

# The basis of reproductive seasonality in *Mastomys* rats (Rodentia: Muridae) in Tanzania

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**ABSTRACT.** Reproduction of the African murid genus *Mastomys*, multimammate rats, is seasonal, starting after the rains and extending well into the dry season. During a two-year study in Tanzania, we tested three hypotheses to investigate the proximal causes of this seasonality. Food availability was no limiting factor since food supply could not induce continuous breeding. Temperature was always high and thus not a restrictive climatic factor. Diet was probably always sufficiently varied and protein-rich to allow reproduction. This contradicts earlier hypotheses that consider *Mastomys* as an opportunistic breeder in which reproduction is seasonally limited by poor conditions; environmental predictors were believed not to be involved since the animals live in an unpredictably unstable environment. However, although the occurrence of rain may be unpredictable, it is highly predictable that heavy rainfall will be followed by good conditions. Laboratory experiments show that sprouting grass has a stimulatory effect on reproduction, suggesting that breeding is triggered by new vegetation.

**KEY WORDS:** *Mastomys*, Rodentia, multimammate rats, seasonal reproduction, reproductive trigger, Tanzania.

## INTRODUCTION

Reproductive seasonality in animals can be explained in two different ways. The first assumes that animals breed continuously unless reproduction is inhibited by changing energetic demands, limited food availability or lowered diet quality (reviews in Bronson 1985, Bronson & Perrigo 1987, Derting 1989, Hammond & Wunder 1991, Millar *et al.* 1991). Such animals have been named 'opportunists' because they breed whenever conditions are good (Bronner *et al.* 1988).

A second hypothesis explains reproductive seasonality as an evolutionary adaptation to temporal instability. An individual will maximize its reproductive success by breeding at such a time that young will grow up in the most favourable conditions (Baker 1938). The proximate causes, the particular environmental conditions which stimulate the parents to reproduce, are often photo-periodic variation but can also be dietary components (e.g. Bronson & Perrigo 1987, Dark *et al.* 1983, Kruczek 1986, Negus & Berger 1987, Olsen 1981); such proximate causes have a predictive value.

In tropical animals such underlying mechanisms are rarely investigated, although breeding seasonality is often apparent. This is also the case for the different species of multimammate rats, *Mastomys* spp., where reproduction is strongly related to rainfall patterns (e.g. Coetsee 1965, Delany & Neal 1969, Field 1975, Hubert 1982, Neal 1977). In our own study population of *M. natalensis* (Smith 1834) in Tanzania, the main breeding season starts after the major rains of March–May and continues until September; if rains at the end of the year are abundant, there is a short additional reproductive period early in the following year (Leirs *et al.* 1989). Also growth patterns and maturation rates are strongly associated with rainfall (Leirs *et al.* 1990). Bronner *et al.* (1988) suggested that, in South Africa, *M. natalensis* is an opportunistic breeder, reproducing continuously unless limited by low temperatures in the dry winter. They presumed that *Mastomys* did not use any environmental predictors to trigger breeding. On the other hand, Linn (1991) reported that 6-methoxy-2-benzoxazolinone (6-MBOA), a chemical present in sprouting grass and known as a reproductive stimulus in *Microtus* (reviews in Korn 1989, Negus & Berger 1987), has a stimulatory effect on ovarian weight in *Mastomys coucha* (Smith 1836) and could thus possibly be a reproductive trigger.

In this paper, we will present our findings in a natural population of *M. natalensis* in Tanzania, in order to answer the following questions:

1. Is reproductive activity related to changing conditions of temperature, rainfall and photoperiod?
2. Is reproduction seasonally limited by food availability?
3. Is reproductive seasonality related to changes in diet composition?

Furthermore we will report on laboratory experiments with a mutant strain of *M. coucha*, attempting to answer a fourth question:

4. Is sprouting grass a possible stimulus for reproduction in *Mastomys*?

## METHODS

### *Field study*

Our study took place in fallow land on the campus of the Sokoine University of Agriculture in Morogoro, Tanzania (6° 51' S, 37° 38' E). Details about the habitat and the field work were published elsewhere (Leirs *et al.* 1990). Basically, we collected data between 1986 and 1989 in monthly removal captures (2916 individuals) and, *c.* 2 km away, in a capture-mark-release study on two 1 ha grids, 100 m apart, with 100 trap stations each (8715 captures of 3351 individuals). Analyses of population dynamics, reproduction, growth and survival have been published by Leirs *et al.* (1989, 1990, 1993). There were virtually no other small mammals on the study plots. In addition to our own removal study, we used data collected by Telford (1989) on the same site between 1981 and 1985.

