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WATER PHYSIOLOGY AND POPULATION DYNAMICS IN INSULAR POPULATIONS OF *MASTOMYS HUBERTI* (*RODENTIA, MURIDAE*)

During a two-year study of population dynamics, two island populations of *M. huberti* were shown to display variable survival rates, resulting in a highly fluctuating density on the smaller island, whereas immigration processes probably accounted for the relative stability on the other. Water metabolism results indicated that one of the island populations seemed better adapted to water shortage. A halt to growth during the dry season may be a consequence of harsh environmental conditions, but may also enable individual survival.

Key words: Island biology, population dynamics, water metabolism, *Mastomys*, adaptation.

1. INTRODUCTION

Since the famous book of M a c A r t h u r and W i l s o n (1967) and even before, island biology has been a fertile ground for testing hypotheses and elaborating theories about the functioning and evolution of animal communities

and populations. Besides the numerous works on insular communities, many studies have taken a population approach (see references in Granjon 1987), and a few syntheses have summarized and theorized current knowledge in different fields, such as population dynamics and its regulation (Gliwicz 1980), behavioural ecology and interindividual relationships (Stamps and Buechner 1985) and body size evolution (Lomolino 1985), among others. The "island rule" (after Van Valen 1973) so described (i.e. "the graded trend from gigantism in the smaller species of insular mammals to dwarfism in the larger species", Lomolino 1985) has few exceptions, for which environmental constraints have often been invoked as responsible. However, the consequences of the harsh conditions associated with particular insular habitats for the characteristics of island populations have seldom been considered.

We here present data on populations of an African murid rodent, *M. huberti*, which is known to live preferentially in outdoor humid zones of West Africa (Petter 1977, Duplantier and Granjon 1988). Surprisingly, this species has been found to occupy the sandy islands of the Saloum region (Sénégal), whereas the congeneric *M. erythroleucus* was by far the dominant species on the nearby mainland (Granjon and Duplantier 1989). Moreover, field data suggested that insular *M. huberti* were of small size compared with their mainland counterparts, and that this was associated with a reduced growth rate in captivity (Duplantier 1988). These various preliminary findings led us to start a long-term field study of the population dynamics and demography in some of the populations. As one of the starting hypothesis was that part of the "non-classical" characteristics of these insular populations was due to the particular environment of the Saloum islands, we also performed a study of water metabolism in the same samples (comparisons between island and mainland populations will be published elsewhere). These two sets of results are presented and discussed together, to try to understand how environmental constraints can interact with the "usual" evolutionary trends in island habitats.

2. MATERIAL AND METHODS

2.1. STUDY SITES

Capture-Mark-Release (CMR) programs were undertaken at two sites of the Saloum islands region (Fig. 1). The climate and geography of this region have been described in details by Granjon (1987) and Granjon and Duplantier (1989).

The first station (Betanti) is about one kilometre south of the village of Betanti (13°41' N, 16°38' W), on the coast near a vast island group known as "iles de Betanti". The vegetation of the study site is mainly herbaceous, with grasses (*Sporobolus robustus*, *Andropogon gayanus*, *Pennisetum pedicellatum*, *Cassia* sp. and *Eragrostis tremula*) and halophilous plants such as *Philoxerus vermicularis* and *Cressa cretica*. Bushes (*Maytenus senegalensis*) and shrubs (*Acacia albida*, *Phoenix reclinata*, *Tamarix senegalensis*, *Strophautus sarmentosus*, etc.) are also present, together with baobabs (*Adansonia digitata*).
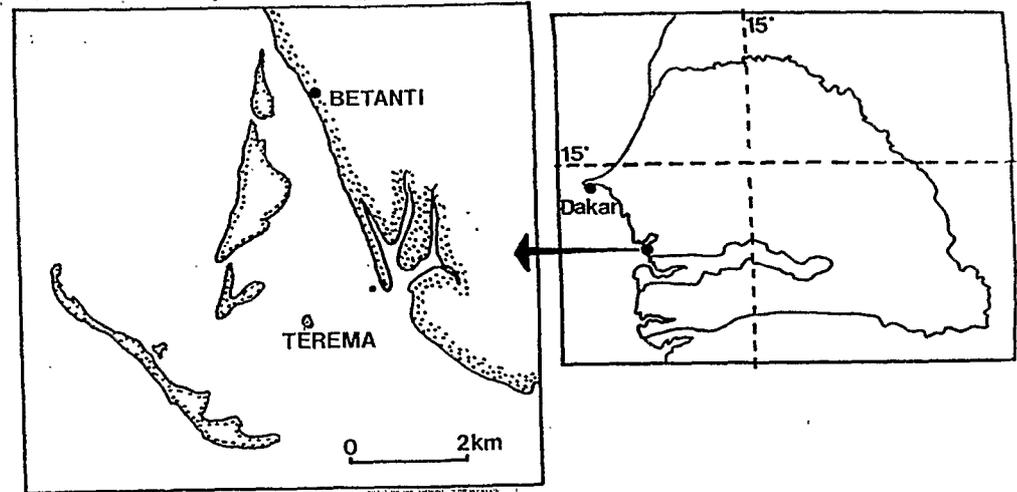

