The population dynamics of rodents at Settlers, Transvaal, South Africa

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Abstract

Studies of populations of *Mastomys natalensis* and *Rhabdomys pumilio* have shown that densities increased in late summer and peaked in midwinter. Numbers were low in spring over midsummer. Small numbers of *Otomys angoniensis* were caught throughout the year. Breeding in *M. natalensis* ended in March–April and recommenced in August–September. Breeding in *R. pumilio* ended in May and recommenced in August. Reproductively active adult *O. angoniensis* individuals were present throughout the year. There was a small peak in juvenile numbers of *M. natalensis* and *R. pumilio* in spring, but little juvenile recruitment over midsummer. The mean body mass of *M. natalensis* and *R. pumilio* declined from a peak in March to low values throughout the winter, followed by a slight increase in spring. The body mass of *O. angoniensis* was highly variable. The low numbers of *O. angoniensis* caught are ascribed to trap-shyness rather than low density in the field. *O. angoniensis* was probably present in fairly high numbers throughout the year.

Introduction

Rodent population census, by trapping, has been done extensively at various localities in South Africa, but usually at monthly intervals, or longer. In order to ascertain possible subtleties in rodent demography, trapping was instituted weekly. A prior study by Mendelsohn (1982a) found three common rodent species, the multimammate mouse *Mastomys natalensis*, the fourstriped field mouse *Rhabdomys pumilio*, and the angoni vlei rat *Otomys angoniensis* to be resident on the study area at Settlers. This paper deals with the demography of the rodent populations in relation to season and body mass dynamics.

Material and methods

The study site was situated near Settlers (24° 57′ S, 28° 33′ E) on the Springbok Flats, Transvaal, South Africa. This study area fell inside that of Mendelsohn (1982a, b). The topography was flat, but drainage lines produced a gently rolling landscape from East to West. The area was used for mixed farming, with cultivated fields (72 %) interspersed with patches of grazed bushveld (27 %). The entire area was on Springbok Flats Turf Thornveld (Acocks 1975). The rainfall data (Fig. 1) were obtained from Deeside farm, on the southern edge of the study area.

Mastomys natalensis has been separated into sibling species (*M. natalensis* and *M. coucha*) based on chromosome numbers and haemoglobin electrophoresis (Bronner 1986; Green et al. 1980; Meester et al. 1986). Meester et al. (1986) do not give the Springbok Flats (Northern Transvaal) in the distribution of either species. As the *M. natalensis* population at Settlers was not identified to sibling-species level, we will use *M. natalensis* as referring to *M. natalensis* sensu lato throughout.

Two live-trap lines were established, the first (Line A) through grazed bushveld on black turf [Mendelsohn's (1982a) line 2]. This line crossed a dry river bed which was later flooded. The second (Line B) ran along a fence between a tarred road (5 m away) and a cultivated field (5 m away). This line incorporated both black turf as well as red clay [Mendelsohn's (1982a) lines 4 and 5]. Trapping was initiated in February 1986, and in June 1986 the number of traps was increased from 20 to 35 in line A and from 20 to 40 in line B. Both lines were set weekly, for two trapping nights per week. The
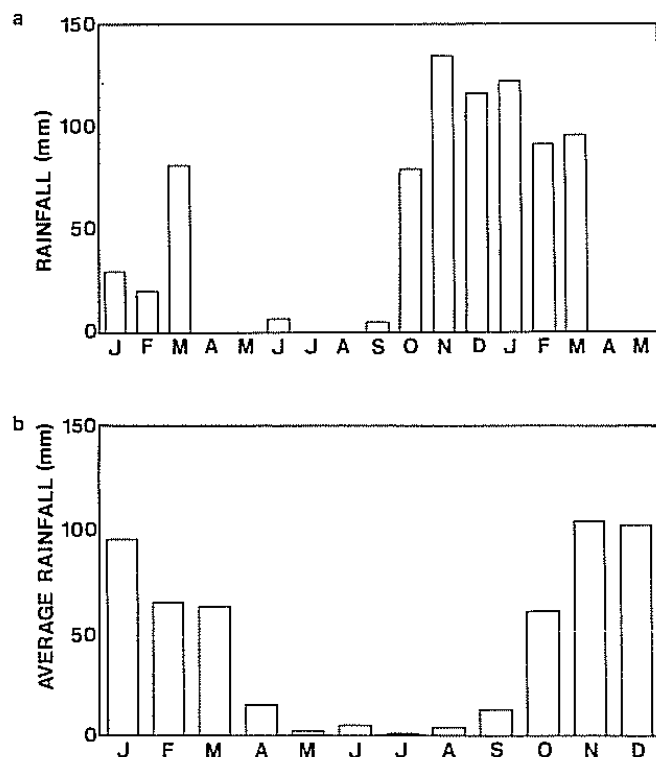
Fig. 1. Rainfall figures at Deeside Farm on the southern border of the study area. a: Rainfall during the study period. b: Average rainfall from 1978 to 1987

