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Seasonal changes in reproduction and diet of the Bushveld gerbil, *Tatera leucogaster* (Muridae: Rodentia), in Zimbabwe

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Abstract

The reproductive ecology and diet of *Tatera leucogaster* were studied in two areas, mixed woodland and Miombo, in the Sengwa Wildlife Research Area, Zimbabwe. Both populations ceased breeding during the cool dry season but one population started breeding three months before the other. The two populations had similar diets, and rainfall and temperature were also similar in the two areas. The difference in duration of breeding in the two areas was probably related to food abundance.

In both study areas the testes mass of adult males made up about 6 % of their body mass. The adult sex ratio was strongly biased in favour of females during the breeding season.

In the mixed woodland area, females had an average litter size of 5.6 ± 0.29 and an annual reproductive capacity of 28 young per adult female. In Miombo, females had an average litter size of 4.8 ± 0.36 and an annual reproductive capacity of 12 young per adult female.

The diet mainly consisted of seeds (50–75 %) and insects (10–40 %), with a small amount of stem and leaf material (< 10 %). There was little seasonal variation in diet.

Introduction

The bushveld gerbil, *Tatera leucogaster*, is widely distributed throughout southern Africa (SMITHERS 1983) and has a variable pattern of breeding. It breeds throughout the year in Botswana (SMITHERS 1971) but mainly breeds during periods of high rainfall in Zambia (CHIDUMAYO 1980) and the Transvaal (PERRIN and SWANEPOEL 1987).

The main objective of the present study was to document the breeding biology and diet of *T. leucogaster* in two similar habitats separated from one another by a distance of 8–9 km. A comparison of the results from the two areas gives one an opportunity to separate the effects of climate (rainfall and temperature), which is similar in the two areas, from the more local effects of the abundance and availability of food. This approach is particularly useful if, as was the case in this study, the breeding seasons in the two areas are very different.

A second objective was to examine certain aspects of the reproductive biology of the males. Adult male *T. leucogaster* have extremely large testes during the breeding season (PERRIN and SWANEPOEL 1987), similar to certain other species of *Tatera* which have the largest proportion of body mass allocated to testicular tissue known for mammals (KENAGY and TROMBULAK 1986). I examine the constancy of this feature within the genus and show how the size of the testes is correlated with adult sex ratios and regression of the testes during the non-breeding season.

Material and methods

Study areas

A total of 300 *T. leucogaster* were collected from a 4 km² area of the Samapakwa plateau (18°05' S; 28°08' E) during the period July 1987 to June 1988, and during the period November 1987 to June 1988 a further 145 animals were collected from a 2 km² area of mixed woodland adjacent to the four square mile area (18°10' S; 28°10' E) in the Sengwa Wildlife Research Area in Zimbabwe.

The Sengwa Wildlife Research Area is described by CUMMING (1975). The study area on the Samapakwa plateau is Miombo (a *Brachystegia-julbernardia* mixed woodland). The commonest trees were *Brachystegia boehmii*, *B. spiciformis*, *Julbernardia globiflora*, *Terminalia sericea*, *Combretum zeyheri*, and *Baphia massaiensis*. The shrub *Xeromphis obovata* was particularly common. Most of the larger trees had been destroyed by elephant a decade or so prior to my study but an elephant reduction program, which ended in 1982, has allowed a prolific regrowth of trees. To prevent a late dry season fire from destroying this regeneration of trees the area has been subjected to cooler annual burns at the beginning of the dry season. Consequently, herbs and grasses were sparse. Common grasses included *Eragrostis viscosa*, *E. curvula*, *E. cilianensis*, *Aristida adscensionis*, *A. pilgeri*, *A. vestida*, *Dactyloctenium gigantum*, *Heteropogon contortus*, *Leptocarydion vulpiastrum*, *Panicum maximum*, *Pogonarthria squarrosa*, *Schizachyrium jeffreysii*, *Schmidia pappoporoides*, and *Setaria pallidifusca*.

The second study area was mixed woodland and bushland dominated by *Colophospermum mopane*, *Combretum apiculatum*, *C. zeyheri*, and *Erythroxylum zambesiaceum*. The area was not burnt and so herbs and grasses were much more abundant than on Samapakwa. Common grasses included *Eragrostis viscosa*, *E. cilianensis*, *E. regidior*, *E. superba*, *Dactyloctenium gigantum*, *Chloris virgata*, *Urochloa trichopus*, *Digitaria eriantha*, *Andropogon gayanus*, and *Schmidia pappoporoides*.