Fig. 1. Map of Senegal (right) and of part of the Saloum islands region (left), showing the study sites

The second site is the island of Terema, around 4 km south of Betanti and 1.2 km off the coast. The nearest land (ile aux Boeufs n°3, 750 m West of Terema) is an island 21 hectares large, also supporting a population of *M. huberti*. The area of Terema is about 0.8 ha, and the highest elevation does not exceed one meter. Most of the islet is covered with grasses mixed with halophilous plants (*Sesuvium portulacastrum* and *Ipomaea pes-caprae*), some stalks of small creeping watermelons (*Cucumis melo*), and a few bushes. Surprisingly, a group of dwarf baobabs remains.

Sampling for water physiology experiments was conducted at these two sites, after the end of the CMR programs. The climatic regime of the region is characterized by a unique annual rainy season lasting from June-July to October, and a mean annual temperature around 28°C (data from Kaolack city).

2.2. TRAPPING PROGRAMS

CMR programs in Betanti and on Terema were conducted from October 1988 to October 1990, on a trimestral basis: every three months, live-traps were set on two grids during five successive nights in Betanti, and three on Terema island. Traps were placed every ten meters on parallel lines ten meters apart. They were baited with peanut butter and checked every morning for captures. The trapped individuals were weighed, marked by toe-clipping and released at their capture site after their reproductive condition was noted. The grid in Betanti was composed of 11 lines of 21 traps covering an area of 2 ha. The whole area of Terema (around 0.8 ha) was sampled with 68 to 87 traps, according to the changing shape of the island edges due to variable seawater currents.

Trapping for water physiology experiments was performed during the last week of May 1991 in Betanti and Terema. This period corresponds to the end

of the hot dry season in this region. Due to a very low recapture rate in Betanti, the sample size in this station is particularly small compared with the other one.

2.3. WATER METABOLISM EXPERIMENTS

In the field, the trapped individuals (except for pregnant and lactating females) were given an intraperitoneal injection of tritiated-water (90 ml of a 5.12 MBq/μl solution of tritiated-water), and maintained in the traps with no food or water supply for 150 to 180 minutes. A blood sample was then taken from the infraorbital sinus, and the animals were released at their capture sites. A second blood sample was taken from the recaptured individuals, around three days (range 2–6) after their initial capture. After a second injection of the tritiated-water solution followed by a 150–180 min period in the trap with no water nor food, the animals underwent a third blood sampling.

