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Body size variability and water balance: A comparison between mainland and island populations of *Mastomys huberti* (Rodentia: Muridae) in Senegal

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Abstract. Generally rodents are found to be larger on islands than on the mainland. However, there are some exceptions to this rule, and the aim of this paper is to examine one of them. On the mainland of Senegal, *Mastomys huberti* occupies humid habitats. However, it occurs also on dry and sandy islands (Saloum delta), where its representatives are dwarf. Since water availability appeared to be the limiting factor in these islands when compared to the mainland, we studied water turnover characteristics in relation to body size, in mainland and island populations at the end of the dry season, under both field and laboratory conditions.

All populations were found to be water balanced in their natural habitats. They presented similar rates of water turnover, even though island animals were subjected to stronger constraints than mainland ones. Laboratory experiments suggested that the physiological plasticity of one of the island populations may be reduced.

Island populations have a higher kidney size to body weight ratio than those from the mainland. We propose that smaller size in the islands allows the maintenance of water balance with a smaller amount of water, and that a higher ratio of kidney filtration surface to body size may help *Mastomys huberti* to survive in dry islands.

We discuss the factors responsible for body size variability and variation in water exchange characteristics and conclude that different factors could explain body size variation among island populations, depending on the species considered and the ecological constraints met within the islands.

Key words. Island dwarfism; water turnover; physiological plasticity; *Mastomys huberti.*

Many species of rodents exhibit larger body size on islands than on the mainland, and many hypotheses have been proposed to explain the observed pattern[1–3]. This pattern was described as part of the island rule by Van Valen[4], and has recently been discussed by Lawlor[5] and reexamined by Lomolino[6] with a larger sample of species and populations. Release from competition and from predation, as well as resource limitations, were suggested to be the major factors affecting the body size of mammals on islands, with resource specificity, trophic level and island carrying capacity as potential additional factors[5,6]. Within this general trend of insular gigantism, a few cases of insular dwarfism in different rodent species were pointed out by these authors. An analysis of body size variation of island rodents with different diets[5] suggested that dwarfism occurred in rodent species characterized by a specialized diet, whereas dietary generalists would follow the rule of increased body size on islands (but see Angerbjörn[7]).

A biogeographical study of the distribution of rodents in the Saloum region (Senegal) indicated a strong decrease in species richness from the mainland to the most isolated islands[8], which is in agreement with the island syndrome (sensu Blondel[9]). However, the only rodent species occurring on these islands, *Mastomys huberti*, is not the most abundant species on the mainland[10], which does not fit the island syndrome. Moreover, on the mainland *Mastomys huberti* is found only in humid regions, whereas the islands of the Saloum region of Senegal in which it occurs are sandy and dry. In these islands, its representatives are dwarf. *Mastomys huberti* is a dietary generalist species, (Hester, unpubl. data), which indicates that the trend displayed by this species is not consistent with Lawlor's argument[5].

Ecological constraints vary with species and habitats, and probably so do factors likely to influence body size. The present study examines to what extent smaller body size in island populations could be related to plasticity of physiological mechanisms, allowing the survival of populations of a species in marginal habitats[8,11]. Water, among other factors, is an important component of habitat quality. Many studies comparing water turnover rates in wild species exist[12,13]. For instance, MacMillen and Hinds[14] have shown that within the Heteromyidae rodent family, the efficiency of water regulation was inversely correlated with body size.

However, very few studies have addressed this problem at a population level[15–18], and to our knowledge none of them have considered water constraints (as a resource limitation) in the frame of body size variation and