traps were placed 6 m apart, adjacent to runways or other signs of rodent activity (to increase the capture rate of *O. angoniensis*). The traps were baited with peanut butter and oats, and left in place throughout the study period. From February to May 1986 all animals caught were removed, but from mid-June 1986 capture-mark-recapture (FLOWERDEW 1976) was instituted, using the toe-clipping method (TWIGG 1875a).

Additional trapping was done using snap-traps, placed randomly along a field verge between two cultivated fields [on black turf (MENDELSOHN 1982a, line 4)]. These traps provided data on population age and sex structures, and body mass.

All animals were identified, aged, sexed, weighed, and their reproductive condition noted. Reproductively active individuals were defined as those that were scrotal (males), or that were perforated, pregnant or lactating (females) (TWIGG 1975b). Body mass was used to separate individuals into juvenile and adult age classes, with the separating mass being: *M. natalensis* – 30 g (DAVID and JARVIS 1983); *R. pumilio* – 30 g (BROOKS 1974, 1982; DAVID and JARVIS 1985) and *O. angoniensis* – 50 g (DAVIS 1973). Individuals which showed reproductive activity although weighing less than the above values, were considered to be adults.

Two indices of population numbers were obtained: a. the minimum number of mice alive (MNA) (DAVID and JARVIS 1985) [MNA = the number of mice actually caught + the number of mice marked before the Ith trapping occasion, which were not caught at the Ith occasion but were captured subsequently (i.e. mice assumed to have been present at time I)]. b. As the number caught per 100 trap-nights (1 trap night = 1 trap set for 24 hours) (CHIDUMAYO 1984; MENDELSOHN 1982a).

Results

Three species dominated the captures: *Mastomys natalensis*, *Rhabdomys pumilio* and *Otomys angoniensis*. Occasionally shrews (*Crocidura* spp. n < 20), the striped mouse *Lemniscomys rosalia* (n = 2) and the pouched mouse *Saccostomus campestris* (n = 1) were caught. The results focus on the first three species.

Population numbers

Numbers of *M. natalensis* (Fig. 2a, b) increased from February to the end of June, and then gradually decreased over late winter. There was a slight peak in late spring, low numbers over midsummer, and an increase towards the end of summer (Fig. 2.1b). The MNA showed fairly constant numbers over winter, a slight increase in late spring and a decrease over midsummer.