The same individuals plus some others were brought to Dakar for laboratory experiments. They were left acclimatizing to the laboratory conditions, i.e. natural photoperiod (13 hours daylight), relative humidity (between 70% and 90%) and temperature (between 20° and 27°C), for 5 to 7 days before the experiments. The laboratory experiment was divided into two phases. During the first one, food and water were available *ad libitum*, while in the second phase the animals were water-deprived. Time constraints did not allow to subject the animals to a gradual water deprivation. In both experimental phases the procedure used in the field was repeated. Radioactivity was counted in 5 to 10 ml of plasma following the procedure described in Sicard et al. (1985). Water flux was estimated from the change in tritium activity in the blood samples before and after the release periods (in the field) or the resting periods (in the laboratory). Changes in body mass and mass-specific water pools were assumed to be linear during these experimental periods (see Nagy and Costa (1980) for discussion). Plasma was assumed to be 95% water, and for each animal, body water contents (BWC, initial and final), water influx and efflux (WI and WE) and water balance (WB) as the difference between WI and WE were calculated (Nagy and Costa 1980). When water metabolism was balanced (i.e. WI not significantly different from WE), the water turnover rate (WT) was calculated as the ratio between the means of water flux (WI and WE) and the means of BWCs (initial and final).

2.4. DATA TREATMENT

CMR data were used to evaluate the dynamics of the two populations studied. Following Leirs (1992), who critically compared the different available estimators of population size, we chose Minimum Numbers Alive (MNA), (Krebs 1966) to depict population changes. Survival rate estimates were obtained through the SURGE program, which aims at modelling survival and capture rates from CMR data (Lebreton et al. 1992, Pradel and Lebreton 1993). Among the different models tested, we retained the "st, p" (time-dependent survival, recapture rate constant) model for comparing the two

populations. The recapture rate having been found equal in both cases ($p = 0.71$), survival rates were directly comparable.

Water metabolism data were compared between and within populations by means of analysis of variance (ANOVA) or non-parametric tests (Siegel and Castellan 1988).

3. RESULTS

3.1. CMR STUDY

During the nine trapping sessions of the two-year study, 425 captures of 160 *M. huberti* were recorded on Terema, whereas 165 different individuals of *M. huberti* were captured on 217 occasions in Betanti. At the former site, *M. huberti* was the only species present, whereas *Tatera gambiana* was found almost as frequently as *M. huberti* in Betanti (121 individuals, 179 captures). The population dynamics of these two species at the two study sites between October 1988 and October 1990 are shown in Figure 2 Numbers were very small at the beginning of the CMR program, with only 2 *M. huberti* trapped on Terema, and 5 *M. huberti* and 2 *T. gambiana* in Betanti. Subsequently, fluctuations of the number of *M. huberti* on Terema were very pronounced, with MNAs ranging from 8 to 97. Variations in the numbers of the two species present in Betanti were more attenuated, with MNAs between 19 and 37 for *M. huberti* and between 7 and 48 for *T. gambiana* (Fig. 2).

Distributions of the trapped individuals into weight classes per trapping period (data from the two years pooled) appear somewhat different between the two sites (Fig. 3). At both stations, there is a regular increase of mean weight from January to October, but the modal value is always the lowest in the population of Betanti. Consequently, the mean weights of the samples captured are in all sessions ($n = 9$) higher on Terema than on Betanti.

Survival rates in these two populations are listed in Table 1. No statistically significant difference was found between the two populations at any period. The variations of these rates seem to follow the same general pattern on Terema as in Betanti, with a regular decrease from the beginning to the end of the year.

3.2. WATER METABOLISM

Global ANOVA pointed out the importance of both experimental conditions (field, *ad libitum* or water deprivation) and origin (Terema, Betanti) on water balance variability over the whole sample. As for water influx and efflux, interaction between the two factors (population and experiment) emerges as significant (Table 2).