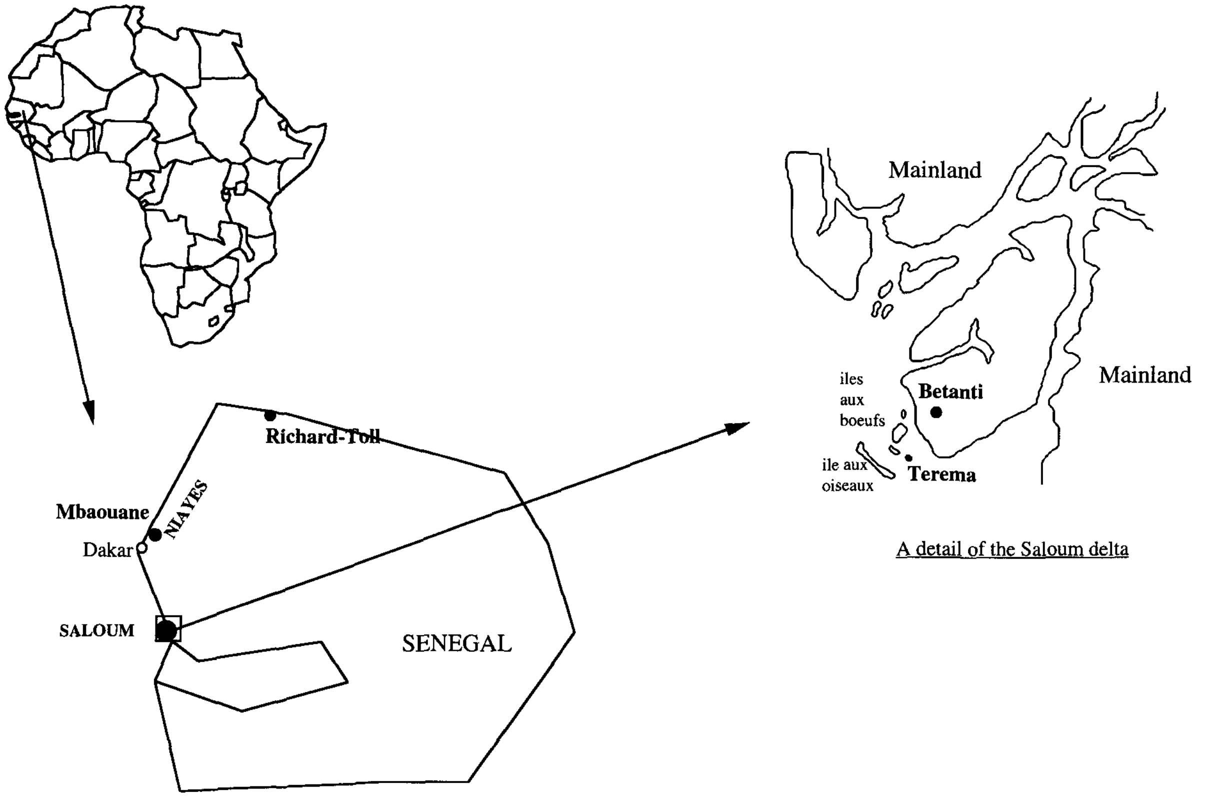

Figure 1. Geographical location of four populations of *Mastomys huberti* sampled for this study (dark circles indicate location of populations).

island biology. The situation of *Mastomys* in the Saloum delta provides an exceptional opportunity to test, under natural conditions, the relation between changes in ecological constraints (water availability) and biological characteristics (dwarfism) in different populations of a species[8]. Water availability seems to be the most constraining ecological factor in the Saloum region, and water needs are often related to body size. Thus, we hypothesized that body size variation of insular *Mastomys* could be partly related to water constraints. We report results from a comparative study of water turnover characteristics between island and mainland populations of *M. huberti* performed in the field and under laboratory conditions, and examine data on body weight variation in the same populations.

