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Productivity of different generations in a population of Mastomys natalensis rats in Tanzania

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In Tanzania three different generation types can be recognized in *Mastomys natalensis* rats. The α-generation is born in the main breeding season and breeds in the next main breeding season. The β-generation is born in the main breeding season but reproduces already after abundant off-season rainfall. Its offspring, the γ-generation, is born in the off-season breeding period and breeds in the same year. Life histories of these three generation types are different. Generation α has a long growth stop, poor survival until breeding but up to six consecutive litters; generation β has a short growth stop, a better survival until reproduction but breeds only once or twice. The γ-generation, however, grows very fast and reproduces at young age. Through their daughters, the β-generation thus produces more than seven times as much young as the α-generation before the end of the following year. The occurrence of these generation types partially explains the relationship between rainfall patterns and population fluctuations.

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Multimammate rats of the genus *Mastomys* are the most common indigenous rodents in subsaharan Africa. They constitute a pest problem in agriculture and public health, particularly in years with rodent outbreaks (Fiedler 1988). Already in early literature it was suggested that such outbreaks followed very wet years (Roberts 1935), but the link between the two phenomena was not understood. It is, however, since long known that reproduction in *Mastomys* is seasonal and related to rainfall (Brambell and Davis 1941, Coetzee 1965, Delany and Neal 1969, Field 1975, Taylor and Green 1976, Neal 1977, Delany and Roberts 1978, Cheeseman and Delany 1979, Chidumayo 1980, 1984, Swanepoel 1980, Hubert 1982, Hubert and Adam 1985).

In our study population of *Mastomys 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 breeding period early in the following year (Leirs et al. 1989). Growth patterns as well as maturation rates are also strongly associated with rainfall (Leirs et al. 1990a). Based on this information, we grouped animals in three different generation types according to period of birth and growth rate. Generation type α is born in the main breeding season around the middle of the year, has a long period of reduced growth and reaches maximal body size in the next main breeding season. A second type (β) groups animals born in the main breeding season as well but, due to abundant off-season rain, they have only a short growth stop and thus reach adult weight early in the following year. The third generation type (γ) is born in the off-season breeding period and is already full-grown in the main breeding season of that same year (Fig. 1).

Such life-history variation may be of great importance in population dynamics: fluctuations of microtine rodents are known to be strongly influenced by the functional age structure of females (Löfgren 1989) and the reproductive effort of different age categories of fe-

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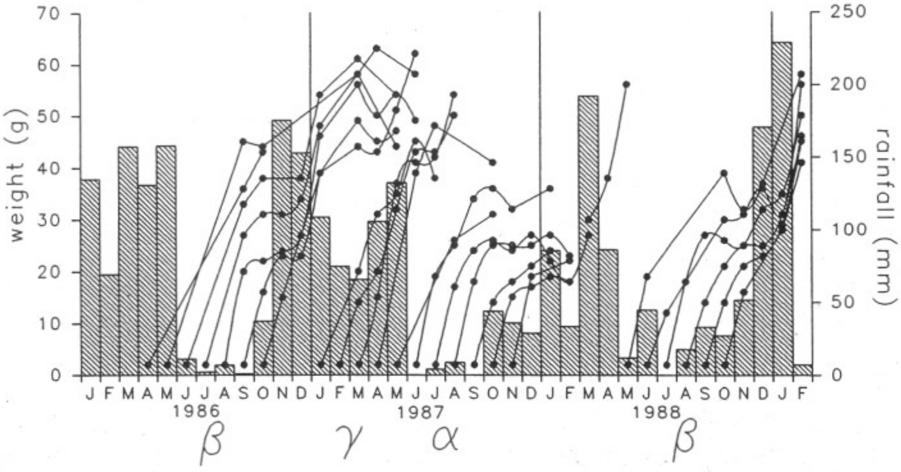

Fig. 1. The evolution of mean body weights per month for monthly cohorts (lines) in relation to monthly rainfall (shaded columns). The vertical lines indicate the start of a new year. The generation type (α,β,γ) is indicated when a new generation is born (after Leirs et al. 1990).

males (Nelson et al. 1991). The purpose of our study was to examine how the variations in reproduction, growth, and maturation combine with survival to define life histories of these three generation types in *Mastomys*. Moreover, we wanted to compare the productivity of these generation types in order to investigate how their occurrence could explain the relationship between rainfall patterns and population dynamics.