In field conditions, no statistically significant difference was found between the samples for BWCs, WI, WE and WB (still the sample size of Betanti is very small). However, important variations in individual body weights were observed between the two injections on Terema, and we decided to split this sample into two parts: one (Terema I) composed of the 20 individuals that lost
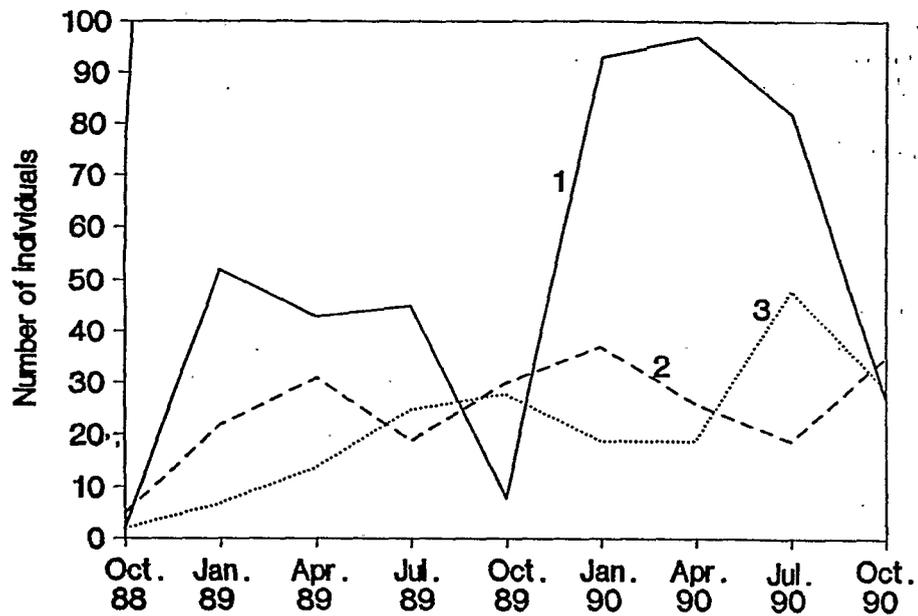
Fig. 2. Population dynamics (Minimum Numbers of individuals Alive) of the rodent species trapped in Betanti and on Terema between October 1988 and October 1990

1 – M. huberti, Terema; *2 – M. huberti*, Betanti; *3 – Tatera*, Betanti

Table 1

Estimated values (and 95% confidence intervals) of survival between successive trapping sessions in Terema and Betanti populations of *M. huberti* sampled by CMR

| Date	Terema			Betanti		
	Estd. value	min.	max.	Estd. value	min.	max.
Oct.88–Jan.89	0.585497	0.048400	0.975142	0.223821	0.032541	0.711998
Jan.89–Apr.89	0.605811	0.417159	0.767441	0.803935	0.376702	0.965301
Apr.89–Jul.89	0.540857	0.337878	0.731127	0.349037	0.174138	0.576892
Jul.89–Oct.89	0.041442	0.010305	0.152189	0.248506	0.088513	0.529650
Oct.89–Jan.90	0.997496	0.000000	1.000000	0.120170	0.037703	0.322550
Jan.90–Apr.90	0.703731	0.566885	0.811702	0.478984	0.278892	0.686053
Apr.90–Jul.90	0.634649	0.493148	0.756177	0.387105	0.184909	0.637480
Jul.90–Oct.90	0.400958	0.270779	0.546794	0.330901	0.128431	0.624029
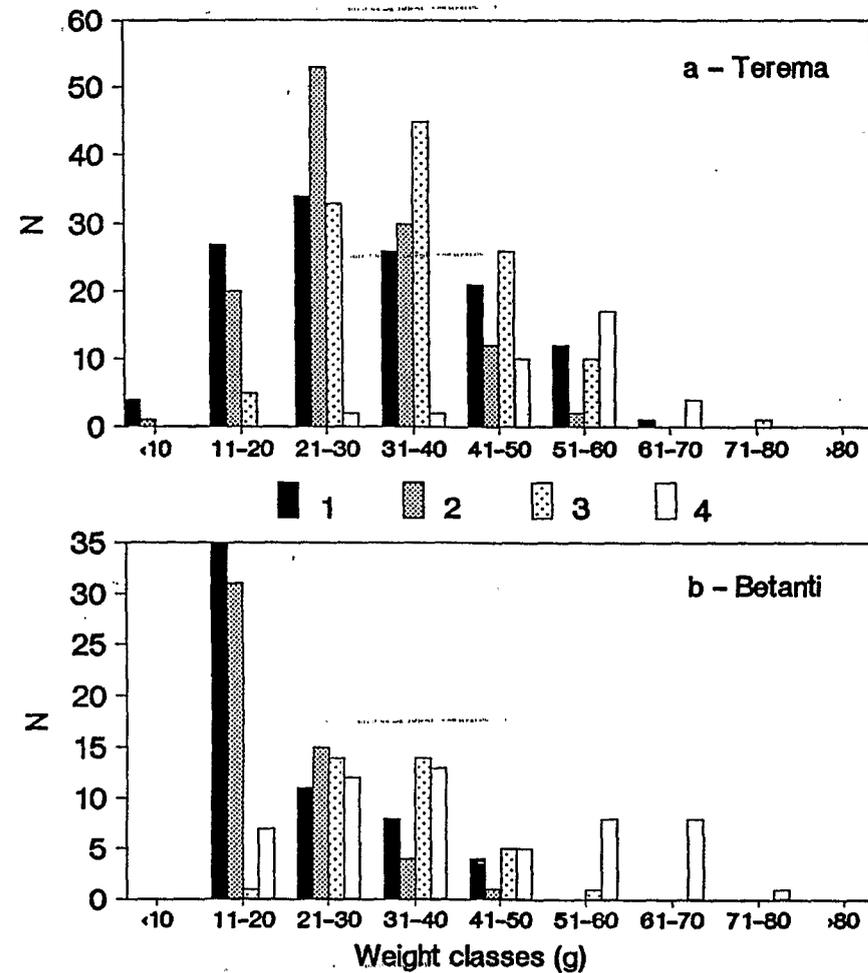
Fig. 3. Distribution of individuals of *M. huberti* into weight classes in each of the trapping periods on the two study grids between January 1989 and January 1990 (data of the two years pooled)

