S. pratensis* are not so clear. Very few *S. pratensis* were captured on the control grid compared to the experimental grids 1 and 3 (Fig. 2). This, however, was probably due to the effects of fire (see below) rather than supplementary food. Thus data were also combined for *S. pratensis* caught on all grids.

Population dynamics

There were no significant deviations from parity in the sex ratios of either *M. minutoides* (30 males, 45 females; chi-square test, $P>0.05$) or *S. pratensis* (23 males, 20 females; chi-square test, $P>0.05$).

Mus minutoides was present on the grids only between June and November, with single individuals being caught in December, March and May (Fig. 3). *Mus minutoides* did not disappear from the grids suddenly, rather numbers decreased gradually from September until January (when none were left).

Although fewer *S. pratensis* were caught than *M. minutoides*, the former species was present in every month of the year (Fig. 2). There were, however, significant seasonal differences in abundance of *S. pratensis* (Table 2; $\chi^2 = 8.518$, df = 3, $P<0.05$). Numbers were highest after the rains in autumn, and lowest in winter. The number of immigrants entering the population also varied seasonally (Table 2; $\chi^2 = 7.694$, df = 3, $P<0.1$). The number of immigrants were highest in autumn, and were proportionally high in winter. Immigrants which entered the population in winter were probably individuals emerging from spells of torpor, while those caught in autumn probably represented juvenile recruitment. Obvious juveniles were, however, not caught during this study, and hence juveniles (born in the same season) could not be differentiated from subadults born in the previous breeding season.

Breeding

Both species displayed periods of sexual inactivity. *Mus minutoides* males had scrotal testes, and females had perforate vaginae, in October and November. The data for this species, however, are incomplete since only two individuals were caught in the rainy season between

December and March. The single female caught in March had a perforate vagina and was obviously pregnant.

Steatomys pratensis males had scrotal testes between October and May, while females had perforate vaginae between November and March (Fig. 4). All individuals of both sexes, with the exception of one female, caught between November and February were in breeding condition. Thus peak breeding coincided with the rains (see Fig. 1). Lactating females were caught in January and March, while the only pregnant individual was caught in March.

Body weight

The mean body weight of male *M. minutoides* (5.8 ± 0.86 g) was not significantly different from that of females (6.0 ± 1.16 g; t-test, $P>0.05$). There were no significant seasonal changes in body weight between June and November (the period in which *M. minutoides* was caught). Similarly, there was no difference between mean body weights of male (28.3 ± 1.39 g) and female (28.5 ± 1.39 g) *S. pratensis* (t-test, $P>0.05$). There were, however, significant seasonal differences in the mean body weight of *S. pratensis* (Fig. 5; $F = 2.935$, $df = 3, 37$, $P<0.05$). Only the body weights of males were used for the seasonal comparison due to the biasing effect of undetected pregnant females in the sample. The Tukey multiple comparison test was able to detect a significant difference in the summer mean body weights of *S. pratensis*. Hence, males were significantly heavier during summer (rainy season) than at other times of the year.

Survival

Mean monthly survival ranged from 1 (all individuals captured in one month were recaptured the following month) to 0 for *S. pratensis*, and from 0.7 to 0 for *M. minutoides.* Table 3 shows mean monthly survival averaged over the four seasons. For *M. minutoides* mean monthly survival rates were twice as high in winter as in spring, and this difference approaches significance ($\chi^2 = 3.394$, df = 1, $P<0.1$). For *S. pratensis* mean monthly survival rates were higher in winter, although this difference was not significant ($P>0.05$).

Home range movements

There were no significant differences in mean distance between captures of male and female *M. minutoides* or *S. pratensis* (Table 4; t-test, $P>0.05$ in both cases). Mean distance between captures of *S. pratensis* (36.1 ± 14.9 m) was significantly greater than that of *M. minutoides* (18.6 ± 9.0 m; t = 3.60, df = 25, $P<0.05$).

Effect of fire

The unscheduled fire burnt exactly half of the two experimental grids 1 and 3, and thus provided the opportunity to study its effects on small mammal populations. The effect of fire on *M. minutoides* cannot be easily gauged from this study since this species disappeared from the study area shortly after the fire. In the three months following the fire five individuals were caught in unburnt sections of grids 1 and 3, and five individuals were caught in the burnt sections. Although this sample is too small for statistical analysis, it does suggest that *M. minutoides* distribution is not influenced by fire. One individual caught immediately prior to the fire was recaptured the following month (after the fire) at the same trap location in the burnt section of the grid. Thus at least some *M. minutoides* are able to survive the direct effects of burning.

In contrast, the fire did appear to have a measurable influence on *S. pratensis*. Prior to the fire, four individuals were captured in the to-be-burnt areas, and five individuals in the not-to-be-burnt areas. In the three months after the fire, nine individuals were captured in the unburnt areas compared with five in the burnt areas. This difference is not significant (Table 5; chi-square test, $P>0.05$). However, in the period January to May (four to eight months after the fire) more individuals were captured on the burnt areas ($n = 24$) than on the unburnt areas ($n = 3$; $\chi^2 = 16.333$, $df = 1$, $P<0.05$). *Steatomys pratensis* thus appeared to select recently burnt areas where grass cover had recovered (see Table 1).