Rainfall and temperature were monitored at the Sengwa Wildlife Research Institute (18° 10' S; 28° 13' E). Monthly means were determined from daily records.

Collection and processing of animals

The two areas were sampled monthly by lines of snap traps placed at irregular intervals adjacent to burrows. Traps were left in place for two days and were then moved. Trapped areas were not retrapped. Animals were measured, sexed and weighed soon after removal from the traps. A clean mass was determined by removing the gut, from the lower oesophagus to the rectum, and also the uterus and embryos of pregnant females.

Seasonal changes in female reproductive activity were assessed as follows. First, females were classed as mature if they were reproductively active (see below) or had been in the past, i.e. had placental scars, otherwise they were classed as immature. Mature females were further categorized as 1. pregnant if they had implanted embryos; 2. reproductively active if corpora lutea were detected in the serially sectioned ovaries or if the uterus was distended with fluid (i.e. in proestrus); 3. remaining females were considered to be reproductively inactive. In addition, females were classed as lactating if milk could be expressed from their nipples. Note that it was possible for a lactating female to be categorized as reproductively inactive.

Seasonal changes in male reproductive activity was assessed in two ways. First the reproductive organs were dissected out and a sperm smear taken from each cauda epididymis. The abundance of spermatozoa for each smear was then quantified as 0 if none were present, 1 if only a few spermatozoa were present, 2 if spermatozoa were common but still scattered on the slide, and 3 if the smear mainly consisted of spermatozoa. An average sperm abundance could be determined for any group of animals. Secondly, the paired testes and seminal vesicles were fixed in Bouin's solution and weighed to the nearest 10 mg. To determine if the reproductive organs of adult males regressed during the non-breeding period the means of the log transformed mass of the testes and seminal vesicles were computed for monthly samples of males in age classes 4-8 (see below). This procedure largely eliminated changes resulting from a seasonal influx of juveniles into the population.

The number of litters and reproductive capacity (production of young per adult female) during the breeding season were calculated using the method described by NEAL (1981, 1982). This method considers that the interval between litters is made up of a non-pregnant period (p_o), a pre-implantation period (p_i), and a post-implantation period (p_v) when embryos are macroscopically visible. The value of p_i was assumed to equal 4 d (see NEAL 1981) and that of p_v was estimated as 24 d because the gestation period, which equals $p_i + p_v$, is 28 d (CHIDUMAYO 1980). The average value of p_o could then be estimated by assuming that the ratio of $p_o + p_i$ to p_v was the same as the ratio of non-visibly-pregnant adults to visibly-pregnant adults. The average interval between litters could then be estimated. The average number of litters and production of young could then be determined knowing the duration of the breeding season and the mean litter size.

The relative age of individuals was estimated using the eruption and subsequent wear of the upper molars as criteria. Eight age classes were recognised, ranging from the condition when the third upper molar was not fully erupted (age-class 1) to the condition when all molars were worn to the state where no enamel was visible on the upper surface (age-class 8).

Stomachs were preserved in Bouin's solution before transfer to 70% alcohol. The stomach contents of animals collected in the same month and area were combined and the composite samples were sent to the Composition Analysis Laboratory at Colorado State University for analysis by microhistological techniques. Details of the analysis are described by NEAL (1984a, b). Food fragments were categorized into four classes: anthropod (mainly insect), seed, plant stem and leaf, and fungi or lichen.

Results

Climate

There were 909 mm of rain during my year of study compared to a yearly average of 670 mm during the previous 22 years. Prior to my study it had last rained on March 26, 1987 and until early February 1988 the monthly rainfall was below the long term average (Fig. 1) except for December 1987. Rainfall was considerably higher than the long term average during the period February–March 1988. Thus, the April–November dry season was longer and more severe than usual, and rainfall was heavier and more concentrated towards the end of the rainy season than usual.

The temperature also varied seasonally (Fig. 1), being at a maximum in November at the end of the dry season and beginning of the rains (mean monthly maximum of 37.0°C; mean monthly minimum of 27.7°C) and a minimum in July (mean monthly maximum of 27.0°C; mean monthly minimum of 8.3°C).

Thus, the year may be divided into three main seasons: a cold dry season from mid-May to mid-August when the daily maxima and minima averaged 27–29°C and 8–11°C respectively; a hot dry season from September to November when the daily maxima and minima averaged 34–37°C and 17–22°C respectively; and a warm wet season from December to April when the daily maxima and minima averaged 31–34°C and 18–21°C respectively. The precise timing of these seasons varies slightly from year to year.