1 – January, *2 –* April, *3 –* July, *4 –* October

10% or more of their initial weight during the experiment, and the other (Terema II) with the 7 animals that have lost less than 10% of their initial weight. Terema I showed a lower WI than Terema II, which resulted in a significant WB deficit (ANOVA, $p \ll 0.001$ and $p \ll 0.05$, respectively; Table 3).

In *ad libitum* conditions, final BWC, WI and WE were significantly different between the two island samples (ANOVA, $p \ll 0.05$), with the Terema sample showing a particularly low value of final BWC and higher levels of water flux.

Table 2

ANOVA 2 tests of the influence of experimental conditions and of origin of the samples on water balance parameters ([**] $p < 0.05$, [***] $p < 0.01$)

Water balance parameter	factor	ANOVA 2 test	Significance
Water influx	experience	$F(2,78) = 32.9$	***
	population	$F(1,78) = 1.1$	NS
	interaction	$F(2,78) = 5.6$	***
Water efflux	experience	$F(2,78) = 12.2$	***
	population	$F(1, 78) = 6.9$	***
	interaction	$F(2, 78) = 4.5$	**
Water balance	experience	$F(2, 78) = 45.0$	***
	population	$F(1, 78) = 14.5$	***
	interaction	$F(2, 78) = 1.5$	NS

Table 3

Weights and water metabolism parameters (mean and standard error) for the two sub-samples of *M. huberti* from Terema island (see text)

	Terema I	Terema II
N	20	7
Initial weight (g)	26.2 (1.9)	31.0 (2.9)
Final weight (g)	22.5 (1.7)	29.6 (2.7)
Initial BWC (%)	73 (2)	78 (2)
Final BWC (%)	71 (2)	78 (2)
WI (ml/kg · day^{-1})	99.0 (8.8)	171.4 (20.7)
WE (ml/kg · day^{-1})	135.3 (12.7)	165.5 (19)
WB (ml/kg · day^{-1})	−36.3 (8.2)	5.9 (14.4)
Water turnover (%)		22.4 (2.4)

In fact, Betanti displayed an increase of BWC between the beginning and the end of the experiment (Wilcoxon test, $p \ll 0.05$). The mean values of WI and WE when compared within each population are not significantly different (t tests), but the t test for matched samples revealed that Betanti individuals were regularly in excess of water ($p \ll 0.05$).