Material and methods

Study sites. Sampling for water turnover experiments was performed in three distinct populations of *M. huberti* (fig. 1). Two of them are located in the Saloum islands region, and the other one in a cultivated zone north of Dakar. Climate and geography of the Saloum region are described in detail in Granjon[19] and Granjon and Duplantier[8]. The first site is located approximately one kilometer south of the village of Betanti (13°41′N; 16° 38′ W), on the coast of a large island (nearly 20,000 ha) which is characteristic of the amphibious zone of the Saloum islands region[8]. The vegetation of the trapping station 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*) as well as shrubs (*Acacia albida*, *Phoenix reclinata*, *Tamarix senegalensis*, *Strophautus sarmentosus* etc.) and baobabs (*Adansonia digitata*). The second site is the island of Terema, around 4 km south of Betanti and 1.2 km off the coast of the amphibious zone. The nearest land (l'île aux Boeufs N°3, 750 m west of Terema) is an island of 21 hectares, also supporting a population of *M. huberti*. The island of Terema is about 0.8 ha in area, and the highest elevation does not exceed one meter. Most of the islet is covered with grasses (as above) mixed with halophilous plants (*Sesuvium portulacastrum* and *Ipomaea pes-caprae*), some stalks of small creeping watermelons (*Cucumis melo*), a few bushes, and a group of dwarf baobabs. The mainland site chosen for comparison is situated in a market garden zone called Niayes, north of Dakar, which represents one of the most common habitats of *M. huberti* on the mainland. The trapping site lies close to the village of Mbaouane (14° 53′ N; 17° 84 W), and is characterized by the adjacent small gardening plots irrigated from wells and separated from one another by grassy embankments. The main market garden products are tomatoes, eggplants, gombos and cabbages, among others. Another mainland sample originating from a similar biotope in the northwest of Senegal close to the city of Richard-Toll was analyzed for body size comparisons only.

Trapping program. The Betanti and Terema populations were sampled between 22.05.91 and 29.05.91, and the Niayes population was trapped between 31.05.91 and 04.06.1991. The Richard-Toll population was sampled at the end of June 1993. This period corresponds to the dry hot season, characterized by a complete lack of rain and a mean temperature of around 25 °C in Niayes and Richard-Toll, and of around 30 °C in the Saloum region. Live-traps (type Manufrance) were baited with peanut butter, set in the afternoon and checked the following morning. The capture/recapture method was used: in Betanti 4 out of 16 animals were recaptured, in Terema 27 out of 46, and in Niayes 11 out of 14 animals were recaptured.

Water turnover study. We used the tritiated water technique. For discussions on the reliability of this technique, see Nagy and Costa[20]. All the precautions recommended by the authors were taken into account in the study reported here.

Field experiment. All captured animals (adults, excluding pregnant and lactating females) were subjected to an intraperitoneal injection of 90 μl of a solution of 5.12 MBq/ml of tritiated water on the morning of their capture. Animals were then maintained in the traps with no food or water supply for 150 to 180 min, after which time a blood sample (50 μl) was taken from the infraorbital blood sinus. They were then released at their capture sites. A second blood sample was taken from the recaptured animals nearly 3 days after their first capture (mainland site: 3.1 ± 0.3 days, $n = 11$; island sites, Terema: 3.3 ± 0.9 days, $n = 27$, Betanti: 3.5 ± 0.3 days, $n = 4$). After a second injection of the tritiated water solution, followed by a rest of 150 to 180 min with no water and food supply, the animals were subjected to a third blood sampling.

All these animals, as well as additional specimens (in order to obtain a larger sample) were brought to Dakar for laboratory experiments.

Laboratory experiments. Animals were allowed to acclimatize to laboratory conditions during 5 to 7 days. During all the experiments they were housed in pairs, and were subjected to the natural photoperiod (13 hours daylight); humidity varied between 70% and 90%, and temperature between 20 and 27 °C. The first part of the experiment lasted 3 days during which food (rabbit pellets containing 11–13% of moisture) and drinking water were available ad libitum. The procedure used in the field to estimate individual water turnover was repeated. All animals recovered well from the blood sampling. Within 2 days after the ad libitum experiment, animals from Terema, Betanti and Niayes were water deprived for 2.2 days, 1.8 days, 2.3 days respectively, and their water turnover estimated again. Time constraints did not allow us to submit the animals to gradual water deprivation. Duration of water deprivation was kept to a minimum, and all animals survived this treatment.

Blood sample analysis and calculation of water turnover rates. 5–10 μl of plasma were obtained from each blood sample and frozen. Later, the plasma samples were thawed and dissolved in 10 ml of scintillation liquid for radioactivity counting following the procedure described in Sicard et al.[17]. Water efflux and influx were estimated from the change in tritium activity of blood samples during the release period (in the field experiment) and during the resting periods (under laboratory conditions), assuming that changes in body mass and mass-specific water pools were linear during the experimental periods. For each animal, body water content, water influx and efflux, and water balance as the difference between water influx and efflux were calculated[20]. When water metabolism was balanced, water turnover rate was calculated as the ratio between the means of water flux and body water content.