Material and methods

The study took place in fallow land on the campus of the Sokoine Univ. of Agriculture in Morogoro, Tanzania. The main grass species on these fields were *Panicum hanningtonii* Stapf, *Rothboellia conchinchinensis* (Lour.) Clayton, *Pennisetum polystachyon* (L.) Schult. and *Cymbopogon* sp. in varying relative importance. Trees were sparsely present, most often kapok (*Ceiba pentandra* Gaertn.) or *Acacia* spp.

Monthly, between September 1986 and February 1989, we collected animals on traplines using Sherman live traps or Museum Special break back traps baited with peanut butter and spaced 5–10 m apart. Trapping went on during a variable number of nights, depending on trap success. Every month the traplines were laid out at different sites some hundred m apart. Captured animals were fixed in formalin and preserved in alcohol. Additionally, a capture-mark-release study (CMR) was performed between March 1987 and February 1989 2 km south on the same vast campus. Monthly, during three consecutive nights, we live-trapped animals in two 1 ha-grids, 100 m apart, of 100 trap stations each. The animals were marked by toe-clipping and body weight and sexual condition were noted before release. In total 2916 animals were trapped in the removal trapping and 3531 individuals were captured at least once in the CMR-study. In addition to our own data, we included (partially published) data collected at the same study site between 1981 and 1985 (Telford 1989).

Population size was expressed as Jolly-Seber estimates and Minimum Number Alive enumerations (Krebs 1989). Individual age-estimates were obtained from the dry eye lens weight or, during the reproductive season in the CMR-study, from the body weight at first capture when this weight was less than 22 g (Leirs et al. 1990a). Our data do not include measurements of early nest mortality or survival of recently weaned young but local survival to reproduction was calculated in the CMR-study as the proportion N_b/N_0. N_0 is the number of individuals that were present in the grid at the end of their season of birth (the number of animals that were present in the last month with reproduction and that weighed less than 30 g in that month or in one of the two previous months). N_b is the number of these individuals that were still present at the start of the following breeding period (main season or off-season). Surviving proportions where transformed to standardized 28-d finite survival rates φ_{28} (Krebs 1989). The association of generation type and sex with 28-d survival was studied in a three-way contingency table (hypothetical numbers of survivors after 28 d) by a loglinear analysis (Freeman 1987, Statsoft 1991).

To avoid the effects of dispersal in such local survival analysis, we assumed that immigration of young is equal to emigration since there was no reason to believe that our study plots would be more or less attractive than the surrounding sites. The analysis was repeated with N_b now being the total number of all animals present when breeding starts, not only those that we had followed since they were young recruits. This results in a "total survival proportion". We could easily count the number of breeding adults that belong to the α or β generations because when these start to reproduce, their parents have disappeared since long and thus all breeding adults belong to the same generation. However, it was not

