

## Reproductive biology of three species of gerbils (Genus *Tatera*) in East Africa

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### Abstract

The reproductive ecology of *Tatera nigricauda* and *T. robusta* was studied in Meru National Park in central Kenya, and *T. valida* was studied in the Ruwenzori National Park in western Uganda. In both areas seasonal changes in photoperiod were negligible, but there was a bimodal pattern of rainfall. Samples of 398 *T. nigricauda*, 61 *T. robusta* and 116 *T. valida*, collected over periods of at least one year, provided information on seasonal breeding activity, litter size, population structure, and reproductive capacity.

*Tatera valida* only bred during the rains in western Uganda. Adult females had the capacity to produce two litters each year. The average litter size was  $4.25 \pm 0.21$ , resulting in an average annual reproductive capacity of 8.5 young per adult female.

*Tatera nigricauda* bred throughout most of the year in central Kenya. Breeding was at a maximum during the rains and immediately afterwards, then declined and ceased towards the end of the dry seasons. However, breeding began again before the onset of the rains. Young were only recruited into the population during the two months after each rainy season, suggesting that litters conceived during the dry seasons died before they were weaned. Adult females had the capacity to produce approximately 5 litters each year. The average litter size was  $5.2 \pm 0.24$ , and the annual reproductive capacity was 25–28 young per adult female.

*Tatera robusta* appeared to have a breeding periodicity similar to that of *T. nigricauda*. The average litter size was  $4.7 \pm 0.43$ .

A comparison of the reproductive characteristics of different species of *Tatera* did not show any significant relationships between body mass, litter size, duration of breeding, and reproductive capacity. It is suggested that food may be the most important factor affecting the breeding pattern of this genus.

### Introduction

There have been numerous studies on the breeding biology of members of the genus *Tatera*, both within Africa (ALLANSON 1958; DELANY and NEAL 1969; GAUTUN 1975; HANNEY 1965; HUBERT 1977; HUBERT and ADAM 1975; MEASROCH 1954; PIRLOT 1954; SHEPPE 1973; SHORTRIDGE 1934; SMITHERS 1971) and the Indian subcontinent (BEG and AJMAL 1977; CHANDRAHAS and KRISHNASWAMI 1974; JAIN 1970; PHILLIPS 1923; PRASAD 1953, 1956, 1961). The Asian studies have been compared, but there has been little attempt to interrelate the various studies on African *Tatera*.

In this paper I document the breeding biology of *Tatera nigricauda* and present notes on the breeding biology of *T. robusta* collected in Meru National Park in central Kenya. To date there have been no detailed studies on either of these species. I also present additional information, to that previously published (DELANY and NEAL 1969), on *T. valida* in western Uganda. Finally, I review the available information on breeding season, body mass, litter size and annual reproductive capacity of both African and Asian *Tatera* to determine what patterns, if any, exist.

The nomenclature of the African species follows DAVIS (1971), but because of disagreement on the status of some named forms (see, for example, MATTHEY and PETTER 1970) the type name is given as a subspecies in some cases. The nomenclature of the Asian types follows ELLERMAN and MORRISON-SCOTT (1951).

## Material and methods

### Collection and classification of material

A total of 116 *T. valida* was collected from the Crater Track region (0° 06'S, 29° 54'E) of the Ruwenzori National Park, Uganda; and 61 *T. robusta* and 398 *T. nigricauda* were collected from the Rojewero Plains (0° 11'N, 38° 10'E) and surrounding areas of the Meru National Park, Kenya. Descriptions of the study areas are provided by NEAL (1970, 1981) and AMENT (1975). Both areas were sampled by standard trap lines, spaced approximately 50 m apart with the traps set at 10 pace intervals. Collections were made each month for periods of at least one year.

Processing and classification of reproductive material was identical to that described by NEAL (1981). Briefly, animals were measured, dissected, examined macroscopically, and a sperm smear was taken from the cauda epididymides of the males, soon after capture. The mass of the various reproductive organs was measured after fixation in Bouin's solution, and the ovaries of the females collected in Kenya were also serially sectioned. Based on the examination of the reproductive organs the animals were classed as immature or mature, and mature females were further classified as visibly pregnant, reproductively active, or reproductively inactive.