Body and kidney size. Animals were weighed at each capture and in each experimental phase in the laboratory. At the end of the laboratory experiments (a month after the capture), animals were weighed again, sacrificed and their body and kidney length and width measured. Since the kidney weight measure was omitted, allometric comparisons will concern length and width data. Measurements were made with a ruler (0.5 mm precision), considering every time the longest length and largest width. The *Mastomys* kidney is sleek and has a classical bean shape.

Statistical analysis. Once the normality and equality of variance had been checked for, the effects of origin and experimental conditions on body weight and water turnover parameters were tested, by one- and two-way Anovas followed by a Fisher protected Least Significant Differences post-hoc test[21]. When two dependent variables were compared, we used Student's *t*-test for matched samples (Statworks Macintosh software). Mean values throughout the text are presented with their associated standard errors (SE). Sex differences were tested at all steps; they were significant as far as body and kidney size were concerned, but were never involved in an interaction effect with another factor. No sexual differences were observed as far as water turnover was concerned, therefore only population differences will be discussed.

Results

Body weight and length variation in the field. Geographical variability of body weight and length is evident in

Table 1. Body weight and length variations in *Mastomys huberti* in Senegal.

Origin[2]	Females			Males			Total[1]	
	Body weight (g)	Head + body length (mm)	n	Body weight (g)	Head + body length (mm)	n	Body weight[a] (g)	Head + body length[b] (mm)
Betanti (island)	18.6 ± 1.3	95.6 ± 1.4	7	24.0 ± 0.0	109.0 ± 2.0	2	19.8 ± 1.3	98.6 ± 2.4
Terema (island)	24.1 ± 1.7	108 ± 2.5	10	30.2 ± 2.2	112.9 ± 2.3	14	27.7 ± 1.8	110.9 ± 2.2
Niayes (mainland)	39.6 ± 3.1	117.9 ± 3.8	10	45.6 ± 3.5	124.8 ± 3.9	6	44.2 ± 2.8	120.5 ± 2.9
Richard-Toll (mainland)	42.2 ± 2.7	121.2 ± 3.0	20	49.9 ± 1.4	131.0 ± 1.4	49	47.6 ± 1.4	128.2 ± 1.5

1a: 2 ways Anova: sex, $F_{1,110} = 5.8$, $p = 0.02$; origin, $F_{3,110} = 29.4$, $p = 0.0001$; interaction, $F_3, 110 = 0.07$, NS.
1b: 2 ways Anova: sex, $F_{1,110} = 10.1$, $p = 0.002$; origin, $F_{3,110} = 19.5$, $p = 0.0001$; interaction, $F_{3,110} = 0.46$, NS.
2a: Comparison of populations, post-hoc test: B-T, $p = 0.04$; B-N, $p = 0.0001$; T-N, T-RT, $p = 0.0001$; N-RT, $p = 0.03$.
2b: Comparison between populations, post-hoc test: B-T, $p = 0.03$; B-N, B-RT, $p = 0.0001$; T-N, $p = 0.004$; T-RT, $p = 0.0001$; N-RT, $p = 0.008$.

this species (see tests in table 1). However, the general trend shows that mainland individuals are heavier than island ones. This pattern is consistent with data obtained during two previous years of sampling (Granjon et al. unpubl.).

Kidney length and width. A comparison of kidney length and width among the four populations shows a significant origin effect (table 2). The Betanti population has significantly smaller kidneys than the three other populations (post-hoc test, $p = 0.0001$; table 2). Since Betanti animals were the smallest, small kidneys could have resulted from an allometric effect. When the ratio of kidney length or width to body length is considered the above pattern disappears.

The Terema population is the only one that is consistently different from the mainland animals when kidney size to body length are considered (table 2; tests: $p > 0.05$, $p > 0.005$). Only kidney width to body weight ratios allow a distinction between mainland and island populations (post-hoc test: $p < 0.05$). When kidney length to body weight ratios are compared, the two mainland populations display the lowest ratios and are not different; Terema has a significantly higher ratio, and Betanti presents the highest ratio (table 2).

