

## Breeding biology of the bushveld gerbil *Tatera leucogaster* in relation to diet, rainfall and life history theory

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The breeding habits of the bushveld gerbil *Tatera leucogaster* were examined in relation to rainfall and diet. Breeding is seasonal and associated with regular summer rainfall. The duration of the breeding season is variable, which is indicative of a temporally dynamic reproductive strategy. Litter size is large, and the punctuated iteroparity of *T. leucogaster* is associated with a xeric environment. The reproductive tactics of *T. leucogaster* are discussed in relation to other gerbils and rodents exhibiting similar reproductive strategies. *Tatera leucogaster* is a selective feeder on transient but seasonally available insects and seeds, but feeds on herbage when preferred foods are unavailable.

Die voortplantingsgewoontes van die bosveldnagmuis *Tatera leucogaster* is ondersoek met betrekking tot reënval en dieet. Seisoenale voortplanting is geassosieer met gereelde somerreënval. Die duur van die paartyd is onbestendig, wat 'n tyd-dinamiese reprodktiewe strategie aandui. Die werpsel is groot, en die gepunktueerde, herhaaldelike voortplanting van *T. leucogaster* is geassosieer met 'n dorre omgewing. Die reprodktiewe taktiek van *T. leucogaster* word bespreek met betrekking tot ander nagmuise en knaagdiers met 'n soortgelyke voortplantingsstrategie. *T. leucogaster* voed selektief op insekte en saad wat tydelik in 'n bepaalde seisoen beskikbaar is, maar eet groen gewasse wanneer hulle voorkeurvoedsel onbeskikbaar is.

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The species of the genus *Tatera* occur in sub-Saharan Africa, the Middle East and South Asia (Swanepoel, Schlitter & Genoways 1979). Summaries of the existing knowledge on this genus in southern Africa are given by De Graaff (1981) and Smithers (1983). The taxonomy of the genus has been briefly discussed (Swanepoel *et al.* 1979), but a critical need for a revision is evident (Schlitter 1978).

Rodents of the genus *Tatera* are members of the subfamily Gerbillinae. Owing to the disagreement on whether the Cricetidae should be included in the Muridae or not, the Gerbillinae which had generally been considered to be part of the Cricetidae, has been placed with the Muridae by Swanepoel, Smithers, & Rautenbach (1980); with cricetids by Honacki, Kinman, & Koepl (1982); and again with murids by Carlton & Musser (1984). For an extensive review of the problem see Carlton & Musser (1984). The genus includes nine species, four of which are known to occur in southern Africa (Swanepoel *et al.* 1980; De Graaff 1981).

In southern Africa *Tatera leucogaster* occurs in Southern Savanna Woodland, the Kalahari and parts of the Southern Savanna Grassland biotic zone and the South West Arid biotic zone (Davis 1962, 1974, 1975; Swanepoel *et al.* 1979; De Graaff 1981).

Despite the common occurrence and wide distribution of *Tatera* species and their importance as a permanent and primary reservoir of sylvatic plague in southern Africa (Davis 1946, 1953, 1964), little is known of their ecology. They are considered colonial, nocturnal, burrowing rodents, preferring sandy soil (De Graaff 1981; Smithers 1983). Population dynamics of *T. brantsii* have

been studied by Davis (1953) in the northern Orange Free State and De Moor (1969) on the Transvaal highveld, and of *T. leucogaster* by Swanepoel (unpublished data) in the northern Transvaal. Although easily handled in captivity they are difficult to breed in the laboratory (Keogh & Isaacson 1978).

Measroch (1954) and Allanson (1958) have contrasted the reproductive biology of *T. brantsii* and *T. afra* (females and males respectively). The studies were of particular ecological interest since they compared the breeding habits of two closely related rodents of similar size but living in different climatic and physical environments. The reproductive biology of three species of East African gerbils, namely *Tatera nigricauda*, *T. robusta* and *T. valida* have been studied by Neal (1982), while the reproductive biology of the Indian gerbil, *T. indica* has been studied by Prasad (1956) and Bland (1969).

The prime objectives of the present study were (i) to define the breeding season and feeding ecology of the Bushveld gerbil, *T. leucogaster*, (ii) to correlate seasonal changes in reproduction with changes in diet composition/quality and climate (rainfall), and (iii) to interpret the results in relation to previous studies of *Tatera* and current theories on the seasonality of reproduction (Stearns 1976).

### Methods

A total of 1266 (651 ♂♂; 615 ♀♀) *T. leucogaster* were collected during the period April 1968 to May 1971 from a 500-ha area situated in the northern Transvaal district of Soutpansberg, 11 km N, 13 km E of Dendron (23°

16° S; 23° 27' E: 2329 AD), 900 m a.s.l. on the farm Amsterdam.

The study area was situated in the Arid Sweet Bushveld type (Acocks 1975). The commonest trees and shrubs were: *Acacia tortilis*, *A. mellifera*, *A. permixta*, *Rhigozum brevispinosum*, *Mundulea sericea*, *Dichrostachys cinerea*, *Commiphora pyracanthoides*, *Maytenus senegalensis*, *Boscia albitrunca*, and *Grewia* spp; and grasses *Eragrostis rigidior*, *Aristida congesta*, *Pogonarthria squarrosa*, *Urochloa mosambicensis*, *Panicum maximum*, *P. colaratum*, *Themeda triandra*, and *Digitaria eriantha*.