Head-body length was used as a criterion of age. It was useful for separating the young, immature animals from the adults, but different cohorts could not be separated after the animals reached adult size.

### Reproductive capacity

I calculated the reproductive capacity (i. e. the potential annual production of young per adult female) of *T. valida* and *T. nigricauda*, and of other species for which information was available in the literature, using the method described by NEAL (1981). In this method the interval between litters is considered to be the sum of the non-pregnant period ( $p_0$ ), the pre-implantation period ( $p_1$ ), and the post-implantation period ( $p_v$ ) when embryos are macroscopically visible. The gestation period ( $G$ ) is the sum of  $p_1$  and  $p_v$ . In most studies females with pre-implantation stages of pregnancy were not distinguished from non-pregnant adults. In these cases the ratio of  $p_0 + p_1$  to  $p_v$  was assumed to be the same as the ratio of non-visibly pregnant adults to visibly pregnant adults. However, MEASROCH (1954) detected all stages of pregnancy. In this case I assumed that the ratio of  $p_0$  to  $G$  was the same as the ratio of nonpregnant adults to pregnant adults.

These equations were solved for  $p_0$  using estimates of  $G$  in the literature (BLAND 1969; HUBBARD 1970; HUBERT and ADAM 1975; MEASROCH 1954), and assuming that  $p_1$  equaled 4d (see NEAL 1981). For those species for which no estimate of gestation period was available a range of values (22–25d) was used. The mean interval between litters ( $p_0 + p_1 + p_v$ ) was then calculated, and the production of young was estimated for a given time period using the average litter size. However, the gestation period can be considerably lengthened due to delayed implantation in lactating females (BLAND 1969; MEASROCH 1954). In those studies where only visible pregnancies were detected the calculation of reproductive capacity is not influenced by delayed implantation, because the error in  $p_1$  is exactly compensated by the error in  $p_0$ . However, in the study of MEASROCH (1954), in which all stages of pregnancy are detected, the increased length of gestation must be calculated. This was determined from her data by assuming that the ratio of  $p_1$  with delayed implantation to  $p_1$  with no delayed implantation (4d) was equal to the ratio of the percentage of unimplanted embryos in pregnant lactating females to the percentage of unimplanted embryos in pregnant non-lactating females.

### Statistics

Seasonal changes in body mass, mass of the testes and seminal vesicles, and litter size were analyzed by one way analysis of variance (SOKAL and ROHLF 1969).

Variation in litter size in relation to eviscerated maternal body mass and season of pregnancy was investigated by analysis of covariance (SNEDECOR and COCHRAN 1967). The sample was divided into those collected during the rains and immediately afterwards (November to mid-January, mid-April to mid-June) and those collected during the dry periods.

The interrelationships between body mass, litter size, reproductive capacity, and duration of breeding of the various species were analyzed by Kendall's coefficient of rank correlation (SOKAL and ROHLF 1969).

## Results

### Body mass

The body mass of embryos of the heaviest litters ranged from 3.6–3.8 g in *T. valida* and 3.5–3.9 g in *T. nigricauda*. The birth mass is estimated to be approximately 4 g in both

Table 1

Adult body mass (g), mean and range (in parentheses), of various species of *Tatera*