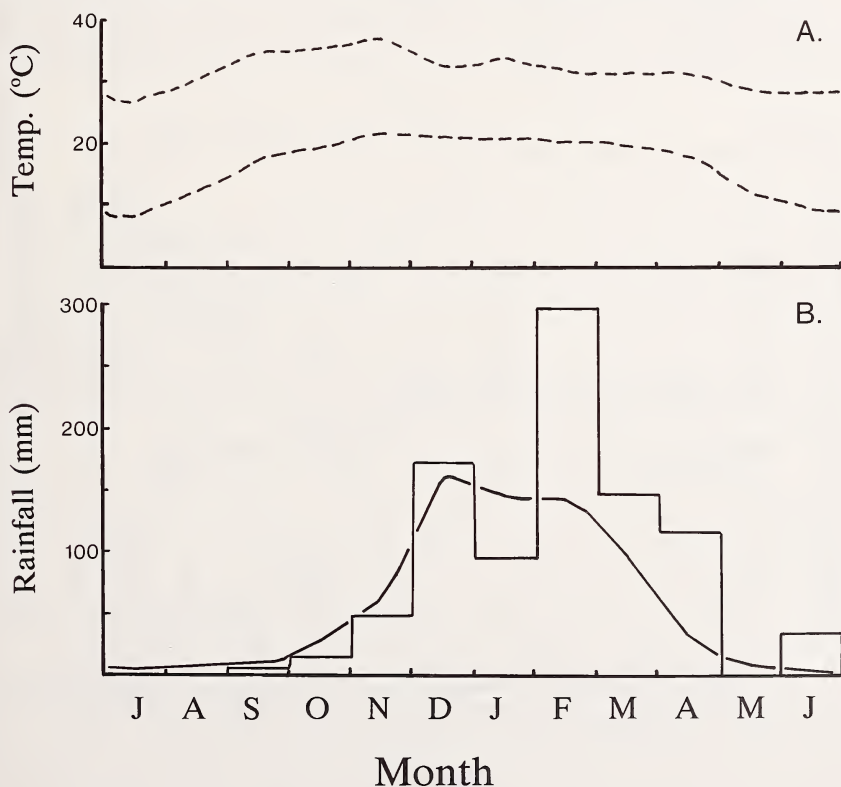


Fig. 1. A: Seasonal changes in mean monthly minimum and maximum temperatures (°C). B: Histogram of total monthly rainfall (mm) from July 1987 to June 1988. The average total monthly rainfall during the period 1965–1987 is also indicated

Body mass

The mean birth mass of 7 young born in the laboratory was 2.8 g (range 2.6–3.0 g) and they were weaned at a mass of 16–22 g at an age of 18–28 d (NEAL 1990). Individuals of both sexes usually attained sexual maturity at a body mass of 60–70 g. The mean body mass of 65 adult males was 79 g (range 58–113 g) and that of 191 adult females was 72 g (range 44–122 g). This slight sexual dimorphism of body mass is consistent with that reported in other studies of this species and for other species of *Tatera* (NEAL 1982). Adult body mass varied seasonally, reaching a maximum during the rains and early part of the dry season and declining to a minimum towards the end of the dry season. For example, parous, non-pregnant females in the Miombo habitat had a mean body mass of 61 g during September–November compared to a mass of 74 g during January–June and the body mass of adult males averaged 72 g and 83 g for the same two periods. Seasonal cycles in body mass have also been reported for *T. nigricauda* (NEAL 1982) and *T. afra* (ALLANSON 1958; MEASROCH 1954).

Sex ratios

The sex ratio of juveniles (i.e. individuals in the youngest two age classes) was not significantly different from parity both in mixed woodland ($\chi^2 = 1.1$; $P > 0.2$) and Miombo ($\chi^2 = 0.4$; $P > 0.5$). Similarly, the sex ratio of adults (i.e. individuals in age classes 3–8) was not significantly different from parity during the non-breeding period, May–November, in Miombo ($\chi^2 = 0.75$; $P > 0.3$). In contrast, the sex ratio of adults during the breeding season was strongly biased in favour of females both in mixed woodland ($\chi^2 =$