A trapline comprising varying numbers (30 to 200) of snap traps, baited with peanut butter and oats, set at irregular intervals depending upon the habitat, for three to four trap nights at a time, was utilized to obtain small mammals from the study area. After such a trapping period, the traps were moved, and no sustained trapping effort was conducted. Therefore, the monthly sample obtained did not necessarily provide an indication of numerical change in the population.

All small mammal carcasses were fixed in 10% formalin, and subsequently identified, sexed, and standard museum measurements were taken. Clean mass was determined by removing the gastrointestinal tract: from the lower end of the oesophagus to the rectum, including the

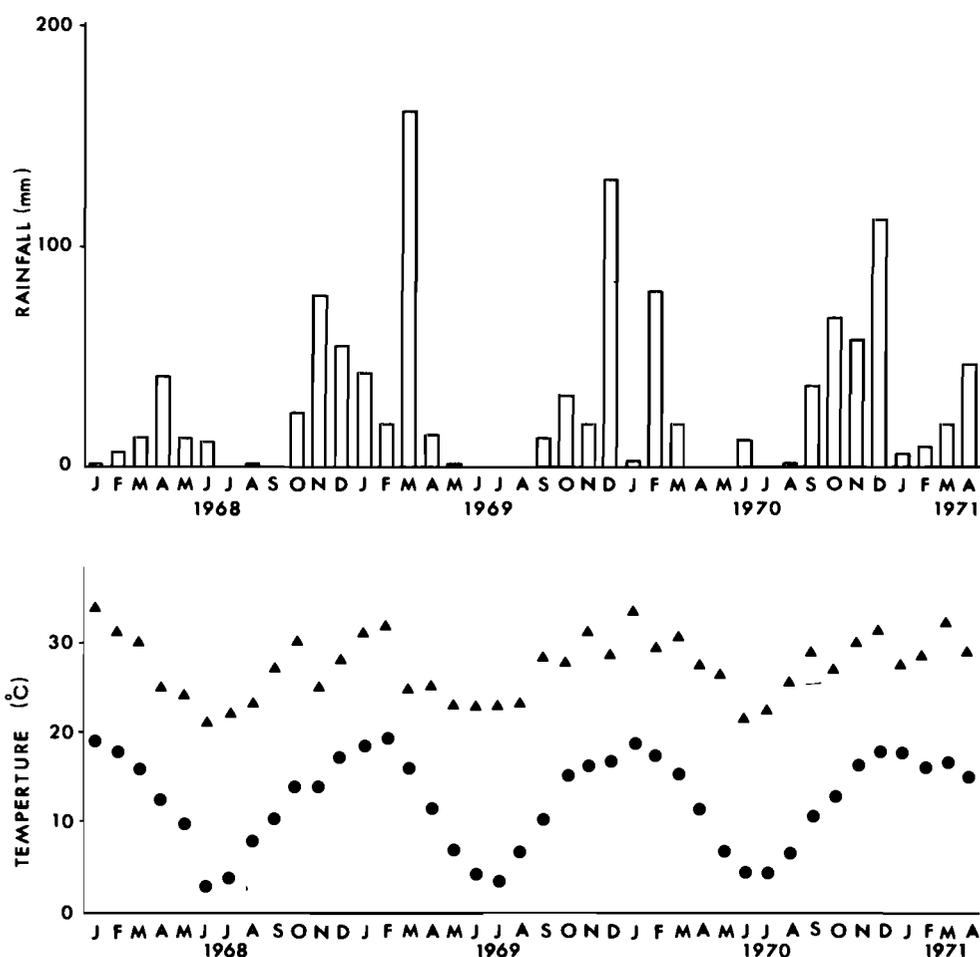
spleen but not the liver. In the case of pregnant females, the uteri and contents were also removed. Subsequently the remaining reproductive tracts, the eye lenses, kidneys, adrenal glands, and gastro-intestinal tracts were removed from the carcass and stored in 10% formalin.

Skulls of all specimens together with a small number of skins were deposited in the Kaffrarian Museum as voucher material.

Mean monthly maximum and minimum temperatures were calculated from standard Stevenson Screen charts obtained from a weather station located on the study area; total monthly rainfall was determined by summing daily precipitation records.

Ten full stomachs from each monthly sample (360 in total) were examined to determine food habits by the macro method of Perrin (1980a). The contents of each stomach were placed in a petri dish beneath a Wild stereo-microscope (6–50 magnification) and divided into plant and insect (and other arthropod) components. For most insects, legs, wings, elytra, mandibles and antennae were conspicuous. Green plant material was isolated from the sample by the subsequent removal of seeds and fruits. Dietary items were placed into three categories, i.e. (i) insects (and other arthropods), (ii) seeds (and fruit) and (iii) green plant matter.