### *Reproduction and weather*

Meteorological data (monthly rainfall, mean relative humidity, mean daily minimum temperature, total radiation) were obtained from the Meteorological Office at the campus, 2 km from the study area. As by Bronner *et al.* (1988), meteorological data and density estimates (Leirs *et al.* 1993) were correlated with arcsine transformed proportions of reproductive activity in adults (scrotal testes in males, oestrus or pregnancy in females) for all months in which adults (males >40 g, females >30 g) were caught.

### *Food availability*

In late 1987 and early 1988, open cans each containing 150 g maize were supplied weekly per trap station in one of the capture-mark-release grids and maize consumption was recorded. The other grid acted as a simultaneous control. Interpretation was sometimes hindered by humidity or termite and bird activity; maize supply was suspended for some weeks when children were seen playing with the cans.

### *Diet composition*

Between April 1988 and February 1989, 145 animals were snap-trapped for stomach collection. The whole stomach contents was removed and fixed in 10% formalin for at least 48 hours, washed and sieved (0.212 mm sieve) with water and cleared in 2% HNO<sub>3</sub> solution for 24 h at 80°C. After sieving again, the dietary particles were preserved in 70% alcohol. A part of each individual stomach contents was poured homogeneously over a microscopic glass slide, mounted with 50% glycerol and scanned in parallel lines under a light microscope at magnification 10 × 6. Each of the observed dietary particles was classified in one of five categories: grass (green monocotyledon leaves), seeds and fruits (endosperm, pericarp and fruit tissue), other plant material (stems, roots, dicotyledon leaves, parts not belonging in the two other plant categories), arthropods and the rest (uncommon food or particles that could not be identified). The size of each particle was estimated by the eye and scores were totalled per category and transformed to percentages. Scanning one slide per stomach was considered to be representative since several readings of the same stomach contents provided no different proportions ( $X^2 = 5.372$ ,  $df = 4$ ,  $P = 0.2513$ ).

### *Sprouting grass laboratory study*

When laboratory experiments started in early 1991, it was impossible for us to obtain *M. natalensis* from the wild. Instead we used the 'Giessen' laboratory strain, a chamois-coloured, pink-eyed *M. coucha* mutant (Coetzee 1980), in order to investigate whether sprouting grass does not only increase ovarian weight (Linn 1991) but actually initiates reproduction. All animals were fed laboratory

mouse pellets and water *ad libitum* and kept in conventional animal rooms at constant temperature with a 12/12 h light/dark cycle.

In a first experiment, 10 young females were removed from the parents after weaning (23–24 days) and paired in a 26 × 20 × 14 cm cage with a male of the same age but from a different nest. Experimental pairs (n = 5) received a mixture of lab pellets and about 20 fresh maize seedlings daily; control pairs (n = 5) received only lab pellets. The maize was grown in the laboratory and harvested between the 3rd and 10th day after germination, i.e. when the concentration of 6-MBOA is highest (Klun & Robinson 1969). To minimize any possible pheromone influence of one cage to another, cages were covered with a filter hood and placed in front of negative pressure horizontal laminar flow cabinets. Pairs were left together in the cage until they were about 200 days old. The age of the mother at first parturition was recorded.

In a second experiment, 14 juvenile females received lab pellets for three weeks after weaning, and afterwards were kept on a diet of dry maize, twice per week supplemented with a few pellets. At an age of about two months, they were paired to males that had already reproduced successfully. The pairs were kept in large cages (100 × 100 × 60 cm or 100 × 60 × 60 cm) in a permanently humidified room. In eight experimental cages, maize seeds, planted two days earlier after soaking in water overnight, had already started germinating; maize seedlings were allowed to grow freely and maize was not replanted. Six control pairs were simultaneously placed in similar cages in the same room but without germinating maize. Litter mates were equally distributed over the control and experimental groups. The time between pairing and conception was calculated by subtracting 23 days (the gestation period) from the date of parturition.

## RESULTS

### *Reproduction and weather*

There were significantly positive correlations between reproduction and rainfall in the previous months. Only negative correlations with temperature were recorded (Table 1).