Body weight variation during water turnover studies in the field and in controlled conditions. A comparison between body weight at capture and at the end of the experiment (1 month later) shows that the island populations put on significantly more weight than the mainland population (table 3, body weight gain/initial body weight: Betanti, 0.40 ± 0.3, Terema, 0.37 ± 0.3, Niayes, 0.13 ± 0.1; $F_{2,36} = 3.4$, $p < 0.05$).

When water was available ad libitum, animals from the three population samples showed the same pattern of weight gain (0.03 ± 0.00 of the initial weight per day). During the experiment of water deprivation, all three samples lost weight at the end (one way Anova, $F_{2,31} = 6.6$, $p < 0.05$; table 3). This pattern was less pronounced in the case of Betanti: 0.04 ± 0.02 of weight loss per day, than in the case of Terema: 0.09 ± 0.01, and Niayes: 0.09 ± 0.00.

In the field, the pattern of weight loss is significantly different for the three populations (one-way Anova,

Table 2. Kidney and body size variations in *Mastomys huberti*.

Population (n)	Body length (mm)	Body weight (g)	Kidney length (mm)[a]	Kidney width (mm)[b]	(K.length/B.weight) × 100 (mm/g)[c]	(K.width/B.weight) × 100 (mm/g)[d]
Betanti (9)	98.6 ± 2.4	26.1 ± 1.8	8.6 ± 0.2	4.8 ± 0.1	33.8 ± 1.7	18.9 ± 1.0
Terema (19)	110.6 ± 2.1	35.8 ± 1.8	10.2 ± 4.7	5.9 ± 0.2	29.3 ± 1.4	17.1 ± 1.0
Niayes (15)	122.7 ± 1.9	46.7 ± 2.2	10.5 ± 0.2	5.9 ± 0.1	22.9 ± 0.8	13.0 ± 0.6
Richard-Toll (69)	128.2 ± 1.4	47.6 ± 1.4	10.7 ± 0.1	6.3 ± 0.1	24.0 ± 0.6	14.0 ± 0.5

[a] 2 ways Anova: $F_{3,107} = 11.7$, $p = 0.0001$.
[b] 2 ways Anova: $F_{3,107} = 13.0$, $p = 0.0001$.
[c] 2 ways Anova: $F_{3,107} = 6.73$, $p = 0.0003$.
[d] 2 ways Anova: $F_{3,107} = 3.39$, $p = 0.02$.

Table 3. Water turnover parameters as measured in 3 populations of *Mastomys huberti* in the field, and during 2 laboratory experiments in which water was first available ad libitum and then withheld.