Species	Locality	Body mass		Authority
		Males	Females	
<i>T. robusta</i>	Kenya	91 (70–130) 103 (80–152)	85 (70–100) <sup>1</sup> 102 (80–130) <sup>2</sup>	This study
<i>T. nigricauda</i>	Kenya	115 (70–170) 132 (80–195)	95 (70–120) <sup>1</sup> 114 (80–161) <sup>2</sup>	This study
<i>T. leucogaster</i>	Zambia	(51–106) <sup>2</sup>		SHEPPE (1973)
<i>T. leucogaster</i>	Botswana			SMITHERS (1971)
	Okavanga	73 (50–96 )	71 (50–110) <sup>2</sup>	
	Kasane	58 (46–79 )	54 (46–78 ) <sup>2</sup>	
<i>T. afra</i>	S. Africa	70 (50–121)	66 (45–90 ) <sup>1</sup>	{ ALLANSON (1958)
<i>T. brantsii</i>	S. Africa	81 (50–116)	74 (50–106) <sup>1</sup>	
<i>T. brantsii</i>	Botswana	96 (82–125)	89 (74–105) <sup>2</sup>	SMITHERS (1971)
<i>T. valida</i>	Uganda	113 (70–140) 129 (90–160)	92 (70–105) <sup>1</sup> 113 (90–130) <sup>2</sup>	This study
<i>T. v. gambiana</i>	Senegal	(100–180) <sup>2</sup>		HUBERT and ADAM (1975)
<i>T. indica</i> <i>hardwickei</i>	India	(80–200+) <sup>2</sup>		CHANDRAHAS and KRISHNASWAMI (1974)
<i>T. i. cuvieri</i>	India	(90–210)	(90–250) <sup>2</sup>	PRASAD (1956, 1961)
<i>T. i. indica</i>	India	(100–213)	(70–193) <sup>2</sup>	JAIN (1970)

<sup>1</sup> eviscerated body mass; <sup>2</sup> total body mass.

species, compared to estimates of 4.5 g for *T. afra* and 5.5 g for *T. brantsii* (MEASROCH 1954), and a recorded birth mass of 4.4 g for *T. brantsii* (MEESTER and HALLETT 1970) in South Africa.

The smallest *T. valida* and *T. nigricauda* trapped had a body mass of approximately 30 g (eviscerated mass 25 g) which is assumed to be the mass of weanlings. Animals normally attained puberty at a body mass of 90–100 g in *T. valida*, 80–90 g in *T. robusta*, and 80–100 g in *T. nigricauda*. Adult body mass varied seasonally in *T. nigricauda*, reaching a maximum during the rains and decreasing 6–7 percent during the dry seasons. The difference was significant in females ( $F_{1,120} = 7.1$ ;  $P < 0.01$ ) and almost significant in males ( $F_{1,126} = 3.3$ ;  $P < 0.1$ ). No seasonal changes in adult body mass were observed in *T. valida* or *T. robusta*.

The adult body mass of the species I studied is compared to those of other species in Table 1. The species, ranked in order of increasing adult body mass, are *T. leucogaster*, *T. afra*, *T. brantsii*, *T. robusta*, *T. valida* and *T. nigricauda*, *T. v. gambiana*, *T. indica*. It may be noted that males are usually a little heavier than females.

### Breeding season

There were two periods of breeding activity a year in *T. valida* in western Uganda, which were correlated with the bimodal pattern of rainfall (Fig. 1 B, D). During the second April–May period of study only 3 adult females were collected, which makes it impossible to deduce anything from the absence of pregnancies at this time.

*T. nigricauda* also had a bimodal pattern of breeding which was correlated with the pattern of rainfall (Fig. 2 B, D). Breeding was at a maximum during the rains and the month following the rains, then declined during the dry season, and ceased in September and March. However, breeding began again before the onset of the rains. One peculiar feature