In water restriction conditions there was a significant difference in WB (ANOVA, $p \ll 0.005$), with a much less pronounced water deficit in the Betanti sample. Only in Terema did the individuals display a loss from their water reserve (Wilcoxon test between initial and final BWC, $p \ll 0.005$). But when the individuals formerly placed in Terema I (9 animals here) were compared with the Terema II ones (4 animals here), it appeared that this loss of BWC concerned only the Terema I sample (t test, $p \ll 0.001$).

Water turnover could be calculated in all but one cases (Terema sample in water deprivation conditions). It was found to be remarkably constant whatever the experimental conditions in the samples from Betanti (between 21.5 and 23.5%), whereas it more than doubled in the Terema sample between field and *ad libitum* conditions (17.8 to 44.5%).

4. DISCUSSION

A number of demographic and socio-spatial traits characterizing island populations of rodents have been summarized by Gliwicz (1980), Stamps and Buechner (1985) and Granjon (1987). Among them, high density and stability of numbers were found to be common features of these populations, although it was noticed that "when environmental conditions on the island are unfavourable to the confined species ... (it can)...cause a large reduction in its numbers" (Gliwicz 1980, 111 p.). An island population of *M. erythroleucus* studied by CMR in 1984–1986, also in Sénégal, typically displayed this relative stability at high density, when compared with a mainland one (Granjon 1987).

Conversely, the pattern found here for the population of *M. huberti* on the small island of Teréma clearly represents an example of highly variable population dynamics: MNA varies by a factor of 50 between October 1988 and April 1990 (see Fig. 2), and by a factor of 12 between October 1989 and April 1990. During the same period, fluctuations in Betanti were much less marked for both species present, and especially *M. huberti*. Data on the population dynamics of *M. huberti* in natural habitats on a "true" mainland are not available, since the species appears quite rarely there. In fact, mainland populations of *M. huberti* are restricted to humid zones, either cultivated or natural (Duplantier and Granjon 1988). In the former their densities seem to be relatively high, due to the abundance of resources. In the latter, *M. huberti* probably occurs in low numbers, except locally (pool edges, swamps etc.) where its densities are likely to fluctuate seasonally. In the Saloum region mainland, *M. huberti* was seldom trapped (Granjon and Duplantier 1989), so the relatively high densities recorded on the two CMR sites (but also on other islands on various occasions, Granjon and Duplantier 1989) can be considered a good example of density compensation (MacArthur, Diamond and Karr 1972) associated with the reduction in species richness on islands.

However, this feature is not associated with stability of numbers, especially on Terema. This can be related to the highly fluctuating survival rate (Table 1) which, on Terema (= closed population), is a direct indication of the mortality rate. This pattern was also found in Betanti, but with a somewhat different meaning: the latter population can be considered an open one, and the survival rate also takes into account immigration-emigration processes, which are probably important in the apparent relative stability of population density in Betanti. This

is particularly true between April and October, when survival rates are very low in Betanti and when, in the absence of reproduction, most of the population is composed of newly-marked adults likely to represent immigrants. It has to be noted that a much less variable pattern of variation of survival rate was found for the insular *M. erythroleucus*, previously studied (Granjon 1987).

Water metabolism in *M. huberti* has been studied by various authors. Maiga (1984) and Yoda (1982, unpubl. results), using different methods, found similar results in *ad libitum* conditions in individuals of a laboratory colony originating from Sénégal. Sicard (1987) studied natural population of *Mastomys* in Burkina-Faso, but the individuals of two cryptic species were probably mixed in what he called *M. huberti* (Sicard and Gautun 1991). Our results are consistent with all these previously published ones, but add much to the knowledge of the physiological abilities of the species in different conditions.