Discussion

The population densities of *M. minutoides* and *S. pratensis* showed seasonal variation, but in opposite directions. *Mus minutoides* was captured in relatively large numbers in winter; its numbers gradually decreased (as did its survival) in spring and almost completely disappeared in summer and autumn. There are no apparent reasons for the disappearance of *M. minutoides* in summer and autumn. *Mus minutoides* population densities are usually reported as being very low eg. 1-2 individuals/ha/month in Uganda (Cheeseman & Delany, 1979), and less than 1 individual/ha/month in the Kruger National Park (Kern, 1981) and the Drakensberg (Rowe-Rowe & Meester, 1982b) of South Africa. Nel (1978) also reported capturing *M. minutoides* from the arid Kalahari Gemsbok National Park in South Africa at relatively low densities, but did not give estimates as individuals/ha/month. In contrast, Monadjem (in press a) reported capturing between 15 and 28 individuals/ha/month in four different seasons at Mlawula Nature Reserve in the eastern lowveld of Swaziland. There is no doubt that the numbers of *M. minutoides* have been underestimated in some studies. Due to the small size of *M. minutoides* (usually weighing less than 7 g) it may be unable to trigger the trap mechanism of some traps.

In line with the findings of this study, most studies have not captured *M. minutoides* on each sampling session. For example, only one individual was caught between November and April in Uganda (Cheeseman & Delany, 1979). In the Kalahari, *M. minutoides* was captured in six out of eleven sampling sessions (Nel, 1978), and in an arid savanna in Mozambique in only one out of four seasons (Gliwicz, 1985). In the Kruger National Park, *M. minutoides* was not captured on every trapping occasion (Kern, 1981). However, Monadjem (in press a) caught *M. minutoides* in every trapping session at Mlawula Nature Reserve and did not observe any changes in its numbers over a one year period.

A number of speculations can be put forward to explain these irregular fluctuations in the numbers of *M. minutoides* in this study. Interference competition from a larger, more aggressive species could possibly exclude *M. minutoides* from traps. This is an unlikely explanation for the present study since *M. minutoides* numbers were greatest when the numerically dominant *M. natalensis* was most numerous (Monadjem, in preparation; Chapter 7). Furthermore, rodent numbers were generally low in spring and summer, during which time virtually no *M. minutoides* were captured. A second explanation is that the *M. minutoides* population was responding to changes in the vegetation. Kern (1981) reported increases in *M. minutoides* numbers following a burn, and did not capture any individuals on the unburnt control grid. This explanation again does not hold for this study since half of both experimental grids were burnt as was large portions of grassland adjoining the study area. Numbers should thus have increased on the burnt areas. It is also possible that *M. minutoides* did not disappear from the study area but simply stopped visiting traps in summer months when natural food (in the form of seeds and insects) would have been abundant. At present this reason cannot be rejected. However, Wirminghaus (1989), who collected monthly samples of regurgitated barn owl (*Tyto alba*) pellets, recorded 73 *M. minutoides* skulls between July and September, but just a single skull between October and June. It is likely that *M. minutoides* numbers do actually fluctuate largely, but the causal factors remain enigmatic.

In contrast to *M. minutoides, S. pratensis* numbers were lowest in winter and gradually increased to a maximum in autumn. *Steatomys pratensis* is known to go into torpor when ambient temperature drops below 20°C (Hanney, 1965; Richardson & Perrin, 1992), the length and depth of which is increased below 15°C (Ellison, 1995). This has been used to account for the low numbers caught in the cool dry season (Sheppe & Haas, 1981). In the present study, fewer *S. pratensis* were caught during the winter months which may have been due to the animals going into torpor on the cooler winter days.

Steatomys pratensis showed a strong preference for recently burnt grassland where regrowth of the vegetation had occurred. Thus *S. pratensis* was absent from burnt areas of the grids for the first three months after the fire when the grass cover was sparse. By the fourth month both grass height and cover had recovered to former levels, and *S. pratensis* selected these areas almost exclusively. Kern (1981) observed similar trends in the Kruger National Park. *S. pratensis* populations were highest in areas burnt every three years, and were absent from grids immediately following a burn. Burning, however, does not appear to directly kill *S. pratensis* as marked individuals were caught in burnt areas after a fire in both this study and in Kern's (1981). *Steatomys pratensis* is a burrower (De Graaff & Nel, 1992) and may escape the fire by retreating into its burrow.

In this study, *S. pratensis* in reproductive condition were captured between October and May with a peak between November and March. Kern (1977 in Skinner & Smithers, 1990) captured reproductive individuals between December and March in the Kruger National Park. In the mammal surveys of Botswana and Zimbabwe lactating or gravid females were captured between October and April and September and May respectively (Smithers, 1971; Smithers & Wilson, 1979). Rautenbach (1982) captured a lactating female in the former Transvaal province of South Africa in February. *Steatomys pratensis* is clearly a seasonal breeder in southern Africa, breeding in the warm wet summer months.