In order to assess diet quality, the proximate con-



**Figure 1** Seasonal changes in total monthly rainfall (mm) and mean monthly minimum (●) and maximum (▲) temperatures (°C) at the study area from January to April 1971.

stituent concentrations of protein and fat were computed; since stomach contents were used for the identification of food items they were not available for chemical analysis. The following previously determined values (see Perrin 1980a) were employed; insects 42% protein, 44% fat; seeds 13% protein, 13% fat; plant matter 16% protein, 2% fat. Fat and protein levels were examined because both are important in rodent reproduction (Richardson, Godwin, Wilkes & Canman 1964) but are relatively scarce as a food resource; fat content can also be used as an index of calorific value in animal tissues/diets (Allen, Grimshaw, Parkinson & Quarmby 1974).

To quantify the seasonality and intensity of reproduction the following procedures were adopted. Testes were examined for spermatogenesis and the mean paired testis mass determined for the entire sample. Males were considered sexually mature if the testes were scrotal and spermatogenic, and if the accessory organs were large. The mean mass of all uteri were determined after being examined for placental scars. Embryos were counted, and their mass determined. Females were considered sexually mature if they were pregnant and/or lactating, or if they possessed a perforate vagina and hypertrophied uterus.

Age classes were established on the basis of eye lens mass employing the method of Perrin (1979). A detailed account of age determination and population age structure of *T. leucogaster* has been prepared (Perrin, Clarke & Swanepoel, unpublished data). Animals placed in age class one or two were classified as juveniles and sub-adults respectively; all other individuals were regarded as adults. Eye lens mass has been accepted as one of the more accurate and precise methods of age determination in small mammals (Morris 1972).

Comparisons between means were effected using Student's *t* test and were considered significant when  $p < 0,05$ .

## Results

The study area is located in the summer rainfall area, receiving 400 to 500 mm per annum on average (Weather Bureau, Department of Transport 1972). Rainfall data recorded from the study area are shown in Figure 1. Variation in precipitation among months and seasons was marked during the study, but a definite annual pattern was discernible. Total annual rainfall was considerably higher in 1968/69 (401 mm) than in either 1967/8 (206 mm), 1969/70 (313 mm) or in 1970/1 (285 mm). Rainfall, although low, was predictable in summer.

Mean minimum monthly temperature changed rhythmically throughout the year, while the mean maximum monthly temperature was more erratic (Figure 1). Mean change in daily temperature was  $14,7 \pm 2,7^{\circ}\text{C}$  (*S.D.*), and was similar to seasonal change between monthly maxima ( $13,4^{\circ}\text{C}$ ) and minima ( $17,7^{\circ}\text{C}$ ). The highest temperature ( $44^{\circ}\text{C}$ ) was recorded in January 1969 and the lowest ( $-3^{\circ}\text{C}$ ) in June 1968.

## Reproduction

Table 1 shows the number of specimens caught per month, their sex, and sex ratio. There were no significant departures from parity in the sex ratio in either the wet or dry seasons, and hence overall. Considerable recruitment occurred in the dry seasons of 1969, 1970 and 1971 which followed breeding during the preceding rainy seasons. Little recruitment was apparent during 1968

**Table 1** Number of captures, sex and sex ratio of *Tatera leucogaster* sampled over three years in the northern Transvaal

Date	Number of males	Number of females	Sex ratio ♂ / ♀	Total numbers
<b>1968</b>				
May	7	8	1,14	15
June	21	17	0,81	38
July	5	0	—	5
Sept	15	15	1,00	30
Oct	13	8	0,61	21
Nov	10	12	1,20	22
Dec	3	4	1,33	7
<b>1969</b>				
Jan	10	21	2,10	31
Feb	10	4	0,40	14
Mar	31	32	1,03	63
Apr	7	6	0,86	13
May	—	—	—	—
June	11	24	2,18	35
July	15	15	1,00	30
Aug	66	64	0,97	130
Sept	40	39	0,98	79
Oct	21	14	0,67	35
Nov	11	3	0,27	14
Dec	—	—	—	—
<b>1970</b>				
Jan	16	16	1,00	32
Feb	20	15	0,75	35
Mar	22	22	1,00	44
Apr	47	40	0,85	87
May	32	31	0,97	63
June	42	42	0,95	84
July	42	41	0,98	83
Aug	29	20	0,69	49
Sept	12	9	0,75	21
Oct	28	18	0,64	46
Nov	11	10	0,91	21
Dec	6	11	1,83	17
<b>1971</b>				
Jan	10	8	0,80	18
Feb	4	7	1,75	11
Mar	5	8	1,60	13
Apr	9	7	0,78	16
May	7	4	0,57	11
<b>Sub-totals</b>				
Dry season	420	402	0,96	822
Wet season	231	213	0,92	444
<b>Total</b>	<b>651</b>	<b>615</b>	<b>0,94</b>	<b>1266</b>

which was a dry year.