First, interindividual variability must be stressed, as it appears as a probable key-feature of the adaptation of the populations to their environment, and especially to the sahelo-sudanian dry season: Over the whole range of experiments reported here, individual water flux ranged from 10.2 (Betanti, *ad libitum*) to 530.5 ml/kg.d. (Terema, *ad libitum*), and mean values from 91.5 (Terema, water-deprived) to 325.6 ml/kg.d. (Terema, *ad libitum*). This plasticity is apparent in laboratory conditions, and may reflect the capacity of the species faced with the changing natural conditions through the year. One extreme of these is represented by the end of the dry season, when water is at minimum in the vegetation, this being particularly obvious in the two insular sites considered here. Then, interindividual differences are less, and mean values tend to be close to the ones obtained in water restriction conditions. This is particularly true for WI, whereas WE is higher in water restriction than in field conditions. This may be due to the sudden transition between *ad libitum* and water deprivation conditions, which prevented the animals from adapting their water exchanges, but may also reflect a better control of water loss in the field through behavioural adaptations.

Secondly, comparison of the results in the different experiments indicates that individuals from Betanti are less flexible in their response to the experimental conditions, keeping relatively low water flux even in *ad libitum* conditions, with a remarkably stable water turnover. This can be interpreted as a loss of plasticity in this population, as a result of strong selection pressure for low water flux. The consequence is that even in water deprivation conditions, WB is at equilibrium, which is not the case in the other sample. However, when the sample from Terema is split into two parts on the basis of weight change during the field experiment, it appears that the fraction that did not lose weight deals better with the shortage of water, in the field or in water restriction conditions. Thus, where overall plasticity seems high, selection would act on those individuals that are best fitted to cope with physiological constrains. This would be accompanied by good overall condition of the individuals, exemplified by their weight stability during the experiment. The pronounced fluctuation of numbers described for the Terema population could be related

Table 4

Mean weight (g) variations of groups of *M. huberti* between different successive trapping sessions (standard error in parentheses, *** $p \ll 0.001$ for Wilcoxon signed-rank test)

	Terema		Betanti	
	Juveniles	Adults	Juveniles	Adults
Jan. to Apr.	N=28 20.5 (3.4) to 27.7 (4.6)***	N=25 42.5 (9.8) to 39.6 (6.7)		N=4 33.0 (8.4) to 32.5 (8.6)
Apr. to July	N=6 16.3 (2.6) to 29.0 (5.0)***	N=40 30.1 (7.8) to 42.9 (9.0)***	N=17 18.3 (2.5) to 18.7 (2.6)	N=11 18.5 (2.8) to 28.7 (5.3)***
July to Oct.		N=17 36.2 (8.1) to 53.5 (7.9)***		N=6 31.0 (7.5) to 60.2 (7.6)***

to the physiological variability of its members: only one fraction of this population seems to cope with the harshness of the environment, and the other fraction might be the one that does not survive to the end of the dry season.

Body weight is also of major importance in the adaptation to dry environments: Whereas BWC variations under the different experimental conditions were small, and might not have a very important biological impact, individual body weights varied quite a lot during the experiment (see above). Weight variations of individuals between the different periods of the CMR program are also of interest (Table 4). The critical period for growth is obviously between January and April, where weight gain of young is limited on Terema, and completely stopped in Betanti. Furthermore, weight increases slightly between April and July, and then significantly between July and October (rainy season), when the few adults still alive achieve "normal" adult weight for the species. This halt in growth, associated with environmental conditions, has already been noticed in *Mastomys natalensis* (Leirs 1992) and, to a lesser extent, in *M. erythroleucus* (Hubert and Demarne 1981). In these two cases, water and food availability were rconsidered as the principal factors. This hypothesis is confirmed by the results of Buffenstein and Jarvis (1985). They have shown that juveniles of *Aethomys namaquensis* and *Tatera leucogaster* reared in the absence of water gained little weight compared with juveniles not water-deprived. In our case, this growth delay seems to be an important characteristic of these Saloum islands populations, as it is still observed in laboratory-born individuals (Duplantier 1988).

The observed growth slackening, imposed by environmental constraints, may allow better efficiency in controlling water efflux during the dry season in the Saloum island populations of *M. huberti*, and especially in Betanti. This relation has already been found, on an interspecific scale in heteromyid rodents (MacMillen and Hinds 1983: small-sized species occur in the driest environment), and may be the ultimate means of survival for rodents populations in extreme environments.

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