Hanney (1965) suggested, based on a captive specimen, that the normal longevity of *S. pratensis* is several years. In this study, however, the longest time interval between first and last capture was only four months (five months for *M. minutoides*). In addition, monthly survival was not very high. Individuals of both *Mastomys natalensis* and *Lemniscomys rosalia* were recaptured after 11 months (Monadjem & Perrin, in press; Monadjem, in preparation; Chapters

7 and 10). This observation, however, may have been due to the small numbers of *S. pratensis* captured. A larger sample is required to establish the survival rates of *S. pratensis*.

Acknowledgment

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Table 1. Vegetation characteristics of the experimental grids 1 and 3 and the control grid between September 1995 and May 1996

	Grid 1						Control			Grid 3					
	Unburnt			Burnt						Unburnt			Burnt		
Month	Cover index	Height	Green (%)	Cover index	Height	Green (%)	Cover index	Height	Green (%)	Cover index	Height	Green (%)	Cover index	Height	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

Table 2. Number of immigrants and total number of individuals of *Steatomys pratensis* caught in winter (June-August), spring (September-November), summer (December-February) and autumn (March-May)

Season	Number of immigrants	Total number of individuals
Winter	6	11
Spring	8	19
Summer	11	24
Autumn	18	29

Table 3. Mean monthly survival averaged over the four seasons (see Table 2 for season definitions) for *Mus minutoides* and *Steatomys pratensis*. Sample sizes are given in parentheses

Season	*M. minutoides*	*S. pratensis*
Winter	0.47 (87)	0.73 (11)
Spring	0.24 (34)	0.58 (19)
Summer	-	0.45 (24)
Autumn	-	0.45 (20)

Table 4. Mean (± standard error) distance between successive captures of male and female *Steatomys pratensis* and *Mus minutoides*. Sample sizes are given in parentheses

	Mus minutoides	*Steatomys pratensis*
Males	15.7 ± 2.4 (9)	34.1 ± 4.6 (10)
Females	25.0 ± 4.7 (4)	41.3 ± 7.4 (4)
Sexes combined	18.6 ± 2.5 (13)	36.1 ± 4.0 (14)

Table 5. Number of *Steatomys pratensis* individuals caught in the four months before the fire (June-September), between one and three months (October-December), and four and eight months (January-May) after the fire, on burnt and unburnt sections of experimental grids 1 and 3

	Number of individuals captured	
Period	Burnt	Unburnt
June-September	4	5
October-December	5	9
January-May	24	3