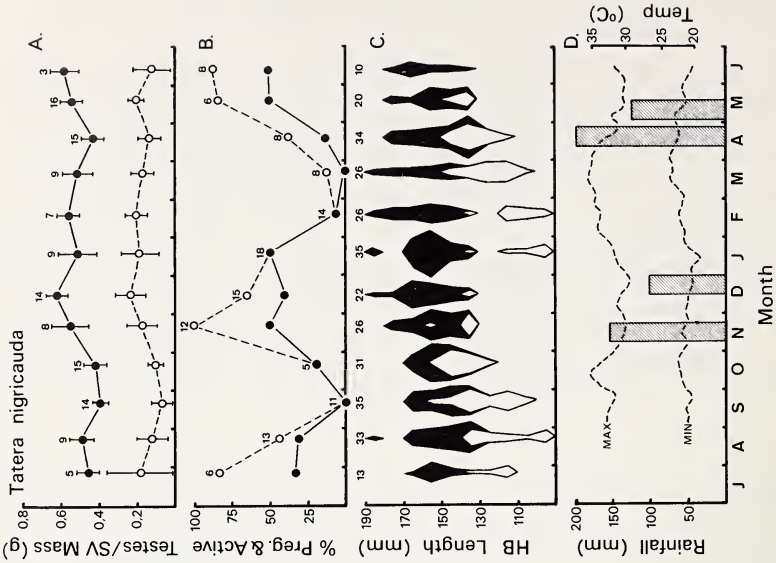


Fig. 2. Seasonal changes in reproductive activity of *T. nigricauda* in relation to rainfall and temperature. Notation as in Fig. 1 except B. ●—● percentage of adult females visibly pregnant, and ○—○ percentage of adult females with corpora lutea

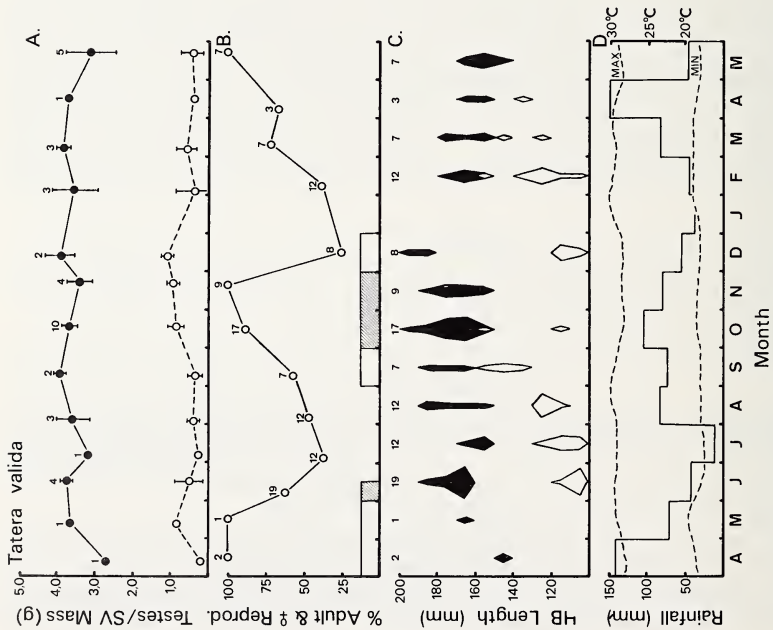


Fig. 1. Seasonal changes in reproductive activity of *T. valida* in relation to rainfall and temperature. Numbers in figures A-C represent sample sizes. A: ●—● adult testes mass, ○—○ adult seminal vesicles mass. Data points represent means and vertical lines  $\pm 2 \times$  S.E. B: Percentage of adult animals in samples ○—○, and pregnancies observed ■ or inferred □



of the breeding pattern was that breeding activity declined and ceased much more rapidly during the January – mid-April dry season compared to the June – October dry season. This pattern was also observed in *Arvicanthis* (NEAL 1981), and may be associated with increased temperatures at the end of each dry season.

Pregnancies were observed in *T. robusta*, or inferred from the presence of lactating females, during the periods July–August and November–January. It seems likely that the pattern of breeding is similar to that of *T. nigricauda*.

The mass of the adult testes and seminal vesicles of *T. nigricauda* were significantly greater during the rains and the month following the rains, compared to the dry seasons. There was no evidence in the three species I studied that males became sexually inactive during the periods of the year when females were not breeding. In contrast, the testes regress, and the males become sexually quiescent during the periods of the year when females are in anoestrus, in *T. afra* (ALLANSON 1958), *T. leucogaster* (HANNEY 1965), and *T. indica* (BEG and AJMAL 1977; CHANDRAHAS and KRISHNASWAMI 1974; PRASAD 1956).