There was a distinct breeding season in *T. leucogaster* (Figure 2). The initiation and cessation of breeding activity was synchronized within and between sexes, although males became sexually mature (fertile) earlier than females in the shortened breeding season of 1969/70. The duration of the breeding season in 1968/69 and in 1970/1 was eight months (September to April), while it was reduced to five months (November to March) during 1969/70. A bimodal tendency (i.e. an early summer peak and a late summer peak) was apparent in the fertility of both male and female *T. leucogaster* in the 1970/1 season, which appears to be correlated with rainfall. The other two breeding seasons show an indication of this bimodality but it is not as obvious as in the 1970/1 season. During the breeding seasons a high proportion of adult males and females were fertile (Figure 2).

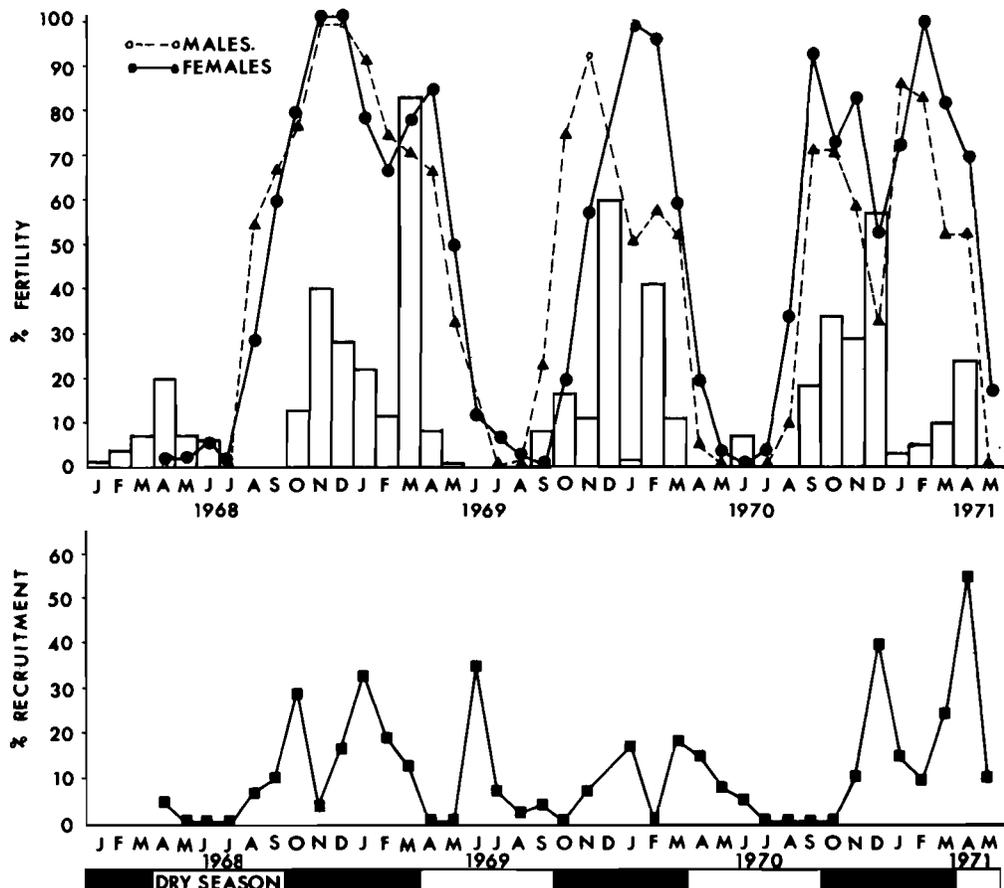
Recruitment (i.e. the percentage of the total population comprising juvenile or sub-adult individuals) was pulsed (Figure 3) in that many young-of-the-year were trapped in some months and none in others. This was a likely consequence of synchronized maturation and conception by female *T. leucogaster*, caused by the same cues for development and a constant periodicity between pregnancies during the breeding season.

The tendency for a recession in fertility at the centre of the 1970/1 breeding season (Figure 2) was confirmed

when testis and uterus masses were examined (Figure 3). A bimodal pattern was evident for female *T. leucogaster* for the other seasons investigated. The overall sex ratio (651♂ : 615♀) and those for the wet (231♂ : 213♀) and dry (420♂ : 401♀) seasons were not significantly different from parity. Skewing of the monthly sex ratio, usually to favour males, was sporadic, often associated with a small sample size, and aseasonal. Mean litter size determined from embryo counts was 4,38 (±1,20 n = 69), while the mean placental scar count was 4,44 (±1,63 n = 148): there was no significant difference between these data. The data did not indicate age-specific fecundity (Figure 4), but fertility appeared to be markedly age-specific (Figure 5). However, this was most likely the consequence of seasonal recruitment and maturation, rather than the result of some socio-physiological mechanism.

**Diet**

*Tatera leucogaster* is classified as a granivorous insectivore that feeds on herbage when preferred foods are unavailable. The stomach contents of the 360 samples examined, comprised 41,4% (±7,3) insects, 26,4% (±5,9) seeds and 32,2% (±6,7) herbage. There was a marked seasonal change in diet composition (Figure 6); insects and seeds predominated in the breeding season when rainfall and temperatures were high, while herbage



**Figure 2** Seasonal changes in the % fertility (sexual maturity / activity) of male (▲...▲) and female (●...●), and % recruitment (■...■) of *T. leucogaster* in the study population (n = 846). The black bar represents the wet season and the white bar the dry season; the histogram indicates monthly rainfall.