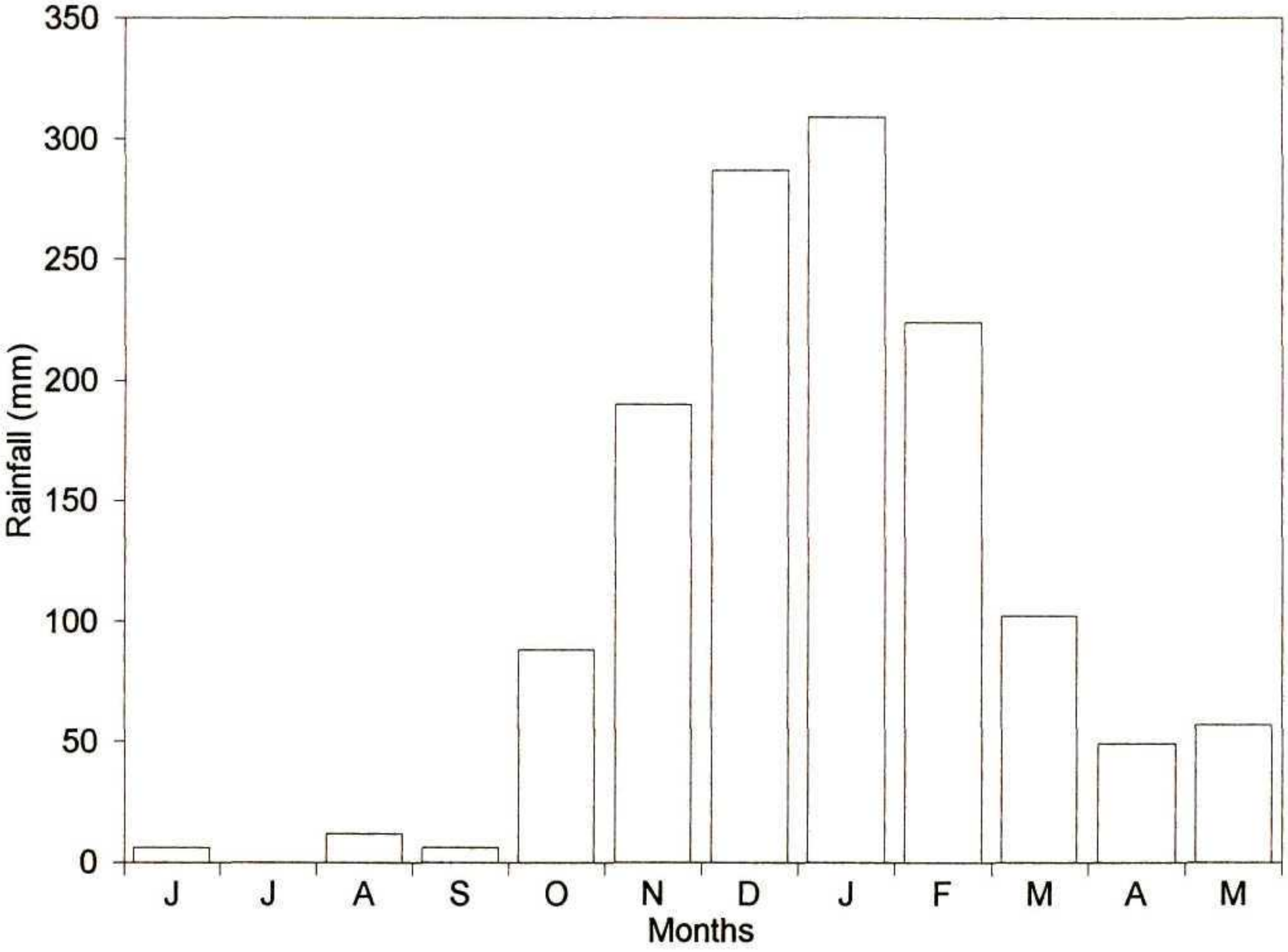

Fig. 1. Total monthly rainfall at eKundizeni Farm, Swaziland from June 1995 to May 1996.

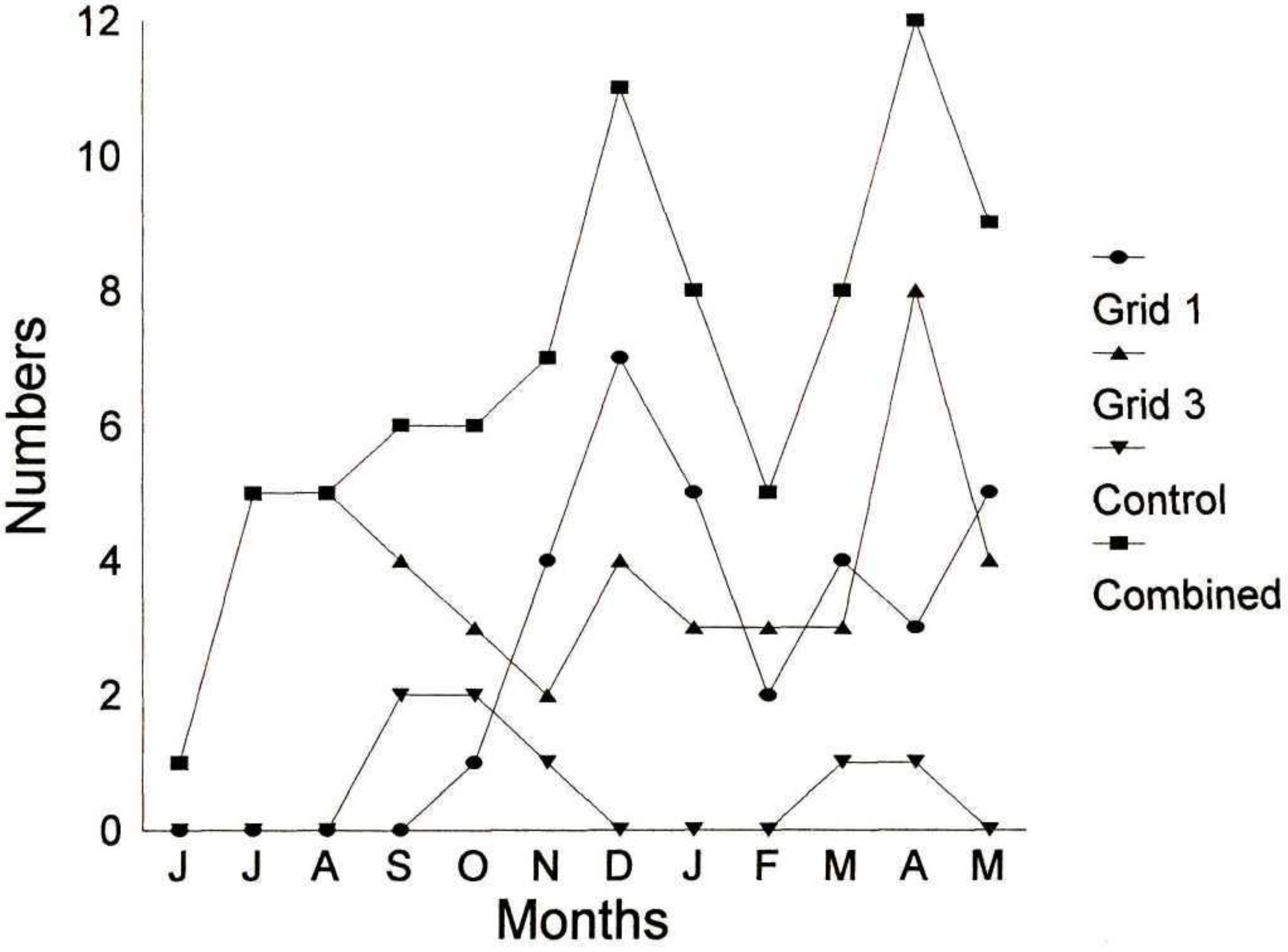

Fig. 2. Minimum number of *Steatomys pratensis* alive on the three grids separately and combined between June 1995 and May 1996.