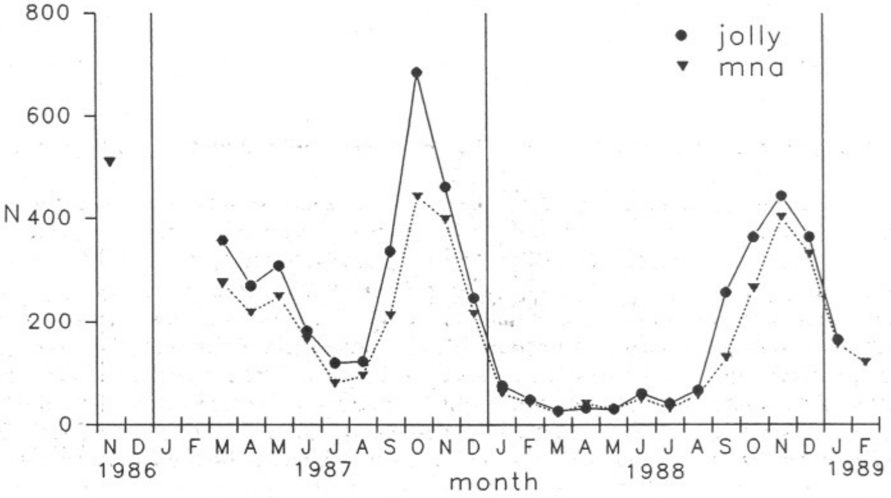

Fig. 2. Population size expressed as Jolly-Seber estimates or MNA-counts. Vertical lines indicate the start of a new year.

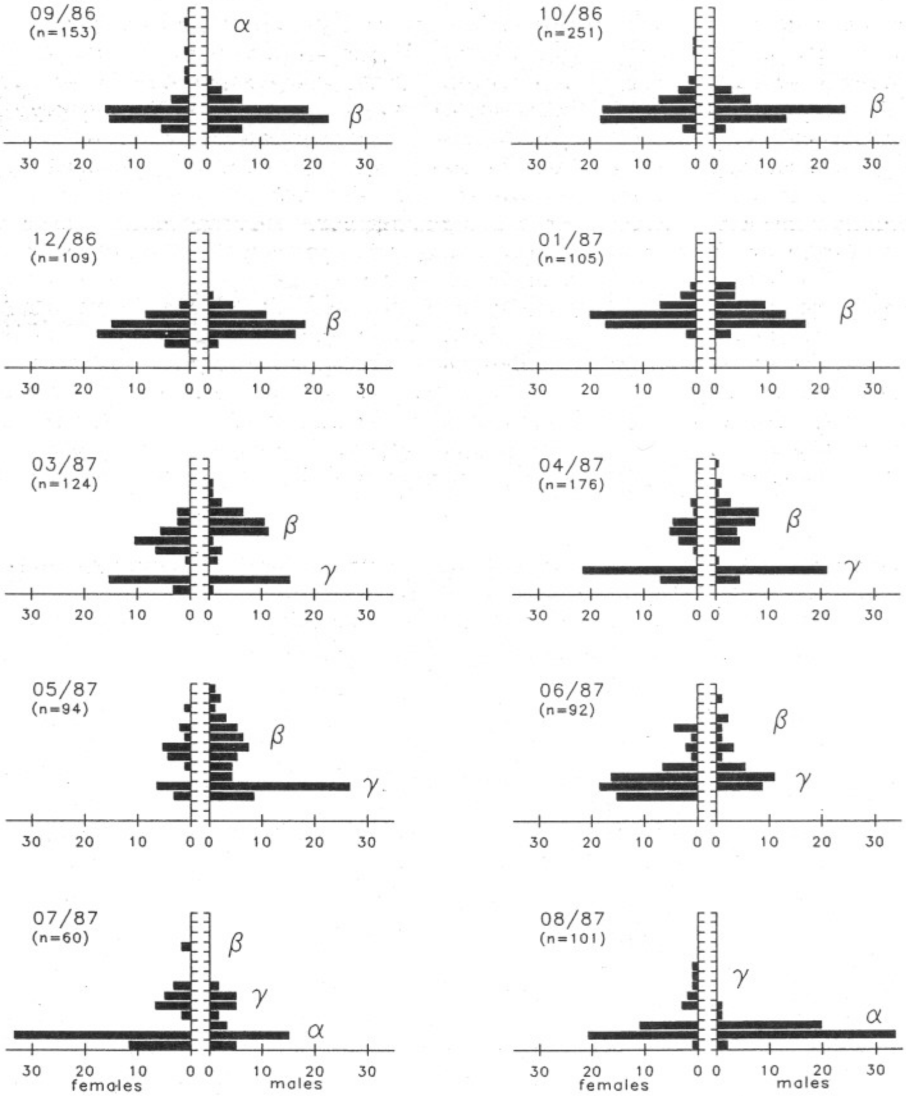

Fig. 3. Age-structure of the population in different months in 1986 and 1987. The individuals are grouped in age-classes of one month and the proportional share (%) of each age-class is represented by horizontal bars. Cohorts of similar ages belong to the same generation type.