Origin (N)	Field conditions					Ad libitum laboratory conditions			Water deprivation laboratory conditions		
	Terema total (27)	Terema I (20)	Terema II (7)	Betanti (4)	Niayes (mainland) (11)	Terema (18)	Betanti (7)	Niayes (mainland) (15)	Terema (16)	Betanti (7)	Niayes (mainland) (11)
Initial body weight (g)											
mean	27.4	26.2	31.0	16.5	46.0	28.9	20.6	41.2	31.1	22.0	42.6
range	13 to 43	13 to 43	20 to 38	13 to 21	31 to 55	16 to 45	15 to 24	16 to 54	17 to 49	17 to 27	17 to 58
S.E.	1.7	2.0	3.1	2.0	2.1	2.1	1.3	2.9	2.2	1.5	3.4
Final body weight (g)											
mean	24.2	22.5	29.6	16.2	45.5	30.2	22.0	43.5	24.6	20.3	32.0
range	10 to 38	10 to 38	21 to 37	14 to 18	31 to 54	16 to 47	17 to 27	17 to 58	14 to 41	15 to 24	13 to 41
S.E.	1.6	1.7	2.9	1.0	2.3	2.1	1.5	2.9	1.9	1.2	2.8
Initial body water content (%)											
mean	72.9	73.0	73.0	67.6	67.4	73.0	69.0	73.9	74.8	79.0	77.0
range	55 to 86	55 to 85	58 to 86	56 to 76	54 to 85	60 to 84	63 to 77	67 to 81	61 to 87	72 to 87	64 to 89
S.E.	1.9	2.2	3.7	3.7	2.8	1.9	2.0	1.3	1.9	2.0	2.3
Final body water content (%)											
mean	72.6	71.0	78.0	67.0	69.5	72.5	79.0	77.2	67.0	72.6	73.0
range	56 to 88	56 to 88	72 to 82	62 to 77	57 to 83	63 to 84	72 to 87	54 to 89	53 to 85	61 to 84	56 to 85
S.E.	1.7	2.0	2.0	3.7	2.4	1.4	2.0	1.9	2.7	3.3	2.8
Influx (ml/kg.d)											
mean	117.7	99.0	171.4	137.6	146.8	325.6	195.6	368.5	91.5	140.7	112.4
range	23 to 252	24 to 176	104 to 252	56 to 207	46 to 297	76 to 530	66 to 325	128 to 815	131 to 258	34 to 239	10 to 254
S.E.	10.5	9.1	22.3	39.3	28.7	30.7	39.2	57.7	24.9	26.3	26.0
Efflux (ml/kg.d)											
mean	143.1	135.3	165.5	136.7	144.2	309.2	148.2	322.9	202.3	182.0	212.8
range	37 to 268	36 to 268	94 to 246	30 to 211	37 to 285	104 to 529	10 to 266	45 to 755	39 to 398	124 to 255	77 to 375
S.E.	11.0	13.1	20.6	38.6	30.0	29.8	34.6	61.8	25.7	21.1	32.6
Water balance (ml/kg.d)											
mean	−25.4	−36.6	5.9	0.9	2.5	16.4	47.3	45.6	−110.8	−41.2	−100.4
range	−92 to 87	−92 to 41	−26 to 87	−28 to 26	−34 to 41	−77 to 95	8 to 80	−10 to 124	−219 to 19	−99 to 30	−156 to −44
S.E.	8.0	8.4	15.5	13.2	8.03	10.7	10.9	10.8	12.2	18.7	11.3
Water turnover rate (100 × flux/volume)											
mean	17.8	*	22.4	23.0	21.7	44.5	23.5	46.8	*	21.5	*
range	7.7 to 30.8		13 to 30	6 to 38	11 to 111	11 to 80	5 to 41	11 to 111		10 to 31	
S.E.	1.3		2.6	7.8	4.5	4.6	5.1	8.5		3.0	

*When water flux were not balanced water turnover rate could not be calculated.

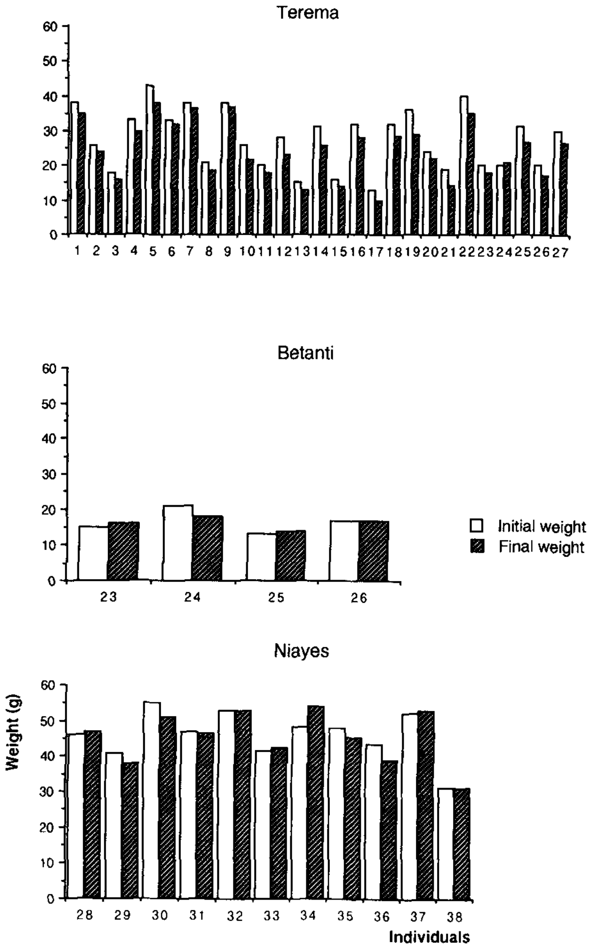

Figure 2. Body weight variation during capture and recapture sessions in the field.