Fewer *P. pumilio* were caught (Fig. 3a, b) than *M. natalensis*. *R. pumilio* showed the same seasonal trend in numbers as *M. natalensis*, with the exception of the spring peak. No *R. pumilio* were trapped after the end of October.
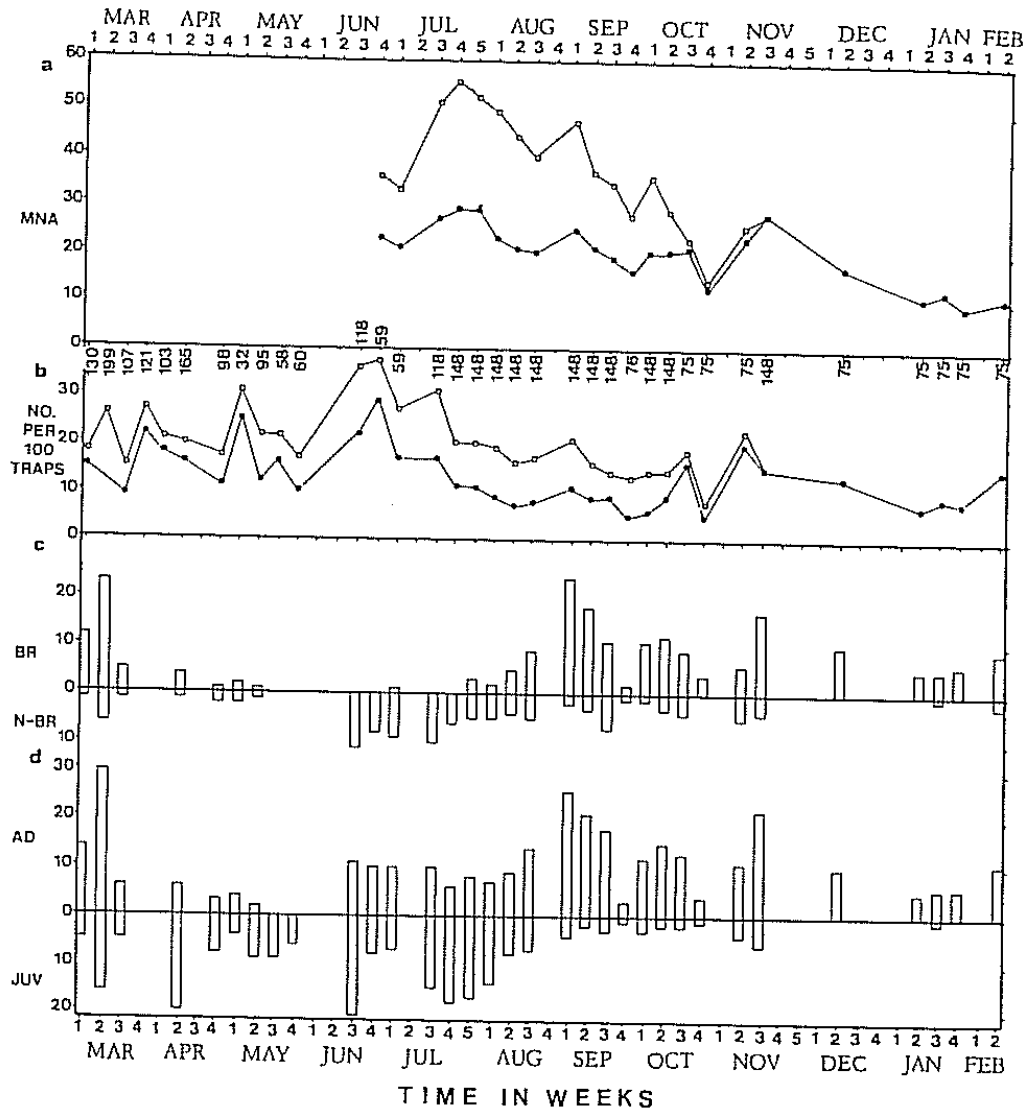

Fig. 2. The population demography of *Mastomys natalensis* at Settlers during the study (see text for details). a: The minimum number of mice alive (MNA) through the study period. b: The number of individuals caught per 100 trap nights through the study period. c: Breeding season: the number of adult individuals in breeding (BR) and non-breeding (N-BR) condition. d: Age structure: the number of adults (AD) and juveniles (JUV) present, o——o = all species trapped; ●——● = *M. natalensis*. Numbers between a and b indicate the number of traps used in each trapping session
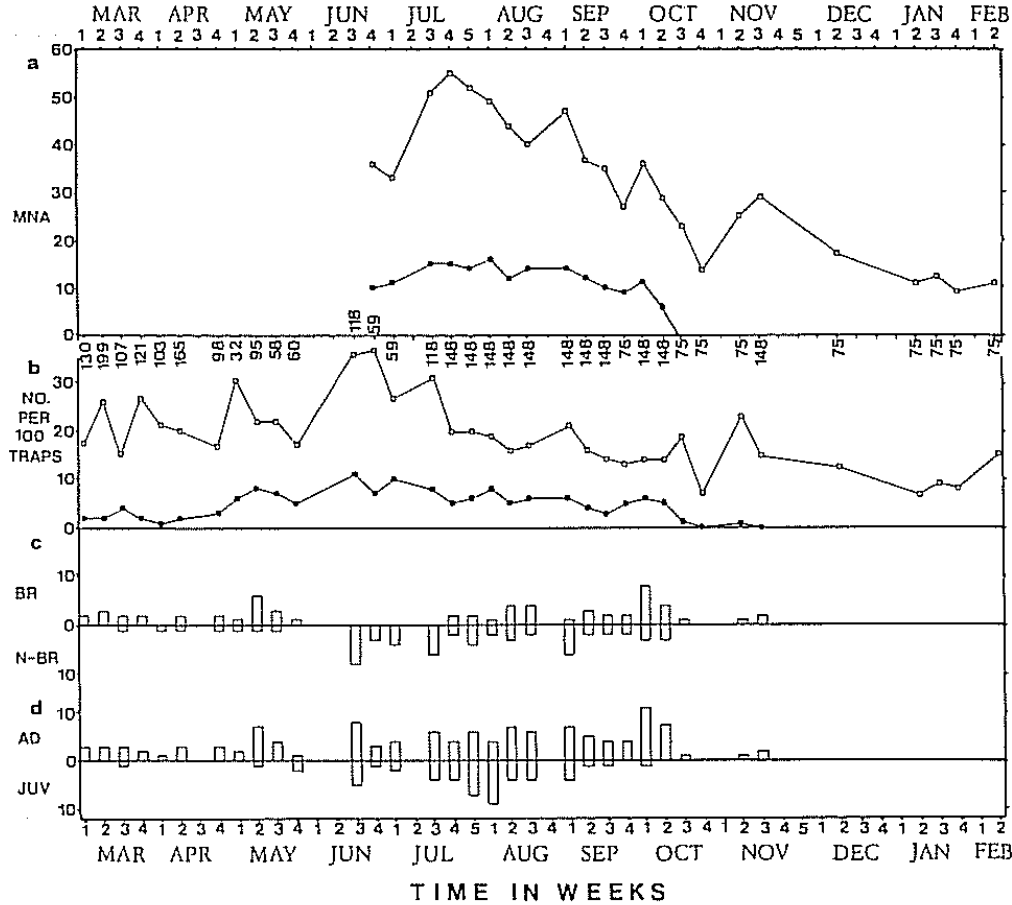
Fig. 3. The population demography of *Rhabdomys pumilio* at Settlers during the study (see text for details). a: The minimum number of mice alive (MNA) through the study period. b: The number of individuals caught per 100 traps nights through the study period. c: Breeding season: the number of adult individuals in breeding (BR) and non-breeding (N-BR) condition. d: Age structure: the number of adults (AD) and juveniles (JUV) present. o——o = all species trapped; ●——● = *R. pumilio.* Numbers between a and b indicate the number of traps used in each trapping session