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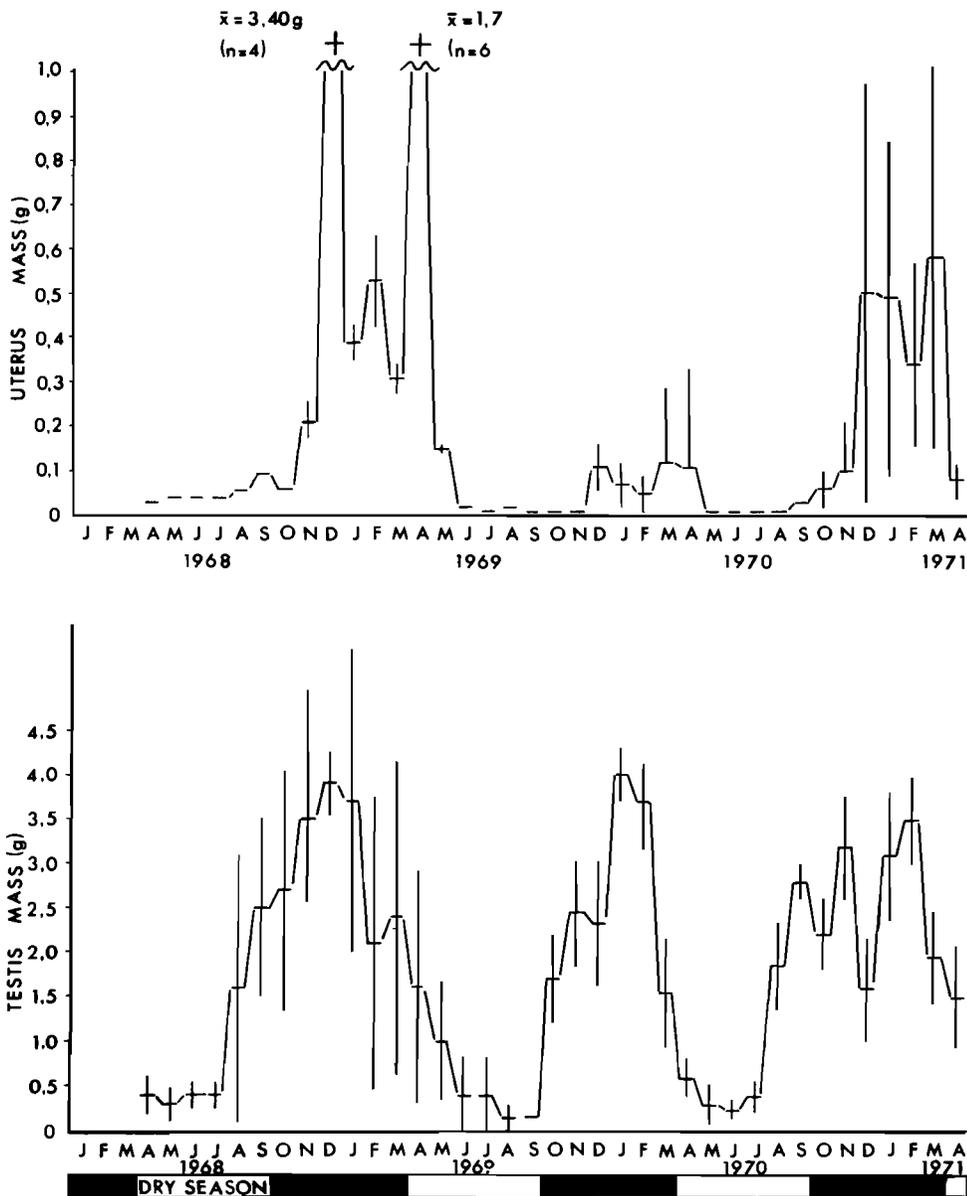


Figure 3 Seasonal changes in mean ( $\pm S.E.$ ) uterus mass (g) and mean ( $\pm S.E.$ ) paired testis mass (g) of *T. leucogaster* in the study population. The black bar represents the wet season and the white bar the dry season.

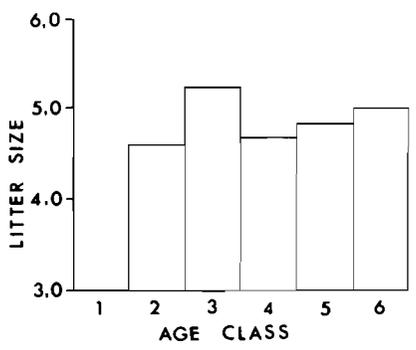


Figure 4 Age-specific fecundity (litter size) of *T. leucogaster* (n = 217).