There is little consistency in the seasonal pattern of breeding in relation to rainfall in the genus *Tatera* (Fig. 3). In Africa, the delay between the onset of the rains and the start of the breeding period, or period of peak breeding activity, increases as one proceeds further from the equator. However, the opposite trend occurs in Asia (Fig. 3). In *T. afra* in South Africa (MEASROCH 1954) and *T. i. indica* in Pakistan (BEG and AJMAL 1977), the cessation of breeding is associated with the coldest season of the year.

#### Litter size

Only five pregnant *T. valida* were collected: four of which had 4 embryos each, and one 3 embryos. The average litter size of 16 animals that were either pregnant or had a single set of placental scars was  $4.25 \pm 0.21$  (range 3–6). DELANY (1964) records a female with 4 embryos in Uganda, and HUBERT and ADAM (1975) record that *T. v. gambiana* has 2–6 young per litter in Senegal.

Five pregnant *T. robusta* were collected: single individuals of which had 2, 6 and 7

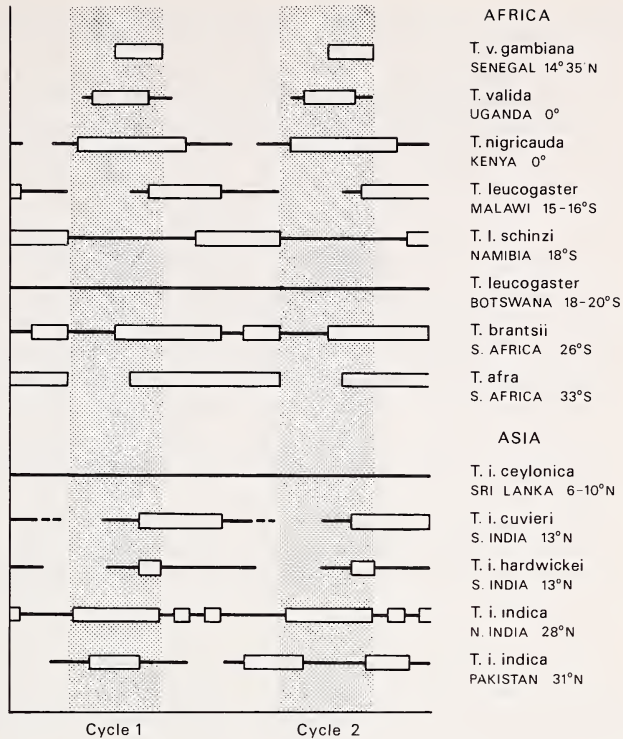


Fig. 3. Period of pregnancies in relation to wet and dry seasons. The shaded areas represent rainy periods which have been given a common length. Where a locality has two rainy seasons each year these are represented by two cycles; if there is only one rainy season then the information is duplicated in the two cycles. The open blocks represent the periods when pregnancies are particularly numerous, the solid line periods when few pregnancies are observed

embryos, and two individuals each had 4 implanted embryos which included a single resorbing embryo. The average number of implanted embryos of 13 animals that were either pregnant or had a single set of placental scars was  $4.69 \pm 0.43$  (range 2–7). SHORTRIDGE (1934) records an average litter size of 4–5 young in this species.

The mean number of implanted embryos (resorbing embryos included) of 37 pregnancies in *T. nigricauda* was  $5.43 \pm 0.23$  (range 1–8); that of live embryos only was  $5.22 \pm 0.24$  (range 1–8). Litter size increased significantly with increase in maternal body mass ( $F_{1,34} = 12.9$ ;  $P < 0.001$  for implanted embryos,  $F_{1,34} = 7.1$ ;  $P < 0.025$  for live embryos), and this relationship was the same in the wet and dry seasons. However, the average litter size during the wet seasons ( $5.7 \pm 0.21$  implanted embryos,  $5.54 \pm 0.22$  live embryos) was significantly higher ( $F_{1,35} = 5.34$ ;  $P < 0.05$  for implanted embryos,  $F_{1,35} = 6.37$ ;  $P < 0.025$  for live embryos) than that recorded during the dry seasons ( $4.56 \pm 0.65$  implanted embryos,  $4.22 \pm 0.64$  live embryos). This difference in litter size was largely accounted for by the difference in size of the mothers in the two seasons. The average eviscerated body mass of pregnant females during the wet seasons was 102 g compared to 90 g during the dry seasons. Litter size has also been observed to vary seasonally, and be positively correlated with maternal body mass in *T. afra* (MEASROCH 1954) and *T. i. cuvieri* (PRASAD 1961).