Breeding season

The breeding season of *M. natalensis* came to an end in March–April, with few reproductively active animals caught from June to July (Fig. 2c). Breeding began again in August–September and reproductives were present throughout spring and summer. Seasonal changes in recruitment (juveniles present – Fig. 2d) showed a slight peak in numbers in November, and an absence of juveniles from December to February.

Although present data for *R. pumilio* are not as complete as for *M. natalensis*, indications are that reproductive activity ceased in May, and recommenced in August (Fig. 3c). Juvenile numbers increased over winter, but there were no juveniles trapped in spring (Fig. 3d).

Reproductively active *O. angoniensis* adults were present throughout the year, showing no marked breeding season (Fig. 4c). Very few juveniles were trapped, but indications were that juveniles were born throughout the year (Fig. 4d).
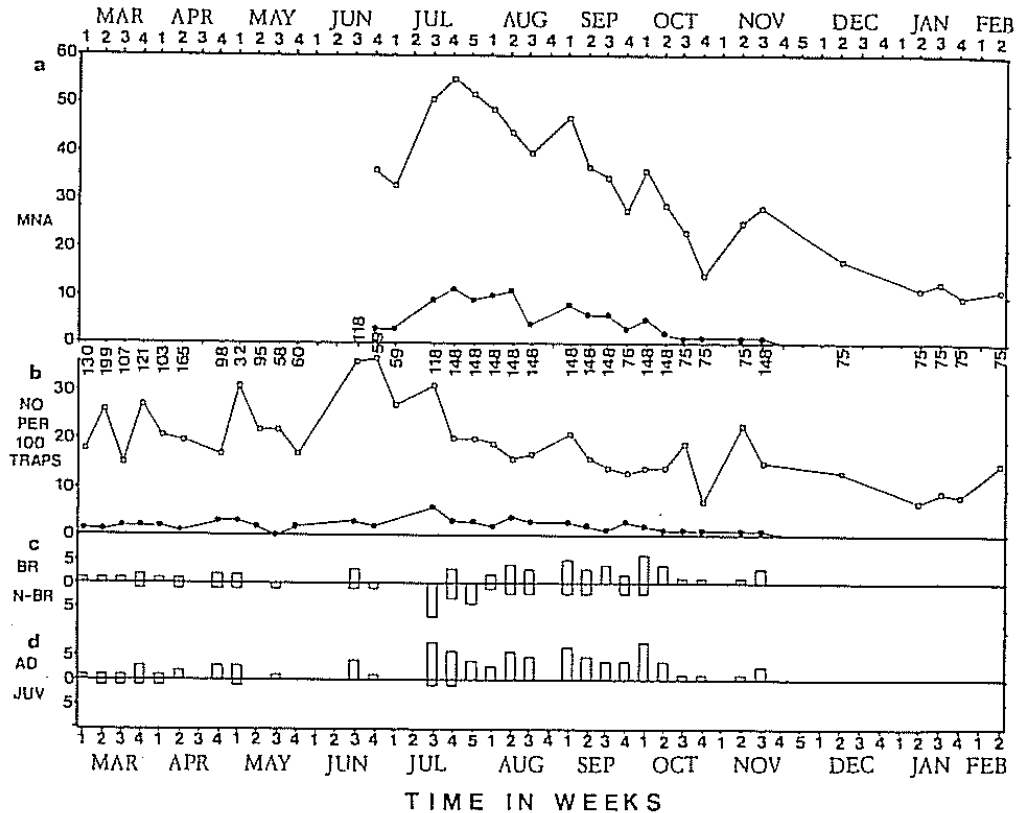
Fig. 4. The population demography of *Otomys angoniensis* at Settlers during the study (see text for details). a: The minimum number of mice alive (MNA) through the study period. b: The number of individuals caught per 100 traps nights through the study period. c: Breeding season: the number of adult individuals in breeding (BR) and non-breeding (N-BR) condition. d: Age structure: the number of adults (AD) and juveniles (JUV) present. o——o = all species trapped; ●——● = *O. angoniensis*. Numbers between a and b indicate the number of traps used in each trapping session