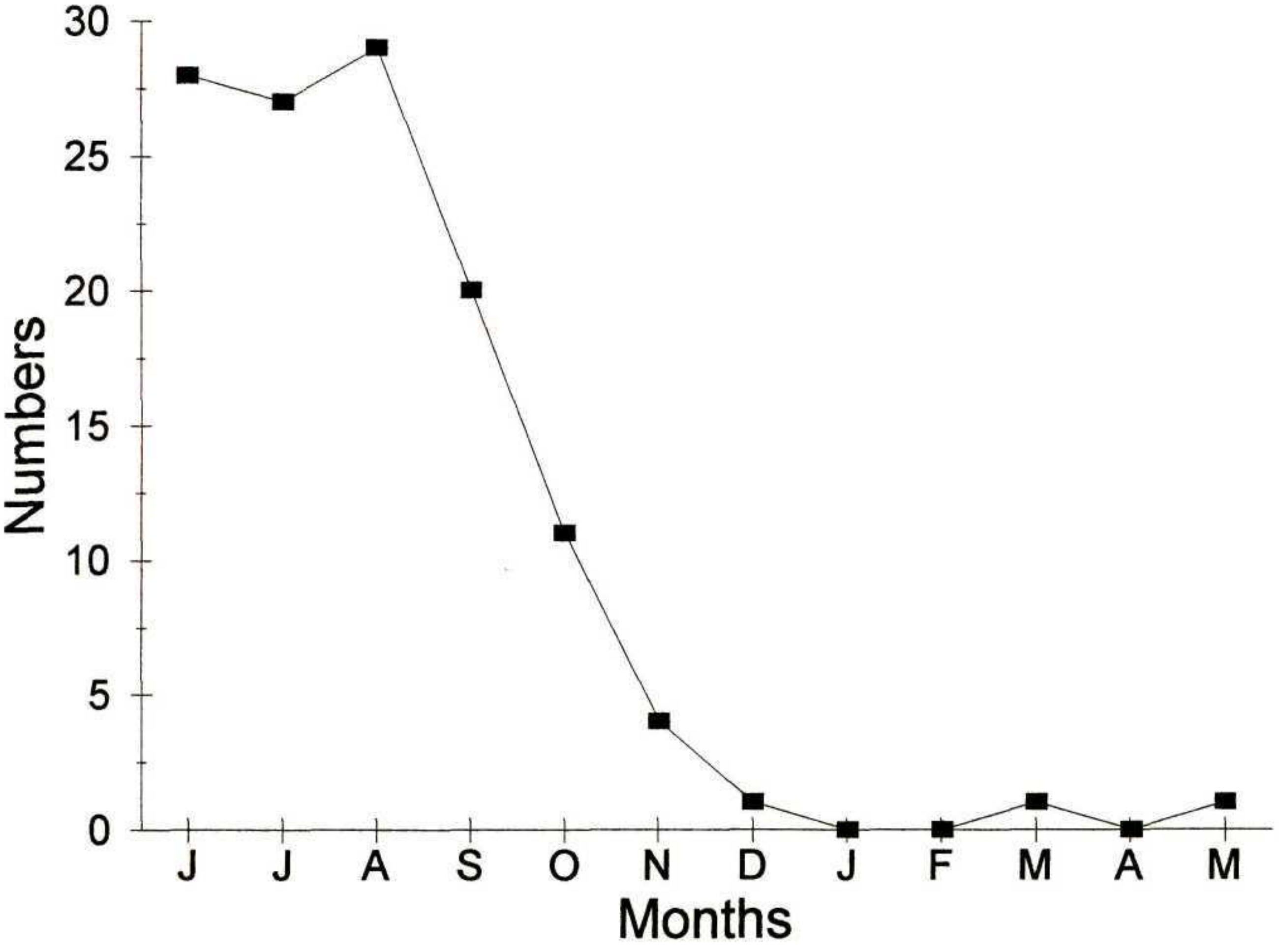

Fig. 3. Minimum number of *Mus minutoides* alive on the three grids combined between June 1995 and May 1996.