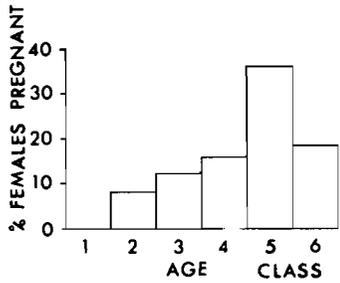
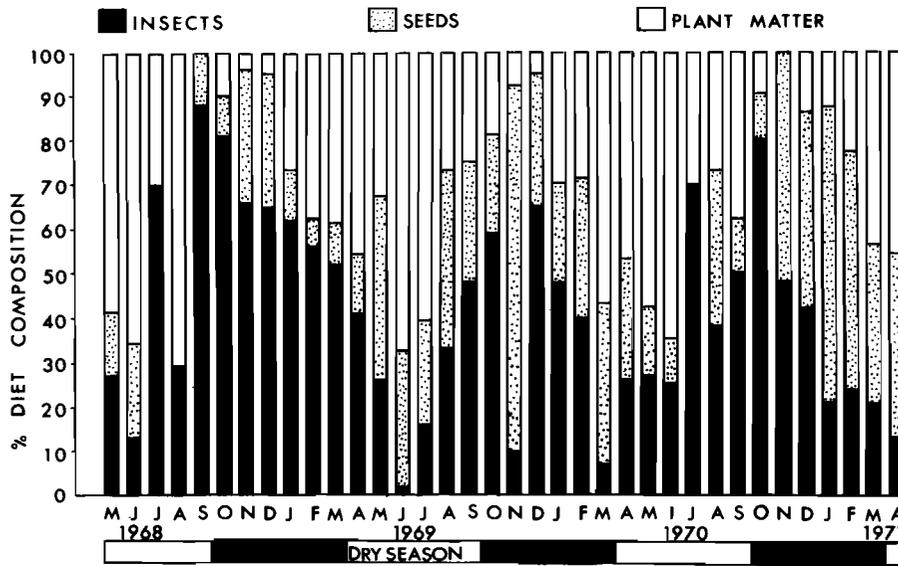


Figure 5 Age-specific fertility (% pregnancy) of *T. leucogaster* (n = 448).

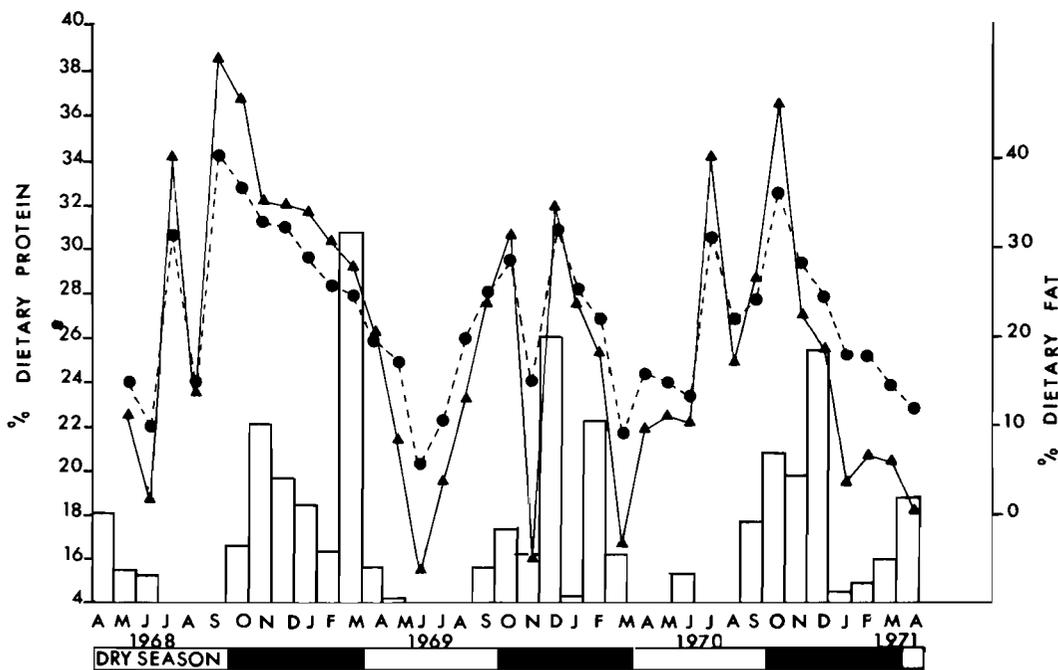
was eaten in large amounts in the non-breeding (dry) season. Fewer insects were present in the diet during the

1969/70 short breeding season; however, the seasonal change in diet composition over the three year study period was remarkably regular.

There were marked changes in the quality (fat and protein content) of the diet of *T. leucogaster* during the



**Figure 6** Seasonal changes in (%) diet composition of *T. leucogaster* in the study population ( $n = 360$ ). The black bar represents the wet season and the white bar the dry season.