Body mass

Mean body mass of *M. natalensis* is shown in Figure 5a, while that of adults and juveniles are shown separately in Figure 5b. Adult body mass (Fig. 5b) was low over winter, and then increased from spring onwards to a peak in January–February. The mass of juveniles increased through autumn to relatively high levels in spring, as they matured.

The mean body mass of *R. pumilio* (Fig. 6b) decreased from a peak in March to lower values throughout winter, and then increased slightly in spring. Body mass of *O. angoniensis* was highly variable throughout the period illustrated (Fig. 6a).

Discussion

The correlation between rainfall and the seasonality of reproduction in many African grassland rodents is generally accepted. LEIRS et al. (1989) in a detailed, three year study of *M. natalensis* at Morogoro, Tanzania, have shown that the breeding season starts soon after the onset of the rainy season in March–April, but if rainfall at the end of the year is heavy, there is a short additional separate breeding period early in the following year.
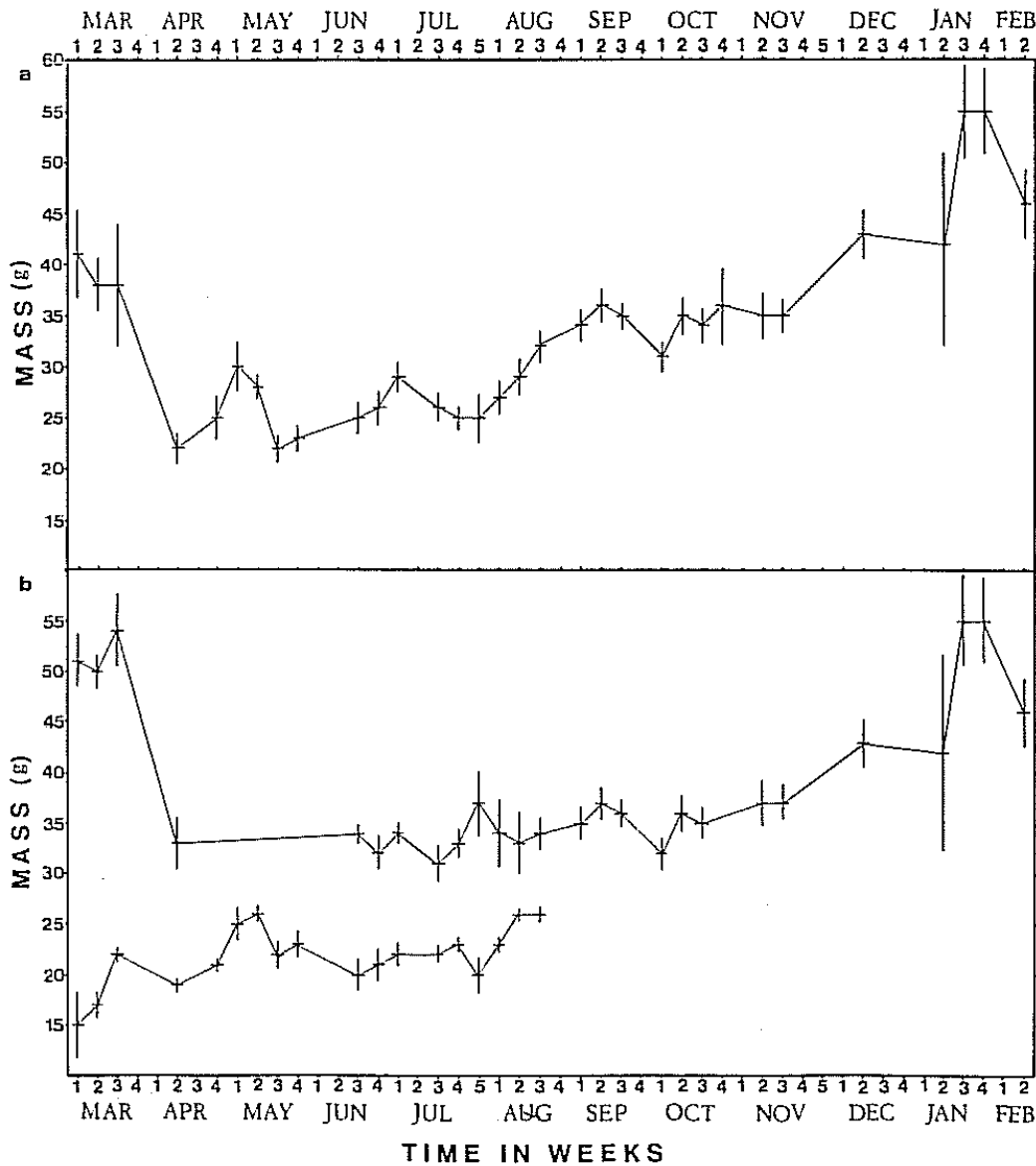
Fig. 5. The body mass of *Mastomys natalensis* at Settlers during the study. a: The body mass of all individuals from each trapping session pooled. b: The body mass of adult and juvenile individuals shown separately. Horizontal lines indicate means; and vertical lines indicate 1 X SE error