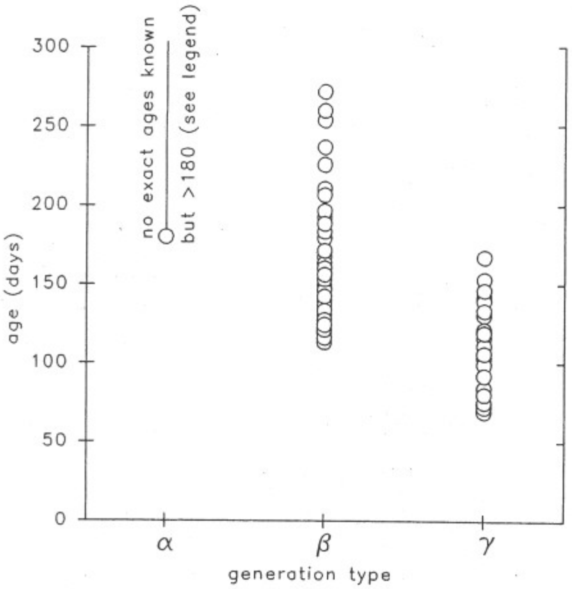

Fig. 4. Recorded ages at pregnancy for animals of three different generation types. Lens-age estimates were available for 94 β-generation and 29 γ-generation animals (born in middle 1986 and 1988, and in early 1987, respectively) but not for generation type α. However, in 1988 reproduction started in April and since there had been no reproduction since October 1987, all breeding animals in 1988 (α-generation) must have been at least 180 d old.

possible to count the γ generation because these animals breed already when some of the parents (β generation) are still present.

The mean incidence of pregnancy I, was calculated for each breeding season as described by Caughley (1977); in short, $I = P/D$ with $P = \Sigma P_j/j$, P_j being the proportion of pregnant females in a month of the breeding season, j the number of months in the breeding season and D the length of the period during which gestation can be recorded externally (10 d in live *Mastomys*) measured as a fraction of the length of the breeding season. Multiplying the mean number of litters per female during the whole breeding season (I) with the mean litter size (counted in utero in females from the removal study) yields the reproductive output, i.e. the average number of young produced by a female during the breeding season.

Since most breeding *Mastomys* do not survive the reproductive season (see later), the lifetime reproductive output of a female will in general be equal to its reproductive output in one breeding season. However, only a small part of the females survive the first months of life and reach sexual maturity. When we multiply the probability of survival until reproduction with the average number of young produced in the breeding season, we can calculate the number of young that a newly recruited female can, on average, be expected to produce during her total lifetime.

In order to compare such values between different generation types, we must make several assumptions: 1) since we were not able to follow a whole life cycle of a β-generation, we must combine the information that was obtained in two different years; 2) our information on litter size is limited to in utero counts and there are no data to assess nestling, weanling and early juvenile mortality; we assume that this mortality is equal for all generations and seasons and can thus be ignored when comparing generations. This is not necessarily true in nature (Dapson 1979, Sharpe and Millar 1991). However, the approach seems valuable as it nevertheless will give an indication of the relationships between reproduction of different generations and population dynamics.

Results

Population size

Population size fluctuated considerably (Fig. 2) with peaks in November and troughs in the middle of the year. The decline at the start of a new year was much sharper in 1988 than in 1987 and the peak density in 1987 was considerably higher.