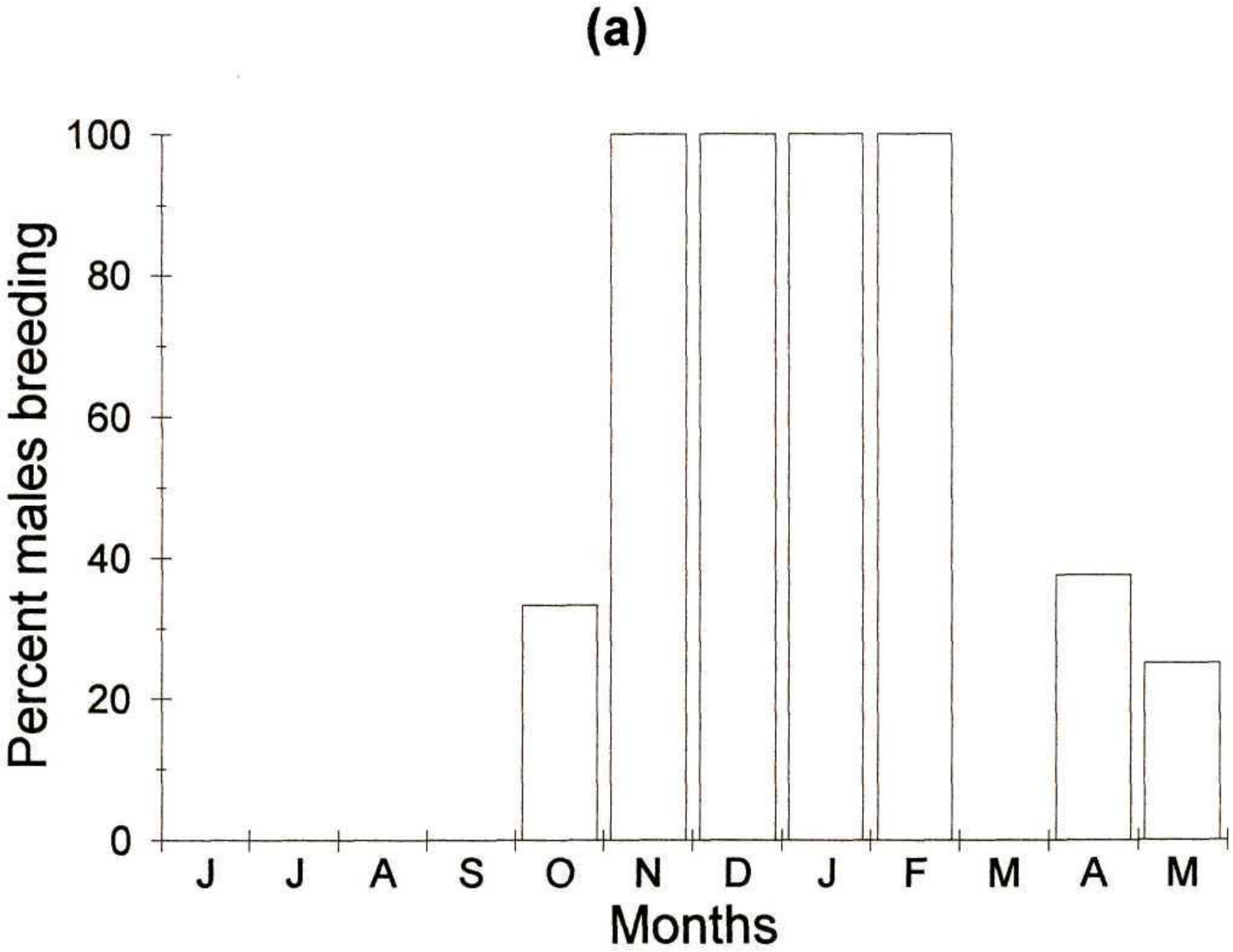

Fig. 4. The proportions of : (a) adult male *Steatomys pratensis* with scrotal testes, and (b) females with perforate vaginae, trapped between June 1995 and May 1996.