Population numbers

M. natalensis numbers at Settlers follow closely the trend found in the same area by MENDELSOHN (1982a). CHIDUMAYO (1984) also found a small increase in late spring followed by lower numbers from November to December. Unfortunately his trapping ended in December. MENDELSOHN (1981) ascribed the small spring peak in numbers to the production of juveniles, and the low midsummer numbers to low rates of juvenile recruitment. This is supported by this study which showed an increase in the number of juveniles at the time of the spring peak, followed by an absence of juveniles over midsummer.
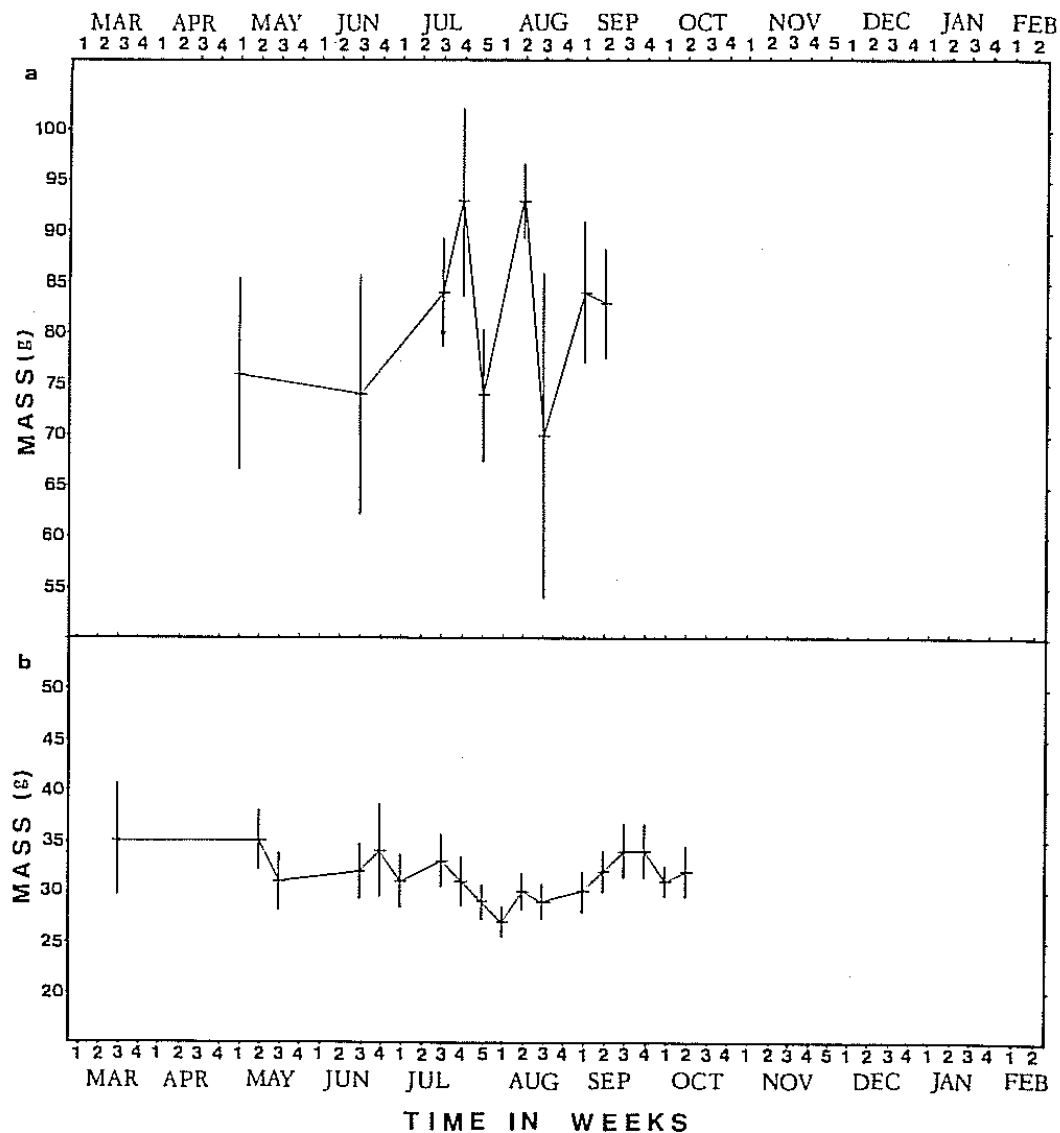
Fig. 6. The body mass of *Rhabdomys pumilio* and *Otomys angoniensis* populations at Settlers during the study. a: The body mass of *Otomys angoniensis* individuals. b: The body mass of *Rhabdomys pumilio* individuals. Horizontal lines indicate means; and vertical lines indicate 1 X SE error