### *Food availability*

Notwithstanding the supply of maize, reproduction ceased late in 1987 (Figure 1). All weekly provided maize was totally consumed at the end of 1987 and the offered amount may not have been sufficient to provoke any effect. From January 1988 onwards, there was always an excess of maize but still reproduction did not start in this grid until April 1988. At that moment however, reproduction had also started in the grid which acted as a control plot. The only effect that we could detect was a slightly higher body weight in the grid where maize was provided (Leirs *et al.* 1990).

Table 1. Correlation between the monthly sexual activity in adult males and females and rainfall in the current month (rain), one ( $rn_1$ ), two ( $rn_2$ ) or three ( $rn_3$ ) months earlier, cumulative rainfall in the previous two ( $rn_{12}$ ) or three ( $rn_{123}$ ) months, mean temperature ( $^{\circ}t$ ), mean relative humidity (rh), total radiation (rad), Minimum Number Alive (mna) and Jolly-Seber population size estimate (jolly). Correlation coefficients (sample size n) have an asterisk or double asterisk when significant at the 0.01 level or the 0.001 level respectively; calculations made for animals in the removal study (1981–1989) and in the capture-mark-release grid without maize supply (1986–1989)

	rain	$rn_1$	$rn_2$	$rn_3$	$rn_{12}$	$rn_{123}$	$^{\circ}t$	rh	rad	mna	jolly
Removal											
♂♂ n=59	0.109	0.087	0.205	0.102	0.180	0.196	-0.066	0.217			
♀♀ n=67	-0.170	0.209	0.398**	0.383**	0.371**	0.488**	-0.663**	0.185			
Capture-mark-release											
♂♂ n=19	-0.326	0.534*	0.653*	0.296	0.692**	0.714**	-0.182	0.470	-0.326	-0.411	-0.436
♀♀ n=22	-0.337	0.384	0.481	0.409	0.502*	0.591*	-0.455	0.017	-0.337	-0.588*	-0.609*