The litter sizes of *T. valida*, *T. robusta*, and *T. nigricauda* are amongst the largest recorded for African *Tatera*, but are generally smaller than the Asian species. The usual litter size of other African species are 4–5 in *T. leucogaster* in Botswana (SMITHERS 1971),

Table 2

Potential breeding rates and reproductive capacity of various species of *Tatera*

Species	Period of reproduction	Interval between litters (days)	No. of litters	Litter size	Prod. young/adult ♀
<i>T. valida</i> (This study)	Rains	109	2	4.25	8.5
<i>T. nigricauda</i> (This study)	Wet	40– 44	3.5–3.8	5.5	19–21
	Dry	97–107	1.4–1.6	4.2	6– 7
	Annual		$\frac{4.9-5.4}{}$		$\frac{25-28^1}{}$
<i>T. afra</i> (MEASROCH 1954)	Aug-Mar	38– 47	5.2–6.4	4.0	21–26 <sup>2</sup>
<i>T. brantsii</i> (MEASROCH 1954)	Mar-Sep	56– 69	3.1–3.8	2.6	8–10
	Oct-Feb	109–133	1.1–1.4	2.6	3– 4
	Annual		$\frac{4.2-5.2}{}$		$\frac{11-14^2}{}$
<i>T. i. cuvieri</i> (PRASAD 1953, 1961)	Aug/Sep– Feb/Apr	60	3.0–4.5	6.3	19–29 <sup>3</sup>
<i>T. i. hardwickei</i> (CHANDRAHAS and KRISHNASWAMI 1974)	Aug–Mar/Apr	95–103	2.6	5.8	15 <sup>4</sup>
<i>T. i. indica</i> (JAIN 1970)	All year	67	5.5	4.8	26
<i>T. i. indica</i> (BEG and AJMAL 1977)	Most of year	42– 52	5.3–6.5	6.3	33–41 <sup>4</sup>

Rates vary according to: <sup>1</sup> estimate of gestation period; <sup>2</sup> delayed implantation; <sup>3</sup> length of breeding season; <sup>4</sup> length of breeding season and breeding rate.

Zambia (SHEPPE 1973), and Malawi (HANNEY 1965); 3–5 in *T. afra* in South Africa (MEASROCH 1954); 2–4 in *T. brantsii* in South Africa (MEASROCH 1954) and Botswana (SMITHERS 1971); 2–3 in *T. inclusa pringlei* in northern Tanzania (HUBBARD 1970). The Asian species have litter sizes of 2–4 in *T. indica ceylonica* in Sri Lanka (PHILLIPS 1923); 5–8 in *T. i. cuvieri* in Bangalore, India (PRASAD 1961); 4–8 in *T. i. hardwickei* in Kolar, India (CHANDRAHAS and KRISHNASWAMI 1974); 3–6 in *T. i. indica* in the Rajasthan Desert, India (JAIN 1970), and 5–7 for this subspecies in Pakistan (BEG and AJMAL 1977).

### Breeding rates and reproductive capacity

The reproductive capacity (potential annual production of young per adult female) of several different species of *Tatera* is compared in Table 2. *T. valida* appears to have a particularly low reproductive capacity, mainly because of a low breeding rate and short breeding season. *T. v. gambiana* probably also has a low reproductive capacity in Senegal, because breeding was confined to two months each year and there were only 2–6 young per litter (HUBERT 1977; HUBERT and ADAM 1975).