Age structure

The age-structure reflects the earlier description of reproductive seasonality but in addition provides information about longevity (Fig. 3). The generation that bred in middle 1986 (α-generation born in middle 1985) has disappeared by September 1986. The new generation (β-generation) is the only present generation from then

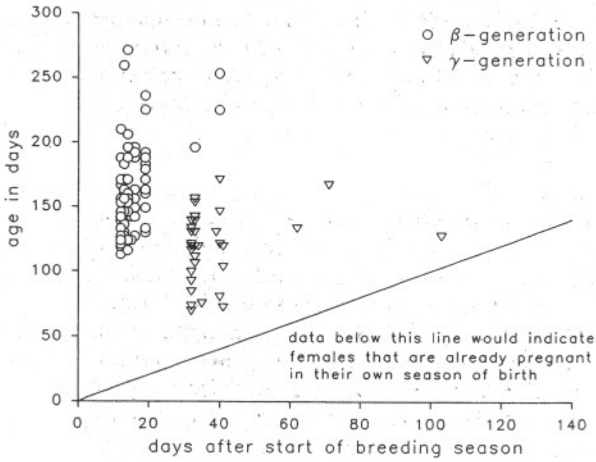

Fig. 5. Age of pregnant females of β- and γ-generations in relation to the time that has expired between the start of the breeding season and the moment of capture. Similar data are not available for the α-eneration.

Table 1. Local survival to reproduction of the different generation types, expressed as the proportion (N_b/N_0) of animals present at the end of their season of birth ($t = 0$) that survive until the start of the next breeding season ($t = b$). The proportion is recalculated as a 28-d finite survival rate φ_{28}.

Type		$t = 0$	N_0	$t = b$	N_b	Survival	φ_{28}
α	♂♂	Nov '87	252	Apr '88	1	0.004	0.349
	♀♀		233		6	0.025	0.498
β	♂♂	Nov '88	162	Feb '89	17	0.105	0.496
	♀♀		131		16	0.122	0.520
γ	♂♂	Apr '87	17	Jun '87	5	0.294	0.550
	♀♀		39		16	0.410	0.646

on, until March 1987 when, as a result of off-season breeding, the γ-generation appears. In middle 1987, when the new α-generation is born, almost all individuals of the β-generation have already disappeared but a small number is still present. The 1988-data are less complete, but show the same patterns.

Sexual maturation

Different generation types grew at different rates (Fig. 1) and reached sexual maturity at different ages (Fig. 4). Moreover, all pregnant females were of such age that they were necessarily born before the start of the breeding season during which they were captured (Fig. 5). The size (head-body length) of reproducing females was not different between the three generation types (Kruskall-Wallis ANOVA $H_{2,130} = 4.518$, $p = 0.10$).

Survival until reproduction

Local survival (i.e. the proportion of female recruits still present at the start of the breeding season) was lowest for the α-generation and highest for the γ-generation (Table 1). This is self-evident because of the different periods that these generations need to mature. The standardized 28-d finite survival rates φ_{28} were much closer to each other but the same trend still exists: local survival was significantly associated with generation type (loglinear analysis partial association $\chi^2 = 9.18$, d.f. $= 2$, $p = 0.010$) and with sex (partial association $\chi^2 = 8.68$, d.f. $= 1$, $p = 0.003$). Also when we eliminated dispersal effects (Table 2), monthly survival was generation-dependent (partial association $\chi^2 = 10.29$, d.f. $= 1$, $p = 0.001$) and sex-dependent (partial association $\chi^2 = 6.05$, d.f. $= 1$, $p = 0.014$). There was no significant interaction between sex and generation type.

Reproductive output

The reproductive output (Table 3) was smallest during the off-season breeding period, obviously because that period is so short. Since some β-generation females were still present during the main breeding season in 1987 following the off-season breeding period in January 1987 (Fig. 3), we calculated the reproductive output in that main breeding season separately for β and γ generations.