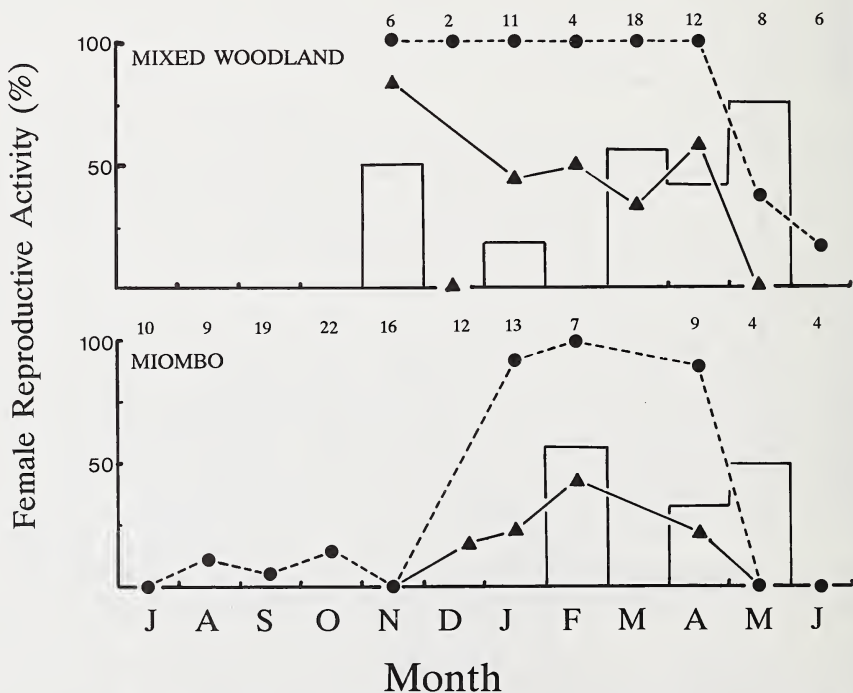


Fig. 2. Seasonal changes in adult female reproductive activity of *T. leucogaster* in two habitats. Percentage of adult females: 1. with corpora lutea or in proestrus (●----●), 2. with implanted embryos (▲—▲), and 3. lactating (histogram). Numbers represent sample sizes

12.2; $P < 0.001$) and Miombo ($\chi^2 = 5.7$; $P < 0.02$). CHIDUMAYO (1980) has also reported 1:1 sex ratios for juveniles and subadults, but a significant excess of old females during the breeding season in *T. leucogaster* in Zambia.

Breeding season

Female breeding activity was seasonal (Fig. 2) and mainly confined to the period of rainfall. The breeding season was longer in the mixed woodland area than in Miombo. Pregnancies were first observed in Miombo during the latter half of December resulting from conceptions sometime after the first week of December. In contrast, when the area of mixed woodland was trapped for the first time during the latter half of November most females were pregnant and the presence of lactating females (Fig. 2) and young juveniles (Fig. 4) indicate that breeding had been in progress for at least two months. Thus, pregnancies occurred at least three months earlier in mixed woodland than in Miombo. Breeding in both study areas ceased coincidentally with the end of the rains at the end of April.

Adult testes mass and seminal vesicles mass were at a maximum during the rains and