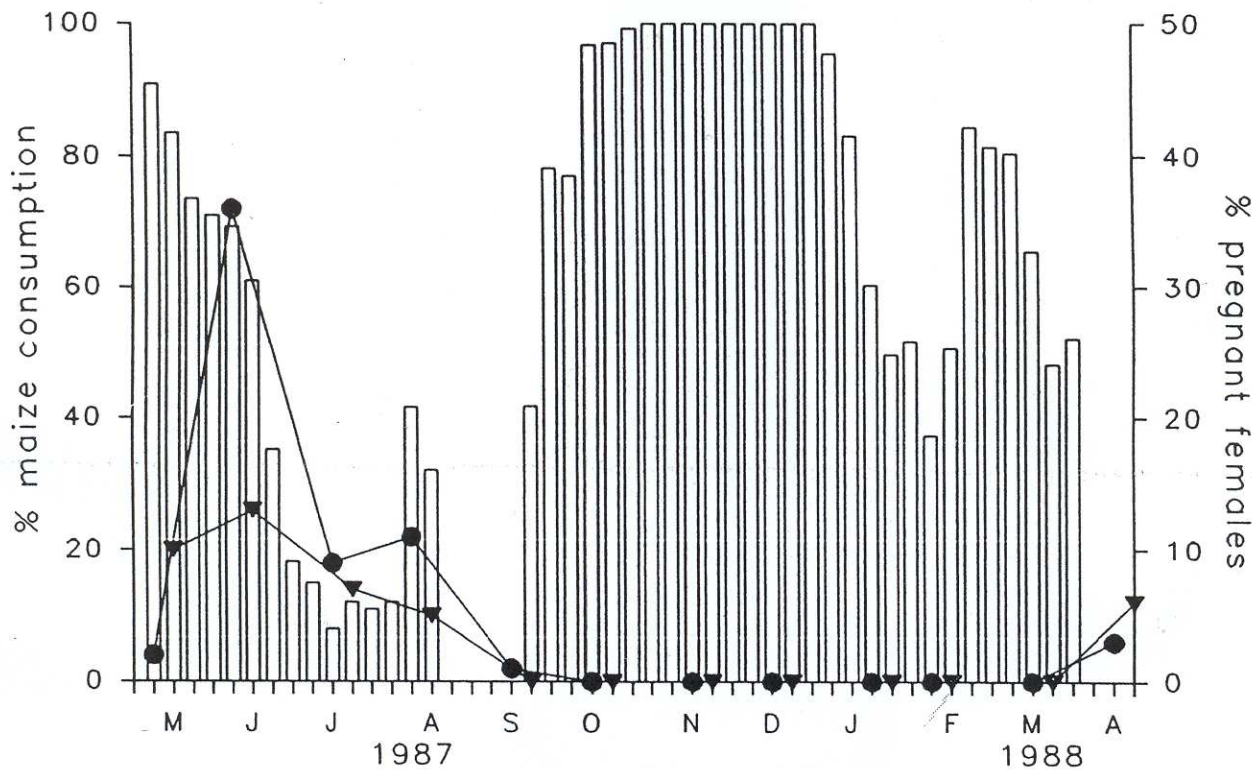


Figure 1. Weekly consumption of 15 kg supplied maize in the experimental grid (vertical bars) and the monthly percentages of pregnant females in the control grid (circles) and experimental grid (triangles). Maize supply was temporarily suspended in September 1987.

### Diet composition

Three quarters of all stomachs contained particles from all different food categories and there was a large variability of food items. In several individuals we found vertebrate muscle tissue and bird feathers. However, not all categories were equally present; only one third of the stomachs (33.7%) contained more than 5% of each category and there was a large interindividual variation in the representation of each food category (Figure 2).