A possible reason for the low numbers over midsummer is the large amount of rain which fell at Settlers from late October through to the end of January. TAYLOR and GREEN (1976) suggest that exceptionally heavy or prolonged rainfall results in very successful reproduction. This would, however, be a longterm effect, the immediate effect perhaps being a decrease in numbers (because of flooding). Individuals may die from overnight exposure when wet (PERRIN 1975), or the decrease in numbers may be because animals moved out of the flooded areas.

R. pumilio numbers were similar to those of MENDELSOHN (1982a), who also found that population numbers were lowest from November to February. BROOKS (1974) showed an increase in *R. pumilio* from May to June, followed by a gradual decrease, with lowest numbers in mid-summer. He trapped in an intensive grid, and the number of animals

trapped per session ranged from a minimum of 40 upward. His results may well be indicative of the trends in the whole Transvaal population, as corroborated by this study and MENDELSOHN (1982a). DAVID and JARVIS (1985), working in the western Cape (winter-rainfall area) found that numbers began to increase from October to November, and rose steadily to a peak in February–March; this was followed by a decline during winter, with lowest numbers in August–September. The general trend was therefore the same as in the Transvaal, but with the cycle shifted three months earlier.

DAVIS (1973) found that *O. angoniensis* numbers were constant from March to December of one year, followed by an increase over the next year to a peak in November. This was followed by a decrease. *O. angoniensis* numbers seem to lack the seasonal fluctuations shown by of the other two species, and rather display relatively constant numbers that vary yearly rather than seasonally.

Breeding season

MENDELSOHN (1982a) found a similar breeding season to this study, with reproductives appearing from July to September, and juveniles showing a slight peak in numbers in September, before very low numbers over summer. He suggested that this was a result of an interrupted breeding season, in which young are produced in spring and late summer-autumn. He found, as in this study, that reproductives were present throughout the summer, and suggested that the absence of juveniles was because environmental conditions were not suitable for the production and/or survival of young. The work of CHIDUMAYO (1984) and TAYLOR and GREEN (1976) agrees with the current results and MENDELSOHN's (1982a, b) data. COETZEE (1965), however, showed that pregnant females are present in large numbers from September onwards (throughout the summer), with 44 % of the adult females caught in December being pregnant. It seems therefore that the *M. natalensis* populations attempt to breed continuously from August to March, but juvenile mortality limits recruitment over midsummer.