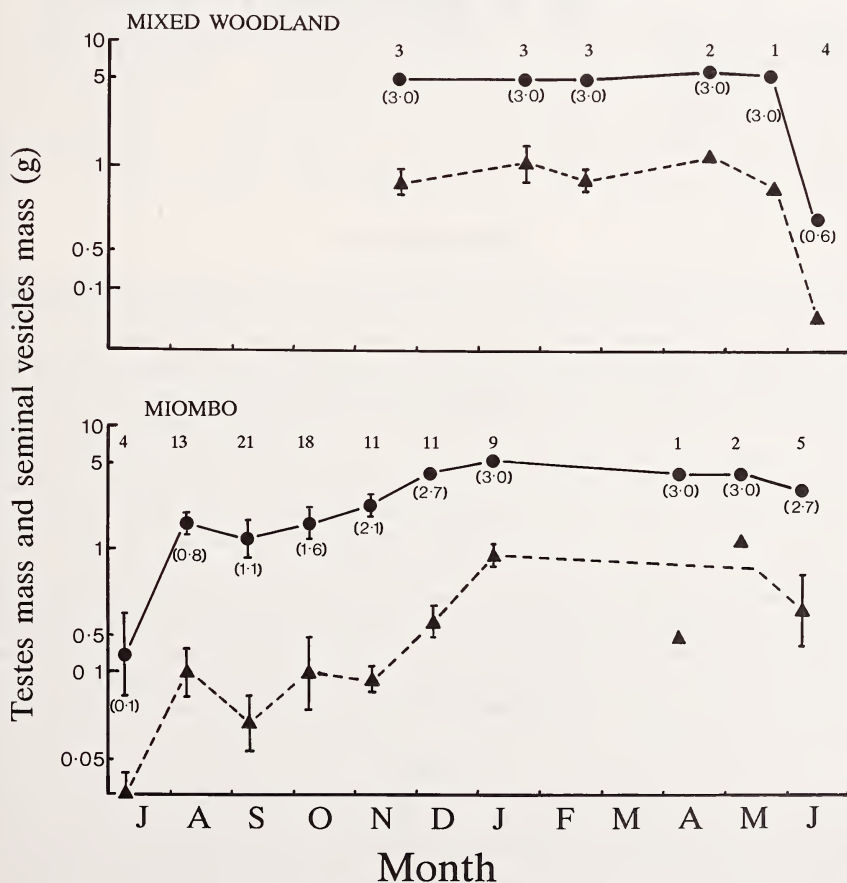


Fig. 3. Seasonal changes in testes mass (●—●) and seminal vesicles mass (▲---▲) of *T. leucogaster* in two habitats. Data points represent means and vertical lines $\pm 2 \times$ S.E. Numbers in parentheses are the average sperm rating of the sample, and numbers above each figure represent sample sizes

regressed during the dry season (Fig. 3), but this regression was subject to considerable individual variation and individuals with large testes and fully mature sperm ratings were present throughout the year.

Litter size

The mean number of live embryos of 25 pregnancies in mixed woodland was 5.6 ± 0.29 (range 3–8) and of 10 pregnancies in Miombo was 4.8 ± 0.36 (range 3–6). In both areas, litter size increased as the breeding season progressed, from a mean of 4.2 during November and December to 6.5 during March and April in mixed woodland, and from 3 in December to 5 during March and April in Miombo. Both the difference between areas and the difference between months were significant when analyzed by two-way analysis of variance. Litter size was not significantly correlated with body mass or age.

Breeding rates and reproductive capacity

The potential annual production of young per adult female was calculated independently for each study area assuming a breeding period from September to April in mixed woodland and from December to April in Miombo. In mixed woodlands females could theoretically have had an average of five litters during the breeding season resulting in a production of 28 offspring, whereas females in Miombo could only have had an average of 2.5 litters resulting in 12 offspring during the breeding season.

Counts of placental scars indicated that no female had more than three litters and that it was unusual for females to have more than two litters. Thus, the high reproductive capacity in mixed woodland must have been achieved by a high turnover rate of adult females.

Population structure

The age structures indicated marked seasonal recruitment of young into the populations (Fig. 4). This was particularly evident in Miombo where most young were produced by females that had survived from the previous breeding season, although a few young matured rapidly and began breeding in April at the end of the breeding season. By the beginning of the dry season in May and June, most of the old animals had died off and been replaced by their offspring. In mixed woodland, the replacement of old animals by their offspring occurred in much the same way, but young began breeding by January and formed the majority of the breeding population by March. Thus, the Miombo population generally consisted of older individuals than the mixed woodland population except during the last three months of the study, and less of the Miombo young bred during the same breeding season of their birth compared to the mixed woodland population. Presumably these differences are mainly related to the length of the breeding season in the two areas.

Similarly, CHIDUMAYO (1980) showed that the main recruitment of young occurred at the end of the rains and beginning of the dry season (March–June) in Zambia. These juveniles advanced in age and formed the majority of the population by the start of the following breeding season, after which they became rare or disappeared from the population.

Diet

The diets in the two study areas were superficially similar (Fig. 5). Seeds formed the bulk of the diet (50–75 %) throughout the year and insects were also commonly eaten (10–40 %). Only a small amount of stem and leaf material was consumed (< 10 %), and this was at a maximum during the rains and early part of the dry season. Towards the end of the rains and early part of the dry season (March–June) a small amount of fungi and lichens were also consumed. However, there was surprisingly little seasonal variation in diet (Fig. 5).