The reproductive capacity of *T. nigricauda* was similar to that of several other species of *Tatera*, and was much higher than that of *T. valida* (Table 2). Adult females had the potential to produce about 5 litters a year, but counts of placental scars showed that no female had more than three litters. Thus, the observed reproductive capacity must have been achieved by having a high turnover rate of adult females.

Reproductive capacity depends on the intensity of breeding activity, the length of the breeding period, and litter size. However, there appeared to be no simple correlation between any one of these parameters and reproductive capacity (Table 2). The reproductive capacity could be low because of a low intensity of breeding, as in *T. valida* and *T. i. hardwickei*; a short breeding period, as in *T. v. gambiana*; or a small litter size, as in *T. afra*.

### Population structure

The population structure of *T. valida* and *T. nigricauda* (Fig. 1 C, 2 C) indicated a marked seasonal recruitment of young into the population. This was particularly evident in *T. nigricauda*, in which recruitment of young was confined to the periods January–February and July–August, even though breeding continued throughout most of the year (Fig. 2 B, C). Thus, young only appeared to be successfully weaned in those litters which were conceived during the rains.

## Discussion

### Reproductive characteristics

The observed positive correlation between litter size and maternal body mass in *T. nigricauda* (this study), *T. afra* (MEASROCH 1954), and *T. i. cuvieri* (PRASAD 1961) is a trend which is probably present in most populations of this genus. The trend is probably related to the increased size of the reproductive tract and increased energy reserves of larger females.

In contrast, when different populations and species of *Tatera* are compared a negative correlation is expected between litter size and maternal body mass (size). This is because longevity correlates positively with absolute body size, and longer lived species generally have lower reproductive rates than shorter lived species (EISENBERG 1981). However, the largest species of *Tatera* had the largest size of litters, although the trend was not statistically significant. In addition there was no obvious correlation between litter size and latitude, contrary to what has been reported for this genus by BEG and AJMAL (1977).

A negative correlation is also expected between reproductive capacity (number of



offspring per adult female per year) and adult body mass (size), for similar reasons to that stated above. However, no such trend is evident in the genus *Tatera* (cf Tables 1 and 2).

Thus, a comparison of the reproductive characteristics of the various species of *Tatera* failed to identify many of the patterns that are normally expected. In this respect, *Tatera* gerbils are similar to the spiny mice of the genus *Acomys* (NEAL 1982a) but differ from the unstriped grass rats of the genus *Arvicanthis* (NEAL 1981) and the elephant shrews (NEAL 1982b).

### Breeding season

*T. valida*, *T. nigricauda* and probably *T. robusta* bred at a maximum during the rains and either ceased or reduced breeding activity during the dry seasons. In *T. nigricauda* there appears to be a strong selection pressure to maintain its seasonal pattern of breeding, because only those litters conceived during the rains were recruited into the population. It is likely that litters conceived during the dry seasons died because of lactation failure. There was a significant reduction in maternal body mass during the dry seasons, so presumably the adults were experiencing some kind of stress at these times.

It is not possible to determine from the data presently available which environmental factors are responsible for the seasonal breeding rhythm of the three species I studied on the equator. Obviously, the most likely factors are rainfall and some aspect of food supply. However, the extreme variability of breeding patterns in relation to rainfall observed in the various species of the genus (Fig. 3) seems to rule out the possibility that rainfall is the only factor controlling the reproductive pattern in this genus. There is some circumstantial evidence which suggests that food affects reproduction in this genus. One feature which appears to be consistent in the genus is a low breeding rate compared to other genera (eg. see DELANY and NEAL 1969). It is unusual for more than 50 percent of the adult females to be visibly pregnant at any one time. One reason for this apparent low breeding rate is a relatively long delay in implantation when females are lactating (BLAND 1969; MEASROCH 1954). The delay in implantation averages 14 d in *T. indica* (BLAND 1969), and I calculate the average delay in *T. afra* and *T. brantsii* as 5 d from the data presented in MEASROCH (1954). This suggests that the energy requirement of lactation is high in *Tatera* gerbils, and that an individual cannot simultaneously lactate and maintain the later stages of pregnancy. If this is the case, then food may be a very important factor governing the pattern of breeding in this genus. The increased energy demands in cold weather might also explain why breeding ceases during the colder seasons of the year at higher latitudes (MEASROCH 1954; BEG and AJMAL 1977).