The absence of spring recruitment in *R. pumilio* could have been because unusually high rainfall from October to January caused high juvenile mortality. MENDELSOHN (1982a) showed the *R. pumilio* breeding season to be similar to that of *M. natalensis*. PERRIN (1980) showed a recession in breeding over midsummer, and attributed this to an environmental factor (drought). ROWE-ROWE and MEESTER (1982) found reproductives present from September to March. Their results also indicated a drop in recruitment in November. The first young entered the trappable population in October, but no juveniles were captured during November. No trapping was done in December, and they trapped juveniles from January onwards. DAVID and JARVIS (1985) showed numbers of reproductives increasing in September, and present until March; juveniles increased from November through to May. This disagrees with the above findings, but they worked in a winter-rainfall area. Survival of young would depend on environmental conditions, and in certain areas (e.g. Settlers) survival may be adversely affected over midsummer, as is the case with *M. natalensis*.

As in our study, TAYLOR and GREEN (1976) found pregnant *O. angoniensis* females throughout the year, with a breeding peak in the wetter months. They found that the number of juveniles trapped varied little. *O. angoniensis* therefore shows little seasonality in reproduction, other than a slight peak in wet months (summer).

Body mass

The decrease in *M. natalensis* adult body mass over winter is documented by several authors (CHIDUMAYO 1984; COETZEE 1965; TAYLOR and GREEN 1976). Growth and maturation seem therefore to be delayed over winter, juveniles not becoming mature until spring.

R. pumilio body mass changes were similar to those of *M. natalensis*. This trend is supported by HENSCHEL et al. (1982) and TAYLOR and GREEN (1976) who suggest that growth and maturation are inhibited during the non-breeding season (winter).

The body mass of *O. angoniensis* varied greatly at each trapping session, and small sample sizes probably disguised trends. DAVIS (1973) found that *Otomys irroratus* lost mass over winter.

General

Numbers of *M. natalensis* and *R. pumilio* peaked in autumn following summertime breeding, but recruitment occurred after the summer rains, when body masses were high. Although adults were reproductively active throughout summer, density did not increase. This apparent paradox has been recorded previously but not adequately explained. It has been inferred that low juvenile recruitment, or infant mortality, is caused by environmental factors, including heavy rainfall (TAYLOR and GREEN 1976), drought or nutrition (PERRIN 1980). However, temporal correlations between environmental variables and demographic events may not be indicative of cause-effect relationships and alternative explanations should be considered.

Changes in the survival and recruitment of young into natural murid populations have been explained by intraspecific competition in the form of aggression (SADLEIR 1965; HEALEY 1967; WATTS 1969). For example, the mortality of young redbacked voles *Clethrionomys grapperi* is greatest during the summertime breeding season, when levels of aggression are higher in adults than young (PERRIN 1981) and when diet is optimal and body growth is greatest (PERRIN 1979). Field experiments, that manipulate density (and hence aggression) and food resources (independently of climate) while agonistic behaviour is being monitored and quantified, are necessary to distinguish between alternative explanations of demographic process. Descriptive studies of the population dynamics of African rodents should now be complemented with experimental investigations.

Acknowledgements

Zusammenfassung

Die Populationsdynamik von Nagetieren in Settlers, Transvaal, Südafrika

Studien über Populationen von *Mastomys natalensis* und *Rhabdomys pumilio* haben ergeben, daß ihre Dichte zwischen Februar und Ende Juni zunahm und in der Mitte des Winters wieder abnahm. Im Frühling gab es ein Populationsmaximum, das während des Hochsommers abnahm. *Otomys angoniensis* konnte ganzjährig in kleinen Zahlen gefangen werden. Die Wurfzeit von *M. natalensis* kam im März/April zum Abschluß und begann wieder im August/September. Die Wurfzeit von *R. pumilio* endete im Mai und fing im August wieder an. Fortpflanzungsfähige, ausgewachsene *O. angoniensis* kamen das ganze Jahr über vor. Die Zahlen der Jungtiere von *M. natalensis* und *R. pumilio* erreichten im Frühling ihr Maximum; wenige Jungtiere ergänzten die Populationen während des Sommers. Karge Umweltbedingungen könnten die Überlebenschancen der Jungtiere im Sommer beeinträchtigt haben. Das Durchschnittskörpergewicht von *M. natalensis* und *R. pumilio* nahm ab von einem Maximum im März bis zu geringen Werten im Winter. Im Frühling gab es eine kleine Gewichtszunahme. Das Körpergewicht von *O. angoniensis* variierte stark. Die niedrige Zahl von gefangenen *O. angoniensis* wird eher der Fallenscheu zugeschrieben, als daß sie die tatsächlichen Populationsverhältnisse widerspiegelt.

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