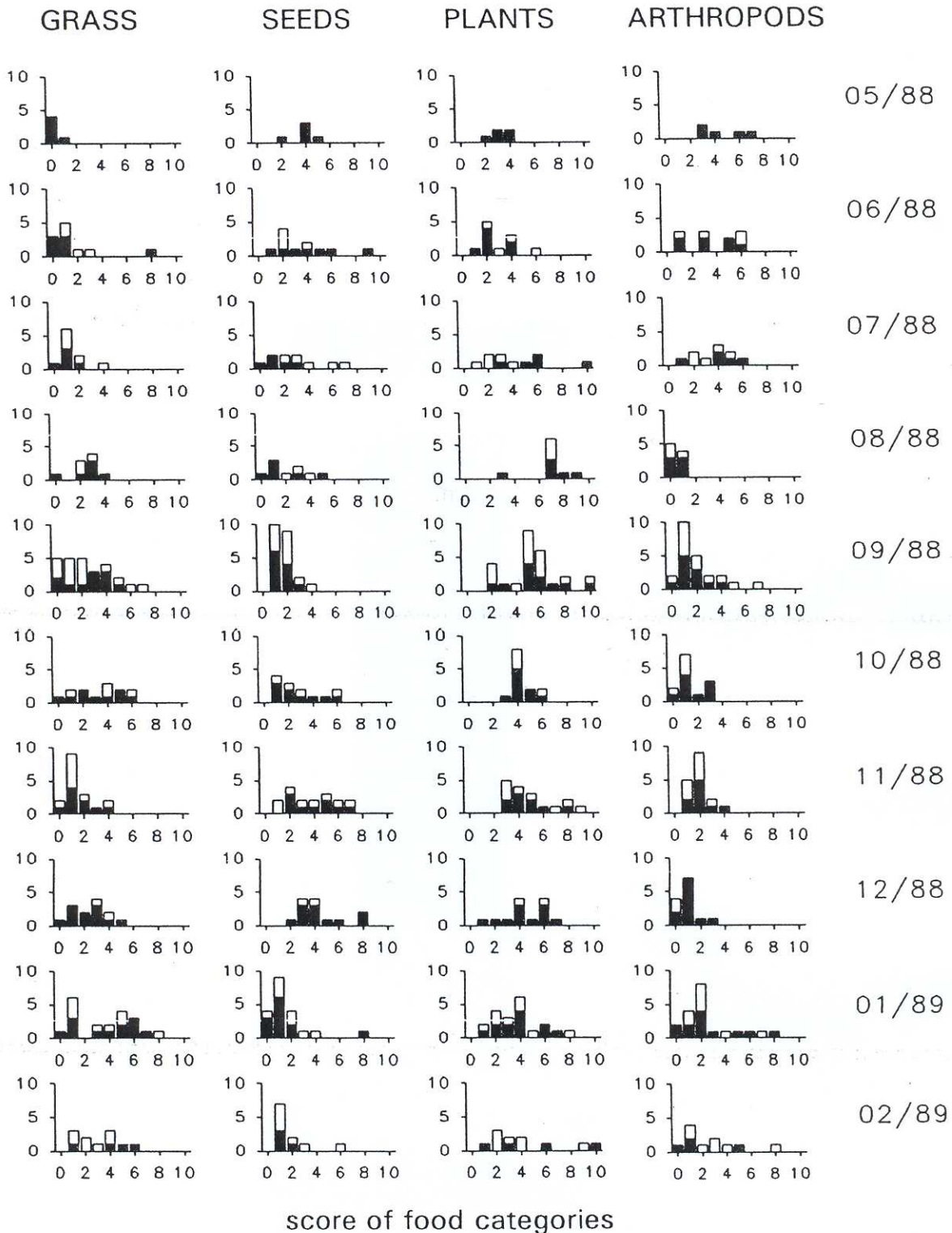


Figure 2. Monthly frequency distribution of individuals according to the proportional score of different food categories in their stomachs. Solid blocks represent males, clear blocks represent females. Proportions distributed in percentage class (0 = 0%; 1 = 1–9%; 2 = 10–19%; 3 = 20–29%; etc.). A distribution skewed to the left indicates the low importance of a food category, a distribution skewed to the right indicates that many animals eat a lot of that category. A flat distribution suggests opportunism.

The relative importance of the different categories changes considerably with the seasons (Figure 3). Plant material is often predominant. Grass and arthropod consumption correspond broadly with the rainfall and reproductive pattern but an arthropod-rich diet is never a feature for the whole population.