$F_{2,39} = 7.716$, $p = 0.015$); in fact, individuals from Terema lost significantly more weight than those from the two other populations (post-hoc test: $p > 0.01$; fig. 2).

An analysis of the Terema sample shows that 74% of the individuals lost at least 10% of their initial body weight between the two capture sessions (range −10 to −24%), whereas the rest of the Terema sample lost only an average of 3% of their weight (range −8 to +5%). Only one animal lost more than 11% of its initial weight in Niayes and the average weight loss of individuals from Betanti and the former site is 0.0 ± 1.0%.

The considerable weight loss observed for a sub-sample of the Terema animals might be attributed to the effect of stress caused by trapping[22], but could not be ascribed to stress induced by the injection or the blood sampling since the same animals did not lose weight during laboratory experiments in *ad libitum* conditions.

Water turnover. A comparative analysis of the 3 populations for the three experimental designs indicates a significant effect of the experimental conditions as far as water influx, efflux and water balance were concerned (respectively $F_{2,107} = 40.8$; 14.8; 92.0; $p < 0.0001$; table 3); geographic origin has a significant effect as far as water efflux and water balance are concerned (respectively $F_{2,107} = 3.1$; 9.7; $p < 0.05$), and there is no interactive effect between geographic origin and experi- mental conditions.

Field conditions. The three populations have comparable water flux and water balance levels ($F_{2,39} = 0.8$; 0.2; 2.7). Since body weight variations have a direct influence on water flux, we considered that the dramatic

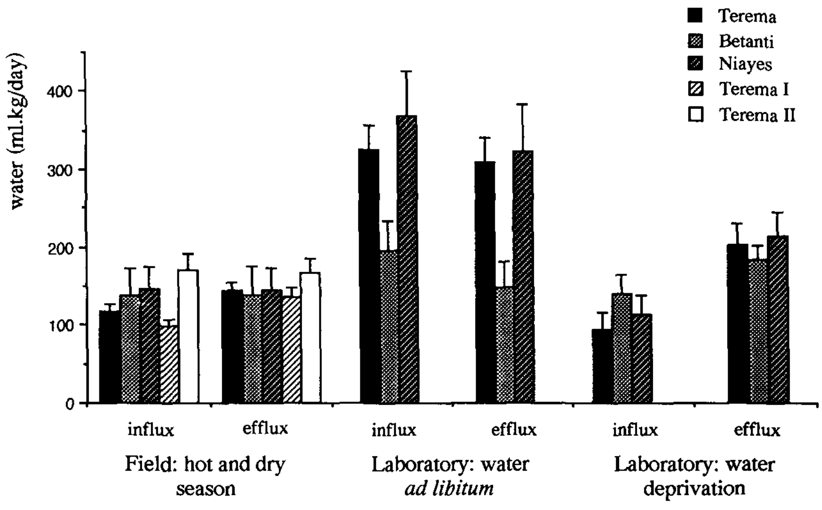

Figure 3. Comparison of water flux measured in three different populations of *Mastomys huberti* in the field and under two laboratory conditions. In the case of Terema two sub-samples were distinguished in the field: Terema I = individuals which lost at least 10% of their weight during the experiment, Terema II = individuals which did not display a significant weight loss. See table 3 and text for more details.

body weight variability displayed by the Terema sample in field conditions justified splitting this sample into two: one fraction of the sample groups the 20 individuals which lost 10% and more of their initial body weight during the experiment (Terema I), while the 7 animals (Terema II) that lost less than 10% of their body mass are placed in the second (see above and table 3).