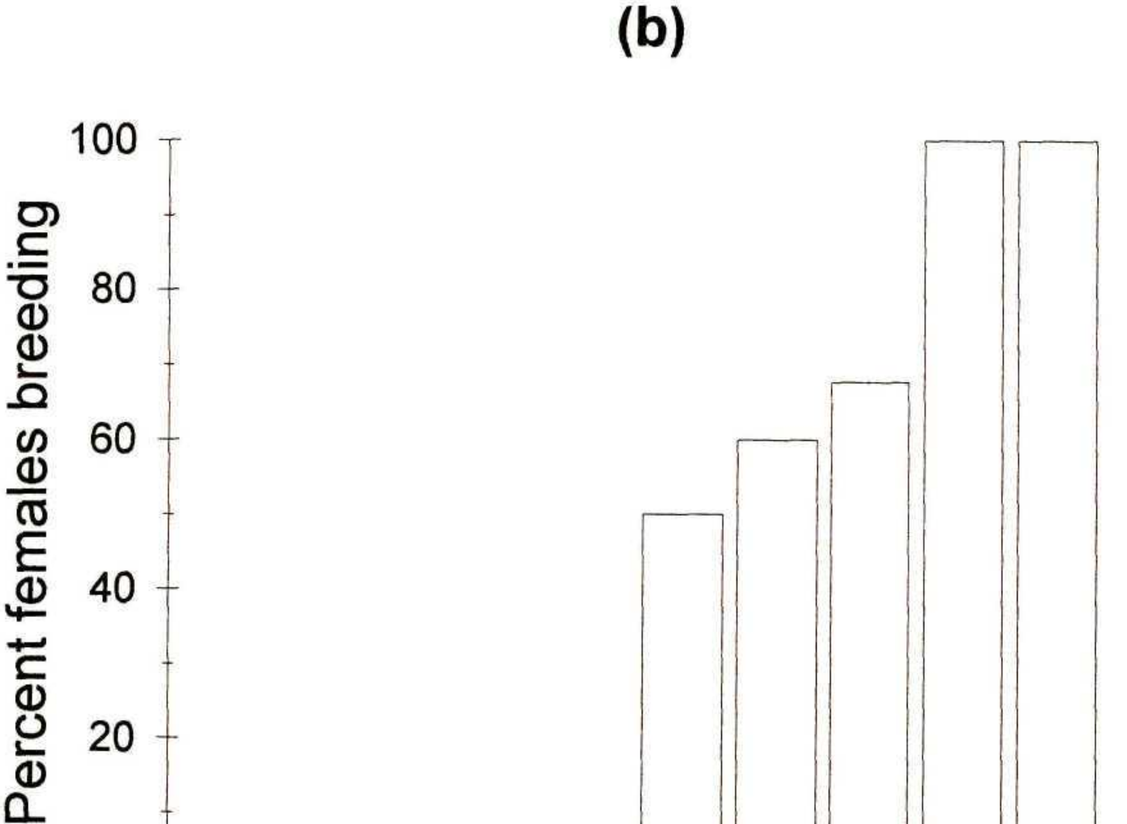

Fig. 4. The proportions of : (a) adult male *Steatomys pratensis* with scrotal testes, and (b) females with perforate vaginae, trapped between June 1995 and May 1996.

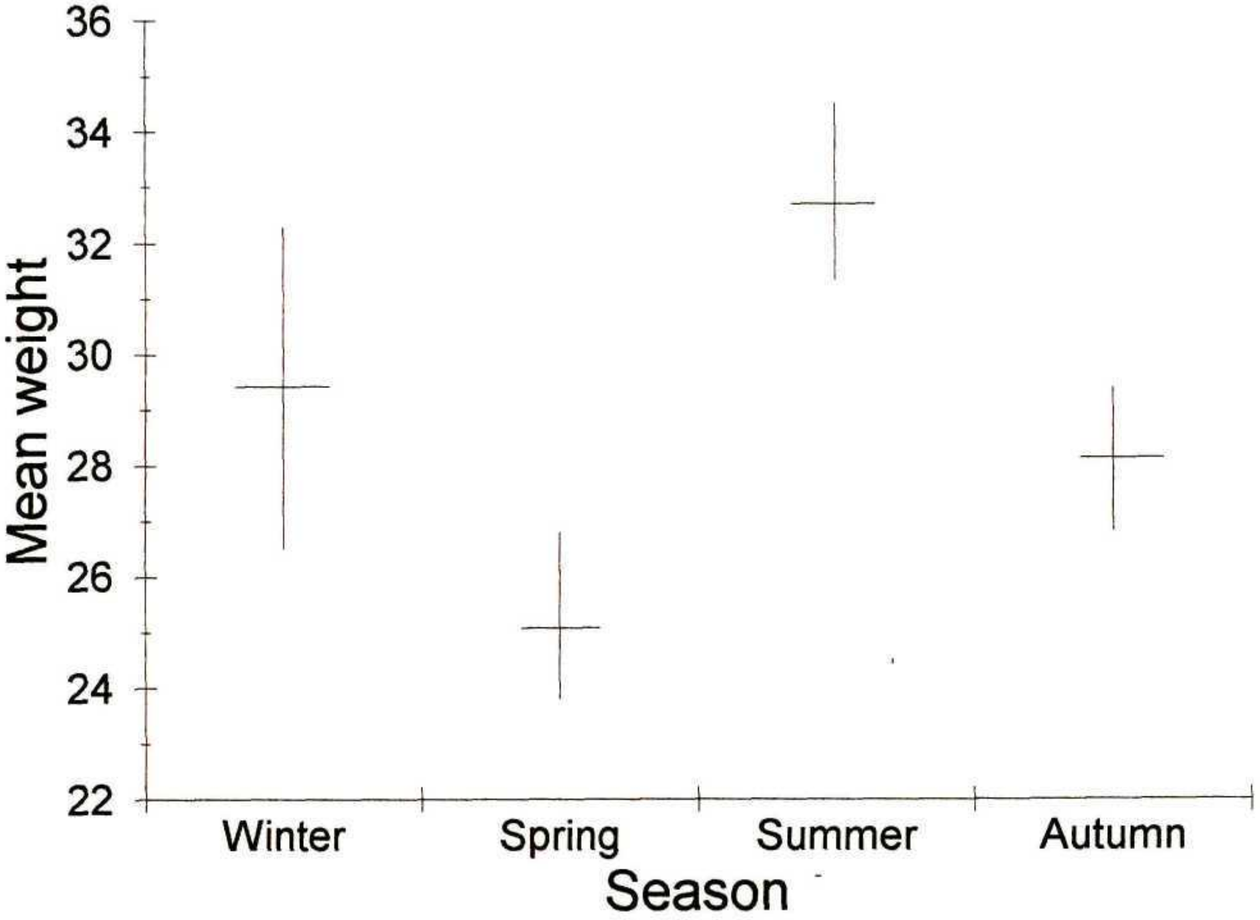

Fig. 5. Mean body weight of *Steatomys pratensis* in the four seasons (see Table 2 for season definitions).