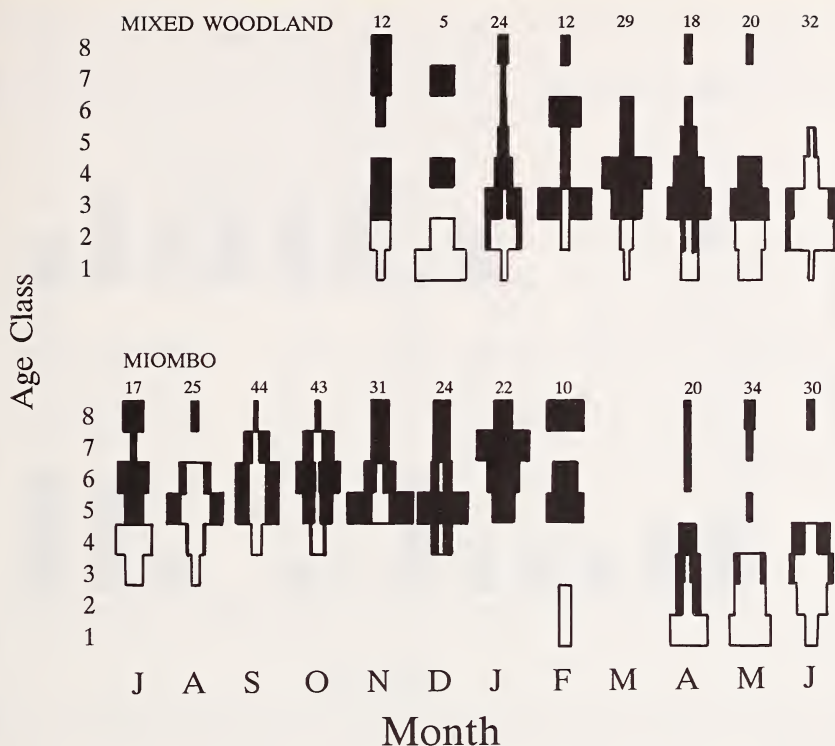


Fig. 4. Monthly age structure of *T. leucogaster* in two habitats. Open blocks represent immature animals and solid blocks represent mature animals. Sample sizes are shown above each figure

In contrast, PERRIN and SWANEPOEL (1987) observed a marked seasonal variation in diet in the Transvaal: insects and seeds predominated during the rains and herbage was eaten in large amounts during the dry season. Overall, the diet consisted of 41.4 % insects, 32.2 % herbage, and 26.4 % seeds.

Discussion

Testes size and sex ratio

Information on adult male body mass, testes mass and adult sex ratios during the breeding season are summarized for different species of *Tatera* in the Table. There is a wide range of testes size in the genus, and the relative size of the testes of *T. leucogaster* is second only to *T. afra* which has the largest proportion of body mass allocated to testicular tissue that is known for any mammal (KENAGY and TROMBULAK 1986).

Testes size in mammals is considered to be related to copulatory frequency and consequently to the type of mating system (HARCOURT et al. 1981; KENAGY and TROMBULAK 1986). There are two broad categories of mammalian mating systems: 1. Single-male systems, where a female mates with a single male, copulation is infrequent and the testes are small, and 2. multi-male systems, where a female mates with more than one male, copulatory frequency is high and the testes are large.

Little is known about the mating systems of most myomorph rodents although many are thought to be promiscuous, i.e. multi-male breeders (KENAGY and TROMBULAK 1986). Based on their study of the relationship between relative testes size and mating system, we

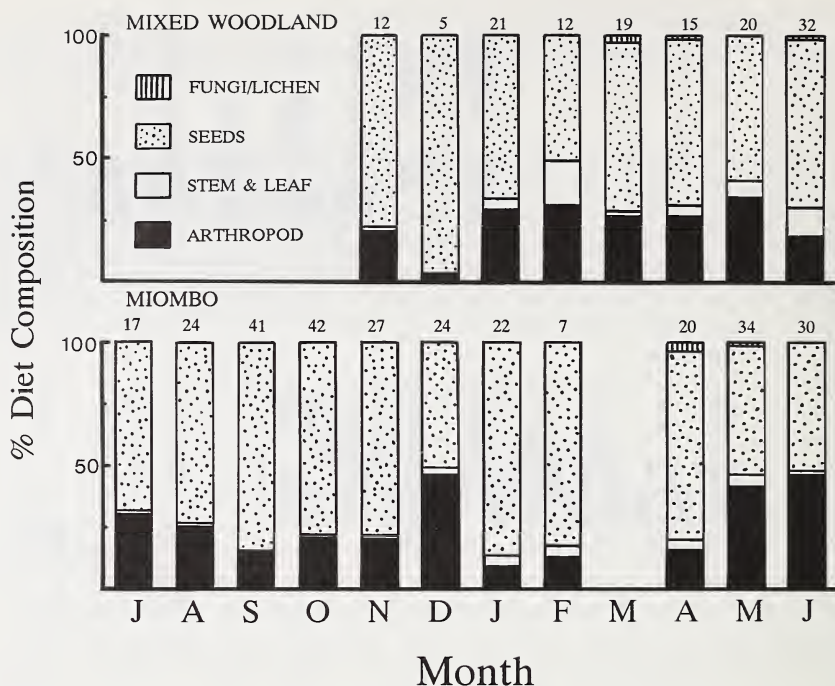


Fig. 5. Seasonal changes in diet composition of *T. leucogaster* in two habitats. Numbers represent sample sizes

would predict (Table) that *T. nigricauda* has a single-male breeding system and the other species have multi-male breeding systems. In this case we would expect *T. nigricauda* to be monogamous and have an even sex ratio (as observed) because the other type of single-male mating system, extreme polygyny in which a single male copulates with all females in a group, is not very likely in a small mammal with a dispersed distribution. The other species of *Tatera* probably have promiscuous mating systems with either even or skewed sex ratios. In fact there seems to be a relationship between adult sex ratios during the breeding season and relative testes size (Table). Species with small testes had even sex ratios and species with large testes had skewed sex ratios in favour of females.