The expected lifetime reproductive performance for each generation type is shown in Table 4. We had no data to estimate survival to reproduction of β-females born in 1986 and used the value obtained in 1988. Moreover, the calculations for the β-generation are more complicated than for the α- or γ-generation because a few β-generation females survive after the off-season breeding period and produce some additional young later in the year. The survival of the β-generation females until the start of the main breeding season is estimated as follows: if the number of heavy weight females (>35 g) in May 1987 ($n = 102$) is compared to the number of light weight females (<30 g) in November 1986 ($n = 263$), a "survival" proportion of 0.388 is obtained. This proportion actually overestimates real survival of β-females since there are already a few heavy

Table 2. "Survival" to reproduction in generation types α and β, estimated as the proportion of animals at the start of the breeding season ($t = b$) to the number of light-weight animals at the end of the prior breeding season ($t = 0$). The proportion is recalculated as a 28-d finite survival rate φ_{28}.

Type		$t = 0$	N_0	$t = b$	N_b	"Survival"	φ_{28}
α	♂♂	Nov '87	252	Feb '88	19	0.075	0.611
	♀♀		233		38	0.163	0.708
β	♂♂	Nov '88	162	Feb '89	60	0.370	0.734
	♀♀		131		62	0.473	0.792

Table 3. Breeding seasons, generation types, mean incidence of pregnancy I, mean litter size and reproductive output (mean number of young produced per female). Separate calculations for the β- and γ-generations were only possible in 1987 because no age-estimates are available in other years.

Season	Generation type	I	Litter size	Reprod. output
Apr '82–Nov '82	α	5.89	11.29	66.5
Feb '83–Mar '83	β	0.17	10.63	1.8
Apr '83–Sep '83	β+γ	4.19	11.95	50.1
Feb '84–Mar '84	β	1.04	9.69	10.1
Apr '84–Oct '84	β+γ	4.99	11.91	59.4
Jan '85	β	0.23	7.44	1.7
Apr '86–Aug '86	α	5.66	11.58	65.5
Jan '87	β	1.73	10.10	17.5
May '87–Oct '87	β	0.89	10.71	9.5
	γ	3.45	10.71	36.9
Apr '88–Sep '88	α	4.99	13.75	68.6
Feb '89	β	1.53	11.87	18.2

γ-generation females in May 1987. With this survival, a β-female will obtain 3.7 additional young in the main breeding season. In total, combining our data for 1986–87 and 1988–89, a β-female that is still alive at the end of its season of birth will on average have produced 12.3 young by the end of the next main breeding season.

Discussion

The age-structures show that older animals are very rare and only few animals live longer than 300 d. This limited longevity has been reported for related *Mastomys* species as well (Hubert 1982, Bronner 1986). After the breeding season, adults disappear from the population and are replaced by the growing young. The total disappearance of older animals could also be observed in the data presented by Coetzee (1980), although the author did not mention it himself. On the other hand, the data on sexual maturation in this study show that no females reached sexual maturity during the breeding period in which they were born. Thus, we can safely conclude that most animals reproduce only in the breeding season following their own season of birth. The only exception are a few females of the β-generation that survive the off-season breeding period and that participate again early in the main breeding season of the same year. Unfortunately, our CMR-study started too late to be certain that these females actually did reproduce in both seasons.

Animals from α-, β- or γ-generations have a different probability to survive until reproduction, not only because it takes a different length of time to reach puberty, but also because standardized survival rates, and thus conditions for survival, are slightly different during this period. These differences are not directly reflected in the expected lifetime reproductive performance estimates. Although the β-generation survives better, it has a lower production of young, resulting in an average lifetime reproductive performance which is only slightly better than that of the α-generation. In years where the reproductive outcome during the off-season breeding is less (Table 3), the β-generation would probably do even worse. However, also the young of the γ-generation, produced by the β-females during the off-season period, will breed in the main breeding season and produce young themselves. Since the sex ratio is not different from parity in this period (73 ♂♂, 62 ♀♀, $\chi^2 = 0.896$), half of the young in the γ-generation are females and each of them can be expected to produce 15.1 young in their turn. Consequently, a female of the β-generation will have produced at the end of the main breeding season a total of, on average, 77.2 young, most of them grandchildren. Thus, the per capita production of young before the end of the main breeding season, will be almost seven times higher in years with a β- and a γ-generation than in years with an α-generation. Although some of our assumptions are rough estimates, the observed differences in production of young are convincing and impressive.