CHAPTER 12

CONCLUSIONS

This study has shown that food availability and vegetative ground cover affect both the distribution and demography of individual species of small mammal, and the structure of the community. The greatest effect was recorded for *Mastomys natalensis*, whose population increased by two- to three-fold following food supplementation. Food supplementation also affected reproduction, body weight, survival and the home range of this species. Food supplementation affected the small mammal community by increasing biomass and decreasing species diversity (both as a result of an increase in *M. natalensis*).

Vegetative cover also significantly affected the small mammal community. A reduction in ground cover resulted a decrease in biomass, species diversity and richness. The species most affected were *M. natalensis* and *Lemniscomys rosalia*. The population of both species decreased following the experimental removal of vegetative cover. The population of *M. natalensis*, however, increased on the low-cover grids with the provision of supplementary food. Hence, both *M. natalensis* and *L. rosalia* avoided low-cover grids, but supplementary food induced *M. natalensis* to venture into the open.

Although these observations have been intuitively known by most African small mammal ecologists for a long time, this is the first African study to have experimentally tested the role of food and cover simultaneously. Some of the insights gained from this study were not immediately intuitively obvious. For example, why did supplementary food extend the breeding season of female but not that of male *Mastomys natalensis* (Chapter 7)? Or, why were the rates of survival of *M. natalensis* (receiving supplementary food) boosted in some seasons but not in others? Some of the observations of this study were perhaps even counter-intuitive. For example, why was the population of *M. natalensis* greatly increased by the provision of supplementary food, while the populations of *L. rosalia* (Chapter 10) and *Mus minutoides* (Chapter 11) appeared not to have been affected?

Problems associated with the current study

The biggest problem encountered in this study was related to the control and manipulation of the environmental factors.

1) The grids used in this study appeared to be floristically very similar (see Chapters 7 and 8). There may, however, have been subtle differences in the soil or vegetation which may have affected the habitat of small mammals. For example, in the second experiment (Chapters 6 and 8) two of the six grids were situated on a cattle farm. Preliminary vegetation examination (at the time when the grasses were dominant) suggested that the grazed and ungrazed grids were floristically similar. After the fire, however, it was noticed that the grazed area supported a far lower diversity of non-grass plant species than the ungrazed area. Thus, there may have been undetected habitat factors that were not adequately controlled for during the study.

2) There were problems associated with the provision of supplementary food. The supplied food may have been eaten by animals other than small mammals. This was especially true in the second phase of the study when it was suspected that cows were eating the supplementary food

on one of the grids (see Chapters 6 and 8).

3) Fire was a major problem. Despite all attempts to prevent them, fires burnt through the study area in September of each year (the effects of fire have been discussed in most of the chapters and will thus not be considered again). Although, the fires confounded the results to an extent, they also provided an insight that may have been otherwise missed (see Chapters 7, 10 and 11).

Future investigation

Experimentation needs to play a much larger role in the study of African small mammals. For experimental studies to be successful, however, the hypotheses that are to be tested must be carefully developed and clearly defined. Probably the biggest problem associated with field experiments is that of confounding factors, some of which are very difficult to control or predict before-hand (*e.g.* the fires that burnt through the study area). This problem is not insurmountable, and should not prevent the design and implementation of experimental studies. As more experimental studies are conducted, more problems are identified; and once a problem is identified, a solution can then be sought.

Many questions have arisen from this study that warrant further investigation. The questions can be divided into two categories. In the first category, the questions deal with the particular design of the study. Questions arising here include *inter alia*: 1) are the results of this study repeatable? 2) Was the supplementary food available to all the species in the community? 3) Did the fire and the presence of cattle on some grids confound the results? If yes, then how did these factors confound the results? 4) Were there subtle habitat differences between the grids that were confounding the results? 5) The study was conducted in a particularly wet period (with well above-average rainfall); would the results of this study have been different if it have been conducted during a dry period?

The questions arising from the second category deal with the findings of this study and include: 1) what are the effects of predation? Very little was known about the small mammal predators of the study area. Marsh owls (*Asio capensis*), slender mongooses (*Galerella sanguinea*), puffadders (*Bitis arietans*) and spitting cobras (*Naja mossambica*) were sighted in the study area, and striped polecats (*Ictonyx striatus*), black-shouldered kites (*Elanus caeruleus*) and blackheaded herons (*Ardea melanocephala*) were sighted in adjoining areas. However, nothing was known about the populations of these predators or their effects on the small mammal community. 2) Why did the populations of *L. rosalia*, *M. minutoides* and other rodent species not increase with supplemental food? Were these rodents not feeding on the supplemented food? Or was the food (rabbit pellets and rolled oats) that was provided not suitable for growth and reproduction in these species? The food was certainly suitable for *M. natalensis* (Chapter 3). *Lemniscomys rosalia*, *Steatomys pratensis* and *M. minutoides* were successfully reared in captivity on a diet of pellets and oats. This, however, does not imply that these rodents will necessarily recognize and feed on this food in the wild. Assuming that these rodents were, in fact, feeding on the supplementary food, why were their populations not affected? Was this perhaps as a result of the social structure of these rodents? Field-based studies (using techniques other than trapping e.g. radio telemetry) investigating the social structure of southern African rodents are desperately required.