The juvenile sex ratio of all species, except *T. brantsii*, were not significantly different from parity. Most juveniles matured between breeding seasons and so it is interesting to note that adult sex ratios outside of the breeding seasons were also not significantly different from parity. This implies that the change in sex ratio occurred at the time of breeding and so may be related to the type of mating system. The skewed sex ratios are probably the result of differential mortality rather than different capture rates because one would expect promiscuous males to be more active than females. In conclusion, it would seem that *Tatera* would make an interesting study animal for mammalian mating systems because of the wide range of testes size and adult sex ratios in different species of the genus.

The testes of *T. indica* (PRASAD 1956), *T. leucogaster* (PERRIN and SWANEPOEL 1987; this study) and *T. afra* (ALLANSON 1958) regress during the non-breeding season, whereas those of *T. nigricauda*, *T. robusta* and *T. valida* (NEAL 1982) show little seasonal variation in size. *T. brantsii* breeds throughout the year (ALLANSON 1958). Thus, the regression of the testes shows a positive correlation with testes size (Table) in seasonally breeding *Tatera*.

Adult sex ratios and percentage of testes mass in relation to total body mass of adult males during the breeding season for different species of *Tatera*

Relative testes size is the ratio of observed mass to that predicted by the equation: Testes mass (g) = $0.031 \times (\text{Body mass g})^{0.77}$ for rodents (KENAGY and TROMBULAK 1986). Sample size is for testes and body mass measurements

	Sample size (n)	Testes/Body mass (%)	Relative testes size	Sex ratio ♂ ♂ / ♀ ♀	χ^2 values	Reference
<i>Tatera nigricauda</i>	52	0.4	0.4	50/59	0.74	NEAL 1982
<i>T. robusta</i>	5	2.2	2.1	5/8	0.69	NEAL 1982
<i>T. valida</i>	23	2.9	2.8	22/23	0.02	NEAL 1982
<i>T. indica</i>	35	2.7	2.9	80/76	0.10	PRASAD 1956, 1961
<i>T. brantsii</i>	10	4.7	4.5	130/202	15.6***	ALLANSON 1958; MEASROCH 1954
<i>T. leucogaster</i> ¹	12	6.0	5.4	20/49	12.2***	This study
<i>T. leucogaster</i> ²	13	6.2	5.5	22/41	5.7*	This study
<i>T. afra</i>	10	7.7	7.3	90/142	11.7***	ALLANSON 1958; MEASROCH 1954

¹ Mixed woodland area. – ² Miombo area. * $p < 0.05$; *** $p < 0.001$.

Perhaps the regression of the testes is related to the energy costs of maintaining mature-sized gonads during the dry season when, presumably, food supplies are more limiting. The gonads and accessory reproductive glands of male *T. leucogaster* and *T. afra* comprise more than 10 percent of their body mass and so considerable savings of energy could be achieved by reducing the size of the reproductive system during the non-breeding season. There was considerable individual variation in the regression of the testes of *T. leucogaster* at Sengwa. During the dry season, the testes and seminal vesicles of animals provided with supplemental food were considerably larger than those of animals from non-supplemented areas (see Breeding Season below; NEAL and ALIBHAI 1991), which suggests that the regression of the testes is related, at least in part, to energy consumption.

Breeding season

The population of *T. leucogaster* in mixed woodland appears to have started breeding in September 1987 approximately three months ahead of the Miombo population which began breeding in December 1987. This difference was not related to rainfall or temperature because these were similar in the two areas, which were only 8–9 km apart. The diets of animals from the two areas were also similar and were virtually identical in terms of the proportions of seeds, stem and leaf, and arthropods consumed in November (Fig. 5) when the mixed woodland population was breeding but the Miombo population was sexually quiescent.