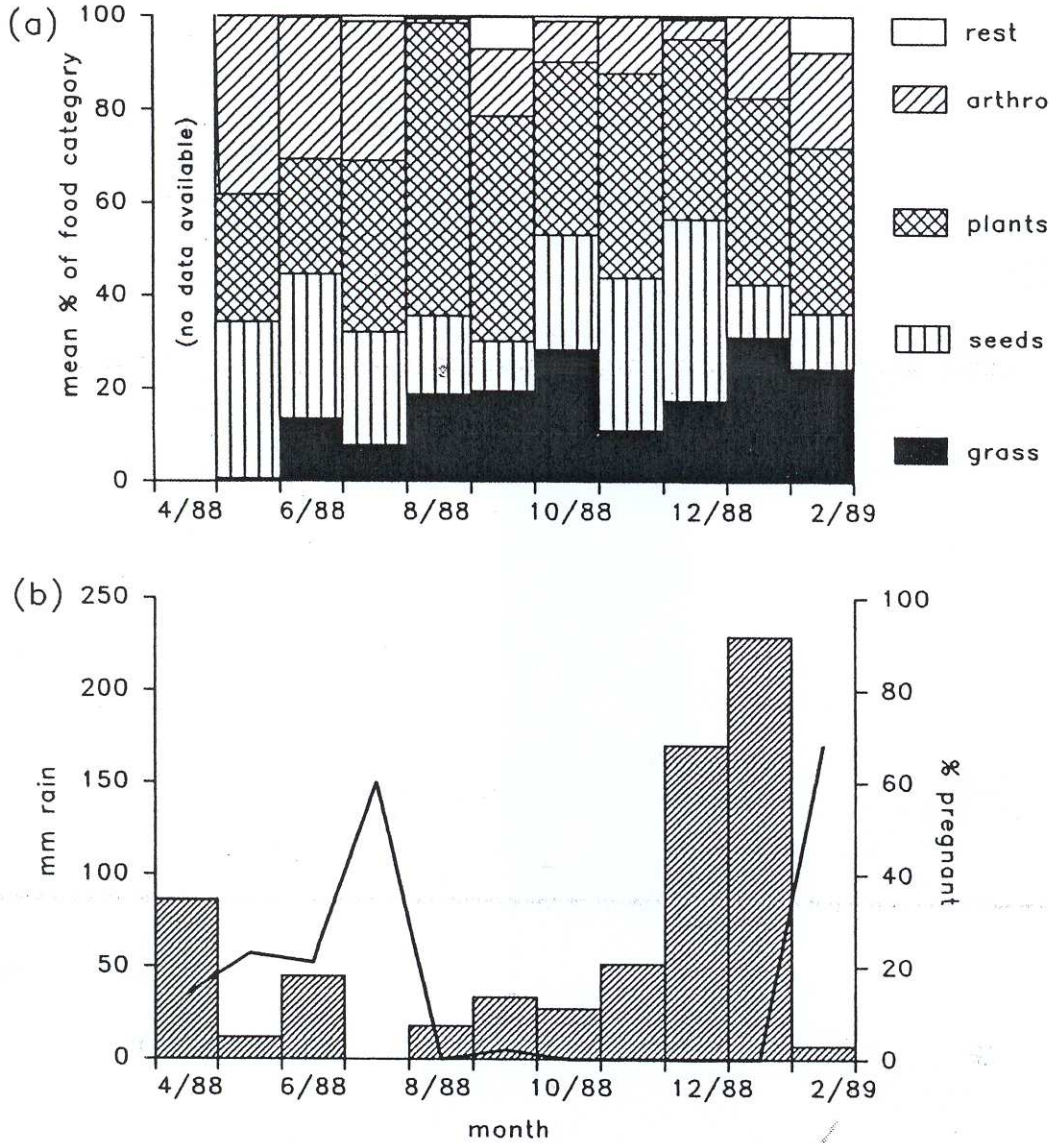


Figure 3. Diet, rainfall and reproduction. (a) mean percentage of each food category per month. (b) shaded columns show monthly rainfall in mm; the curve represents the monthly percentage of pregnant females.

*Sprouting grass*

In the first experiment, the recorded maternal ages at parturition time (85, 96, 106 and 118 days in the group with fresh maize; 96, 97, 160 days in the other group) were not different between the two groups (Mann-Whitney  $U = 4.5$ , one-tailed  $P = 0.325$ ). The animals partook eagerly of the seeds, roots and young stems but, in contrast with an earlier study (Linn 1991), did not consume all the leaves. In the experimental group, one pair never became pregnant until they were 200 days old; in the control group, two pairs did not breed.

The litters in cages with germinating maize in the second experiment were sired 1, 3, 3, 4, 5, 8 and 18 days after pairing of the parents. Animals actively dug up the germinating seeds. In the control cages conception happened 4, 14, 16, 30 and 29 days after pairing. In both groups, one pair did not reproduce within two months. The time between pairing and conception was significantly shorter in the experimental group (Mann-Whitney  $U = 5.5$ , one-tailed  $P = 0.024$ ).

#### DISCUSSION

The positive correlations between reproduction and rainfall confirm the previously reported findings about timing of breeding in *Mastomys*. Abundant rains result in high breeding proportions one to three months later. Environmental temperature on the other hand is negatively correlated with breeding which is the opposite result to that obtained by Bronner *et al.* (1988). This difference may be due to the 10°C higher average temperatures in Morogoro, although the fluctuations are of the same magnitude as in South Africa. Moreover, the data presented by Bronner *et al.* (1988) are limited to only one year. If we recalculate our correlations for two years separately, the correlation between female breeding activity and temperature in the first year (03/87–03/88) is significantly negative ( $R = -0.877$ ,  $P < 0.001$ ), in the second year (02/88–02/89), there is no correlation at all ( $R = 0.032$ ).

Our stomach analysis data confirm that *Mastomys* has an opportunist and generalist diet with some seasonal variation. The seasonal differences in arthropod consumption are due to varying numbers of individuals which fed predominantly on insects, mostly termites. The latter are patchily distributed in the studied habitats which may explain why some stomachs contained many of them, others only very few.

Seeds are an important food category during the breeding season of *M. natalensis*, also in earlier work (Field 1975, Taylor & Green 1976). The large amount of starch in the seeds consumed during the breeding season will help to meet the high energy need in a reproducing organism (Gittleman & Thompson 1988). Kerley & Erasmus (1991) discovered that seed handling strategy in *M. natalensis* indeed maximizes intake of energy-rich parts. Nevertheless, our study provides no evidence for an effect of cereal food supplements on reproduction. Supplied wheat also failed to produce a reproductive response in *Mastomys* in Kenya, although unseasonal breeding occurred in an unseasonal wheat crop (Taylor & Green 1976). This indicates that growing cereal plants are probably more important in triggering reproduction than dry seeds. Hubert *et al.* (1981a) supplied commercial rodent food, cereal-based but probably with a variety of other ingredients, to a population of *M. erythroleucus* in Senegal; they observed a better survival of young and a slight prolongation of the breeding season.