**Figure 7** Seasonal changes in the diet quality (protein  $\blacktriangle$ ... $\blacktriangle$  and fat  $\bullet$ ... $\bullet$ ) of *T. leucogaster* in the study population ( $n = 360$ ). The black bar represents the wet season and the white bar the dry season.

annual cycle; these were evident each year (Figure 7). Fat and protein levels (were closely correlated, and) were high during summer and low during winter. Changes in diet quality were associated with insect abundance in the diet. During the short 1969/70 breeding season diet quality was low relative to the previous and following seasons. The fat and protein levels of the diet showed the bimodal pattern evident in the reproductive parameters and the climatic data.

**Discussion**

All phases of reproduction are subject to selective pres-

ures; and the final selection of the breeding pattern will ensure the temporal placement of mating, gestation, parturition, lactation and weaning that is most beneficial to the survival of the species (Skinner, Nel & Millar 1977).

*Tatera leucogaster* is a seasonal breeder in the arid, summer rainfall area of the northern Transvaal. Breeding occurs typically in the high rainfall months between October and March, but may extend into the months of April, May, August and September. This temporal pattern of reproduction is very similar to that reported for many African taterine gerbils (Table 2). *Tatera afra* breeds after the winter rains in the drier parts

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**Table 2** Reproductive parameters of African female gerbils of the genus *Tatera*

Species	Mean	Range	Sample size	Seasonality	Reference
<i>T. leucogaster</i>	4,6	3-7	21	No pregnancies, April to July	Rautenbach (1982)
	4,5	2-9	53	Young throughout the year	Smithers (1971 & 83)
	4,0	2-7	28	Pregnant Jan. to March, and May to September	Wilson (1975)
	4,4	2-9	217	Bimodal, associated with rainfall	Present study
<i>T. brantsii</i>	3,3	1-5	12	Pregnant May to Aug. and December	Smithers (1971 & 83)
	2,6	1-4	42	Young throughout the year except dry months	Measroch (1954)
<i>T. afra</i>	4,0	2-6	62	August to March, after winter rains	Measroch (1954)
<i>T. valida</i>	4,3	3-6	16	Bimodal, during the rains	Neal (1982)
<i>T. nigricauda</i>	5,2	1-8	37	Maximum during the rains, bimodal	Neal (1982)
<i>T. robusta</i>	4,7	2-7	13	Maximum during the rains, bimodal	Neal (1982)

of the year in the south-western Cape (Measroch 1954), but occurs in the most temperate climate and has the most extreme latitudinal distribution of all the species considered. Positive correlations between the seasonality of breeding and the occurrence of seasonal rains are now well established for many African arid zone rodents (Field 1975; Perrin 1980b; Neal 1982). The positive association between rainfall and breeding activity does not mean that rainfall directly initiates oestrus and / or spermatogenesis, although this is known to occur in the rabbit in Western Australia (Gooding & Long 1957). It appears that the combined effect of rainfall and resultant changes in food supply / nutrition serve to initiate reproduction (Sadleir 1969).

Reynolds (1960) reported two peaks of breeding in Merriam's kangaroo rat, *Dipodomys merriami*, which corresponded closely with periods of new vegetation growth in spring and late summer. The same association was recorded for cottontail rabbits *Sylvilagus floridanus* by Bothma (1969), who also noted that the onset of breeding was correlated with the initial break in drought, and that high temperature and too low or too high rainfall limited breeding. The onset of reproduction following rains in herbivorous mammals may be attributed to oestrogenic effects derived from the growing tips of sprouting vegetation (Bodenheimer & Sulman 1946; Poole 1969; Myers & Poole 1962; Newsome 1966).

According to Measroch (1954) many equatorial mammals lack seasonal breeding periodicity. The results obtained by various workers (Allanson 1958; Chapman, Chapman & Robertson 1959; Delany 1964a, b; Coetzee 1965; Dieterlen 1967; Delany & Neal 1966, 1969), however, indicate that many species of small rodents have a restricted breeding season in tropical and southern Africa that corresponds with the rainy season.

Variation in the length of the breeding season is a primary factor held responsible for numerical change in many rodent populations (Krebs & Myers 1974; Neal 1982), and in arid environments is likely influenced by the extent and pattern of seasonal rainfall (Sadleir 1969).

The length of the breeding season of *T. leucogaster* was shortened during the lower rainfall summer season of 1969/70 and 1970/1. Marked change in the duration of the breeding season is compatible with the concept of a temporally dynamic reproductive strategy (Conley, Nichols & Tipton 1976). This concept was developed following the examination of life history characteristics of certain deserticolous rodents that exhibit shifts in reproductive capacity with time along the *r-k* continuum. In populations of such dynamic strategists, changes in reproductive activity occur within the same individuals in response to variable environmental cues / conditions (Conley *et al.* 1976).

In gerbils with annual breeding seasons, the period of fertility of the two sexes usually corresponds closely although sexual maturation in the male may precede that of the female (Allanson 1958). Such synchrony was clearly evident for *T. leucogaster* during each season. However, during the 1969/70 shortened breeding season, male maturation preceded that of females, whereas during the mid-summer of 1970/1 several adult males became infertile. A similar cessation of breeding activity during mid-summer has been reported for *T. brantsii* in the northern Orange Free State (Davis 1953) and in the seasonally breeding broad niche grassland to semi-arid zone murid *Rhabdomys pumilio* (Perrin 1980c). The cause of the cessation in the present study was not established.