There is circumstantial evidence, however, that food may be more abundant in the mixed woodland area compared to Miombo, which would allow a greater consumption of food and provide more energy for reproduction. First, a large proportion of Miombo is burnt annually at the start of the dry season whereas the mixed woodland area was never burnt. Such burns would decrease the abundance of seeds, which form a major component of the diet, and also of arthropods by reducing the plant biomass. Second, the density of small mammals in the mixed woodland (258 animals at 862 trap locations) was almost twice as high as that in Miombo (178 animals at 1029 trap locations) although the densities of *T. leucogaster* were similar in the two areas (123 *Tatera* at 862 trap locations in mixed woodland and 171 *Tatera* at 1029 trap locations in Miombo). Third, the larger body mass, litter size and reproductive rate of mixed woodland animals compared to Miombo animals

is also more consistent with the proposed availability of food in the two areas rather than other possible causes such as differences in population density or age structure. On the basis of age structure one would expect Miombo animals to be heavier on average than those in mixed woodland but the reverse was true; no relationship was observed between litter size and age; and the density of this species was similar in the two study areas. Finally, a reproductive response to extra food has been demonstrated for this species, at least for males (NEAL and ALIBHAI 1991). A field experiment in August 1987 provided supplementary seeds for a period of 10 d to a population in Miombo habitat. In seed supplemented areas both sexes were significantly heavier, the testes of the males were approximately twice as heavy, and the seminal vesicles were three to four times as heavy as those of animals from control (i.e. non-supplemented) areas.

Thus, the seasonal breeding cycle may be explained as follows. Animals cease breeding in May at the start of the cool dry season. This is probably a response to the rapid decline in minimum temperature (Fig. 1), when the animals are active, although a photoperiod response cannot be discounted. The cessation of breeding does not seem to be linked to the availability of food or moisture because both areas were still lush and green from the previous month's rain, and seeds and insects were plentiful. Breeding starts again at the beginning of the hot dry season in September if high quality food is sufficiently available, as would seem to be the case in the mixed woodland area. If food is insufficient, breeding is delayed until the onset of the rains when the availability first of insects, and then seeds, increases. This would explain the breeding delay in Miombo.

The general pattern of breeding of *T. leucogaster* in Zambia (CHIDUMAYO 1980) and the northern Transvaal (PERRIN and SWANEPOEL 1987) is similar to that described for the mixed woodland area in Sengwa. Food has been suggested to have an important influence on the reproductive cycle of this and other species of the genus (CHIDUMAYO 1980; NEAL 1982; PERRIN and SWANEPOEL 1987), and ROWE-ROWE and MEESTER (1982) have suggested that low temperatures can further influence the timing of reproduction of small mammals in South Africa.

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Zusammenfassung

Saisonale Schwankungen in der Fortpflanzung und in der Nahrungszusammensetzung beim Bushveld Gerbil Tatera leucogaster (Muridae: Rodentia) in Zimbabwe

Die Fortpflanzungsverhältnisse und die Nahrungszusammensetzung von *Tatera leucogaster* wurden in zwei Gebieten (in gemischtem Waldland und in Miombo) in der Sengwa Wildlife Research Region untersucht. In beiden Populationen fand während der kühlen Trockenzeit keine Fortpflanzung statt. Eine Population begann aber drei Monate vor der anderen sich fortzupflanzen. Die zwei Populationen zeigten ein ähnliches Nahrungsspektrum, und Regenfall und Temperatur waren in den untersuchten Gebieten ebenfalls ähnlich. Der Unterschied in der Fortpflanzungsdauer beider Populationen hing wahrscheinlich mit dem Nahrungsangebot zusammen.

In beiden Gebieten betrug das Gewicht der Testes der adulten Männchen etwa 6 % ihres Gesamtkörpergewichts. Das Verhältnis von männlichen zu weiblichen adulten Tieren während der Fortpflanzungsperiode ergab mehr Weibchen.

Im gemischten Waldgebiet hatten die Weibchen eine durchschnittliche Wurfgröße von $5,6 \pm 0,3$. Daraus ergibt sich eine durchschnittliche jährliche Fortpflanzungskapazität von 28 Jungen pro adultem Weibchen. In Miombo hatten die Weibchen eine durchschnittliche Wurfgröße von $4,8 \pm 0,4$.

und entsprechend eine geringere durchschnittliche jährliche Fortpflanzungskapazität von 12 Jungen pro adultem Weibchen.

Die Nahrung bestand hauptsächlich aus Samen (50–70 %) und Insekten (10–40 %) und in geringerem Maße aus Gräsern und Blättern (< 10 %). Es waren nur geringe jahreszeitliche Veränderungen im Nahrungsspektrum festzustellen.

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