Field (1975) already quoted that protein requirements are at least as important during pregnancy. This is consistent with the larger arthropod consumption



in the reproductive period. On the other hand, proteins are present in grasses as well, accounting for over 10% of the dry weight (Nandwa 1973). Swanepoel (1980) found that, in spite of the large seasonal variation in *M. natalensis* diet composition, the dry mass protein concentration varied only between 22.6 and 29.5%; Hubert *et al.* (1981b) reported values between 31 and 43% in *M. erythroleucus* with the lowest nitrogen level in the early breeding season. Protein concentrations of around 10% are sufficient to support pregnancy in laboratory rats or house mice (Bomford & Redhead 1987, Richardson *et al.* 1964). If these data can be extrapolated to multimammate rats, the observed protein concentration is always well above the required minimum and, as already suggested by Field (1975), it becomes unlikely that protein intake alone is a limiting factor in *Mastomys*.

These considerations lead us to the idea that breeding seasonality in tropical *Mastomys* is probably not the result of variations in environmental temperature or intake of nutrients. This means that *Mastomys* cannot be considered to be a purely opportunistic breeder and that, under the alternative hypothesis, we should try to identify which mechanisms the animals use to initiate breeding in anticipation of better conditions still to come. Bronner *et al.* (1988) argued that *Mastomys* cannot use such ecological predictors since it lives in unpredictably changing habitats. However, predictability should always be considered in relation to generation time and lifespan of the studied organism. Although this statement is not a new one (Southwood 1977), it is still not yet widely acknowledged what this means in reality. It is true that the interannual irregularities in rainfall patterns constitute an ecological uncertainty but, more important to a rodent, it is very predictable that after abundant rainfall, the amount of food and cover will quickly increase.

In South Africa, at a latitude of 30° S, photoperiod could be a useful predictor for *Mastomys* (Bronner *et al.* 1988). In Morogoro, much closer to the equator, the photoperiodic changes are very small and can certainly never explain variations between years. Other tropical rodents are known to be reproductively unresponsive to variation in photoperiod (Heideman & Bronson 1990).

Sprouting grass however is known to trigger reproduction in several rodents from arid regions (Beatley 1969, Reichmann & Van de Graaff 1975, Van de Graaff & Balda 1973). Also in our case, it is a much more reliable predictor even if its mere presence cannot be considered to offer optimal conditions of food and shelter. In Senegal, green plant material replaces arthropods as the most important food for *M. erythroleucus* at the start of the breeding season (Hubert *et al.* 1981b). Our laboratory experiments, though based on a small sample, confirm that breeding in *Mastomys* can indeed be stimulated by sprouting grass. In our first experiment, when the rodents were daily fed young maize seedlings for several months, there was no effect. Possibly, there was an inhibitory effect of a too high consumption of stimulatory compounds such as 6-MBOA (Sanders *et al.* 1981). In nature, animals would be exposed to new vegetation for a shorter period. Our second experiment tried to take this into account. The

observed reaction time after consumption of the germinating maize was so short that, if there is a seedling-related mechanism that cues reproduction, it must involve a rapid response. Laboratory experiments with grass-extracts or 6-MBOA provoked a response in several species within hours or days (Linn 1991, Millar 1967, Sanders *et al.* 1981). Under field conditions such responses are much slower and take at least two weeks (Alibhai 1986, Berger *et al.* 1981). Probably this slower reaction can be explained by the variety of other available food and the limited access that individual animals may have to the 6-MBOA food sources, whether artificial or natural. While some environmental influences (e.g. photoperiod) reach all animals in the same way and cause therefore a highly simultaneous response (Sadleir 1969), this is not necessarily the case for triggers that are not equally available to all individuals, such as dietary components. On the other hand, the control animals also started to breed in our experiment, albeit a few weeks later. Laboratory *Mastomys* have been successfully bred on a diet of laboratory pellets without any supply of green vegetation and can mature at young age (e.g. Baker & Meester 1977, Leirs *et al.* 1990, Meester 1960). This reveals that germinating maize is not essential to trigger reproduction but that it has a marked accelerating effect. How sprouting vegetation would interact with other factors that stimulate reproduction in nature, and what these factors are, is not yet known. At least one important difference with the natural situation is that laboratory animals receive plenty of food and never undergo a growth stop as often occurs in nature (Leirs *et al.* 1990).

We conclude that food resources or temperature do not seem to control breeding activity in *Mastomys* but that sprouting grass may have a trigger function. This could explain the observed relation between reproductive seasonality and rainfall patterns.

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