Diet quality was good from June until November but deteriorated from December until April. Since the rodents were fertile from January to April, it is unlikely that a poor diet was the cause of the interruption of reproduction. Brooks (1974), who worked on *R. pumilio* in the Transvaal, suggested that such negative breeding responses were attributable to high temperatures and drought. However, none of these factors alone appear to be a sufficient explanation of the phenomenon observed in *T. leucogaster*. During the cessation, the diet was un-nutritious and the weather was hot and dry. It is possible that protein metabolism was inefficient because of water

shortage (Schmidt-Nielsen & Schmidt-Nielsen 1952) which curtailed reproduction (Richardson *et al.* 1964). It is unlikely that a socio-agonistic factor was implicated since breeding recommenced after only a short cessation.

It is meaningful to compare the reproductive adaptations of *T. leucogaster* with other taterine gerbils (Table 2), since such adaptations influence their demographics. Since frequency of breeding (Neal 1982), litter size and time from birth to weaning (Millar 1978) are the key adaptive variables of mammalian reproduction, because litter size is the predominant factor determining the energy requirements of breeding female mammals (Millar 1977), and since the development of southern African taterine gerbils are very similar (Measroch 1954), litter size can be used for preliminary comparisons. Litter sizes of the six species of gerbils shown in Table 2 are remarkably similar, with the possible exceptions of *T. brantsii* where litter size is relatively small and *T. nigricauda* where litter size is relatively large. The observed differences in litter size do not appear to support a latitudinal gradient explanation, or early theoretical considerations of  $r$  and  $K$  theory (Pianka 1956). This may well be because the frequency of reproduction varies with species, latitude and ecological conditions. For example, *T. valida* (from western Uganda) has a litter size of 4,3 which is not dissimilar from that of 5,2 of *T. nigricauda* (in central Kenya), but the difference in reproductive capacity (i.e. the average number of young produced per adult female per year) is very considerable, at 8,5 versus 25 to 28 (Neal 1982). Such adaptations in reproductive parameters may partially explain the population explosions of taterine gerbils (Davis 1953; Smithers 1971) and the competitive interaction between species (Kern 1981), but other factors such as habitat preference and plasticity in feeding habits must also be significant. (For example, farming activities may create an abundance of food in predator-free space, even when natural rainfall is low).

*Tatera leucogaster*, previously assumed only to take insects occasionally (Smithers 1983), has been shown to be a predominantly granivorous insectivore. Levels of dietary protein and fat in *T. leucogaster* were seasonally variable, but higher than in the omnivorous murid *R. pumilio* (Perrin 1980a). Leatham (1961) has indicated that the optimal level of dietary protein to support reproduction and growth in laboratory rats is 16%, whereas Richardson *et al.* (1964) found that while 14% dietary protein was sufficient to support gestation, 10% was insufficient to support lactation. Although the protein requirements of breeding *T. leucogaster* are unknown, it is unlikely that gerbils were prevented from breeding at any season because of an inadequate supply of dietary protein, owing to the elevated levels of this resource. This is evidently a consequence of optimal foraging rather than digestive system adaptation (Perrin & Curtis 1980), and contrasts with the strategies of omnivorous *R. pumilio* and herbivorous *Otomys irroratus* (Perrin 1980b).

Measroch (1954) associated differences in reproductive tactics between closely related species with dif-

ferent climatic and physical environments. However, *T. leucogaster* and *T. brantsii* may occupy similar habitats in sympatry (Smithers 1971), and yet their litter sizes are dissimilar. What is the rational explanation of this phenomenon? Clearly the two species evolved under a multitude of selection pressures, but food might be a significant factor. Perrin (1980a,b,c) has reported significant differences in reproductive strategies of coexisting rodents in a semi-arid environment that were caused by differences in feeding habits. *Tatera leucogaster* consumes a highly nutritious diet during the summer rainfall period and is able to commit much of its energy and protein into progeny by producing large litters. Evidently rainfall influences diet composition and quality, which, through evolutionary time has led to a regular, seasonal breeding pattern and a large litter size. This strategy, which is based on insectivory, has many parallels with that exhibited by *R. pumilio* in an irregular rainfall area (Perrin 1980a,b,c). It seems likely that although it eats some insects (Smithers 1983) *T. brantsii* has a less nutritious diet than *T. leucogaster* and therefore cannot afford sufficient protein for large litters; or explained differently, it has increased longevity and reduced fecundity owing to environmental pressures.

Alternatively the small litter size of *T. brantsii* may not be caused by habitat *per se* (Southwood 1977) but by age-specific mortality / predation (Murphy 1968; Schaffer 1974). For example, a fluctuating environment that has its impact on juvenile mortality favours reduced reproductive effort, smaller litters, precocial progeny and long-lived organisms. Thus, animals living in a situation that one would expect to select for an increased reproductive effort actually show a decreased reproductive effort (Stearns 1976). No published work presents data that would allow for discrimination between the alternate explanations of  $r$  and  $K$  theory and bet-hedging.

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