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## Zusammenfassung

Fortpflanzungsbiologie von drei Gerbilliden-Arten (Gattung *Tatera*) in Ostafrika

Die Fortpflanzungsökologie von *Tatera nigricauda* und *T. robusta* wurde im Meru-Nationalpark in Mittel-Kenia, die von *T. valida* im Ruwenzori-Nationalpark in West-Uganda untersucht. In beiden Gebieten waren die jahreszeitlichen Änderungen der Photoperiode zu vernachlässigen, hingegen folgten die Regenfälle einem bimodalen Muster.

Eine Gesamtzahl von 398 *T. nigricauda*, 61 *T. robusta* und 116 *T. valida*, die über einen Zeitraum von mindestens einem Jahr gesammelt wurden, gaben Aufschluß über jahreszeitlich bedingte Veränderungen der Fortpflanzungsaktivität, Populationsstruktur sowie Wurfgröße und Fortpflanzungskapazität.

*Tatera valida* pflanzte sich in West-Uganda nur während der Regenzeit fort. Adulte Weibchen konnten zweimal jährlich werfen. Die durchschnittliche Wurfgröße war  $4.25 \pm 0.21$ , was eine durchschnittliche jährliche Fortpflanzungskapazität von 8.5 Jungen pro adultem Weibchen ergibt.

*Tatera nigricauda* pflanzte sich in Mittel-Kenia nahezu während des ganzen Jahres fort. Die Fortpflanzungsaktivität war maximal während der Regenzeiten, nahm dann ab und erlosch gegen Ende der Trockenzeiten. Allerdings begann die Fortpflanzung vor dem Beginn der Regenzeiten. Jungtiere wurden aber nur 2 Monate nach dem Ende jeder Regenzeit gefangen, was nahelegt, daß Würfe, die während der Trockenzeit gezeugt wurden, starben, bevor sie entwöhnt waren. Erwachsene Weibchen konnten fünfmal pro Jahr werfen. Die Wurfgröße war  $5.2 \pm 0.24$  und die jährliche Fortpflanzungskapazität lag bei 25–28 Jungen pro adultem Weibchen.

*Tatera robusta* schien eine ähnliche Fortpflanzungsperiodik wie *T. nigricauda* zu haben. Die durchschnittliche Wurfgröße war  $4.7 \pm 0.43$ .

Ein Vergleich der Fortpflanzungscharakteristiken der 3 *Tatera*-Arten zeigte keinerlei signifikante Beziehungen zwischen Körpergewicht, Wurfgröße, Zeitraum der Fortpflanzung und Fortpflanzungskapazität. Es liegt nahe, daß das Nahrungsangebot der wichtigste Faktor ist, der die Fortpflanzungsmuster in dieser Gattung beeinflusst.

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## Age determination and population characteristics of red foxes from Maryland<sup>1</sup>

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### Abstract

Between 1976 and 1979, 210 red foxes (*Vulpes vulpes*) were collected throughout Maryland to determine the age of each fox based on eye lens weights, epiphyseal closure of the humerus, baculum weight, tooth cementum annuli and skull measurements. Approximately 50 % of the red foxes collected during the trapping season (October–January) were juveniles; 20 % were one year olds; 16 % were 2-year olds; 8 % were 3-year olds; and 4 % were 4-years old or older. An ovulation rate of 6.0 was calculated from the number of corpora lutea per parous female. A mean litter size of 5.0 was determined from the mean number of placental scars per parous female. The peak of the breeding takes place in mid-January. Sixty-seven percent of the adult males produced sperm in October. Ninety percent of the adult males were producing sperm in November compared to 47 % of the juveniles. To assess the physical condition of each fox an adrenal index, spleen index, and body fat index were developed. Adrenal and spleen indices indicated that 5-year olds may be subjected to more stress than

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