Table 4. Expected lifetime reproductive performance (probability of survival until the reproductive season multiplied by the average number of young produced per female in that season) for α, β and γ generation types. The survival probablity for the γ-generation expresses local survival only and thus underestimates real survival.

Type	Birth	Breeding season	Survival to reproduction	No. of young	Lifetime reprod. performance
α	middle '87	May–Sep '88	0.163	68.8	11.2
β	middle '86	Jan '87	?	17.5	?
	middle '88	Feb '89	0.473	18.2	8.6
	middle '86	May–Oct '87	0.388	9.5	3.7
					Total: 12.3
γ	early '87	May–Oct '87	0.410	36.9	15.1

The presence of breeding young of the year and their breeding performance is an important factor in causing density fluctuations of several rodent species (Hubert and Adam 1983, Löfgren 1989, Nelson et al. 1991). In Senegalese *Mastomys erythroleucus*, young of the year participate in reproduction only if the breeding season, which is dependent on the rainy season, lasts long enough; if not so, they have to wait until the following year (Hubert and Adam 1983, 1985). House mouse breeding success in Australia is extended by heavy rains at the end of the planting season, resulting in high densities later (Mutze et al. 1990, Mutze 1991). Also in our study, the presence of a generation that reproduces at young age is important to realize differences in total production of young. While in the cited studies, young of the year can breed in the same year due to persisting rains, the γ-generation in our study is associated with early heavy rains.

Delany and Happold (1979) calculated that one pair of *M. natalensis*, when constantly breeding and in conditions of no mortality, would produce, through themselves, their progeny and their progeny's progeny, over 6700 young in eight months. Our data show that delayed maturation and low survival until reproduction result in a maximum average productivity that is almost 100 times less than the theoretical potential. Only the females of the γ-generation reach sexual maturity at an age that is similar to that in optimal lab conditions (about two months (Oliff 1953)). Thus, *Mastomys* in natural conditions do not always display the short generation time that would be expected in a species which is generally considered to be a typical *r*-strategist (Willan and Meester 1989). Moreover, interannual variations in mortality can mask differences in production of young: the observed peak population sizes differ much less than one would expect from the large difference in reproductive output (Fig. 2). However, overall survival was much lower in 1987: only 91 of 209 animals survived locally from 15 September to 15 November in 1987 while 80 out of 130 individuals survived over the same period in 1988 ($\chi^2 = 10.39$, d.f. $= 1$, $p = 0.001$). Obviously, final population size is not only determined by production of young.

The question remains whether the observed differences between α- and β-generations are the result of different strategies or of a strict order of alternating generation types. In the latter case, a year with a β-generation would necessarily always be followed by an α-generation and vice versa, e.g. due to maternal effects or the effects of adult females on maturation of young (Bujalska 1985, Gilbert et al. 1986). That hypothesis can be ruled out since we observed only β- and γ-generations in two consecutive years, 1983 and 1984 (Table 3). Instead, the presence of a β-generation was always preceded by heavy rains at the end of the previous year (Leirs et al. 1989, Telford 1989). Such rains are also associated with reported rodent outbreaks in East Africa during the last decades (Leirs et al. 1990b). The variation in production of young by different generation types depending on rainfall patterns, helps to understand these outbreaks. The proximate cause of the relationship between rainfall and sexual maturation still needs to be elucidated, but growing grass seems to be an important factor (Leirs et al. unpubl.).

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