An analysis of these two sub-samples reveals that they have different water influx and water balance levels (respectively, $F_{1,25} = 14.2$ $p < 0.001$ and $F_{1,25} = 6.8$ $p < 0.05$, table 3). Terema I shows a lower water influx involving a significant deficit of its water balance (table 3, fig. 3). This indicates that a significant loss of water occurred during the experiment and results in a significant water deficit when compared to the other two populations ($F_{2,32} = 6.1$, $p < 0.01$).

Water ad libitum conditions. An analysis of variation in body water content during this experiment shows a significant effect of the geographic origin ($F_{2,37} = 4.65$, $p = 0.02$). This effect is due in fact to a significantly greater body water content variation in the Betanti sample than in that from Terema (post-hoc test, $p = 0.005$), Niayes showing an intermediate pattern.

A one-way analysis of variance did not show differences in water turnover between the 3 populations. However, the average water flux is relatively lower in Betanti animals than it is in those of Niayes and Terema (table 3, fig. 3). Terema and Betanti animals have different levels of water influx and efflux (one way Anova, respectively, $F_{1,23} = 6.0$ $p < 0.05$; efflux $F_{1,23} = 10.0$ $p < 0.01$). An analysis taking into account individual variations reveals that Niayes and Betanti animals appear to have an excedent water balance (t test for matched samples, respectively: $t = -4.36$, $p < 0.01$ and $t = -4.67$, $p < 0.01$) which may explain the increase in body water content in the two populations.

Water-restricted conditions. Water balance under water restrictive conditions is significantly different in the three samples (One way Anova, $F_{2,31} = 6.4$, $p < 0.01$); the Betanti sample displays a low, not significant, water balance deficit while the two other populations do exhibit deficits (post-hoc test Betanti-Terema $p = 0.001$, Betanti-Niayes $p = 0.009$). The Terema group is the only one to show a significant loss of its water volume (t test for paired samples, $t = 3.63$, $p = 0.002$). However, when Terema I (animals which displayed a water deficit in the field, 9 individuals) is compared to Terema II (animals which were water-balanced in the field, 4 animals), it appears that the loss of body water content involves only the Terema I sub-sample (t paired, $t = 3.32$, $p = 0.01$).

Discussion

Ecological correlates of body size variations. This study points out significant differences in body weight and length between different populations of *Mastomys huberti*. These variations cannot be ascribed to differences in population age structure, since reproduction of murid rodents in the sahelo-soudanian region occurs mainly during and after the rainy season[23,24], and our study took place at the end of the dry season, when the four populations studied were exclusively composed of adults. Thus, at the end of the dry season, adults of *M. huberti* are the smallest in Betanti island and the largest in Niayes and Richard-Toll (mainland samples), whereas in Terema, the smallest island, they are intermediate in size.

Table 4. Ecological characteristics of the 4 localities where the populations of *Mastomys huberti* were studied in Senegal.

Origin	Location	Water availability	Interspecies competition	Intraspecies competition
Niayes	mainland	+ +	+ + +	+ +
Richard-Toll	mainland	+ +	+ + +	+ +
Betanti	island	–	+	+
Terema	island	–	–	+ + +

–very low level or absence; + exists; + + not negligible; + + + potentially important.

Competition is believed to be a cause of body size decrease in populations of some species[3]. However, as far as *M. huberti* is concerned, mainland populations are potentially subjected to more competition than island ones (table 4), but show the opposite trend in body size variation. The smaller size of *M. huberti* in Betanti, as compared to Terema, could be related to the presence of *Tatera gambiana* as a potential competitor in the former site, while in Terema *M. huberti* is the only mammalian species present. *T. gambiana*, a heavier species (about × 2), occurs at similar densities to *M. huberti* in Betanti (Granjon et al. unpubl.), and may temporarily interfere with it as far as resource exploitation is concerned. However, on the whole, competition does not lead to the expected changes in body size between mainland and island populations of *M. huberti*, so other factors have to be considered in order to explain the observed body size variation.

74% of the Terema sample is represented by individuals which lost at least 10% of their initial body weight within the short period separating their first capture and recapture, which indicated that these individuals had coped poorly with the stress of capture when compared to the other fraction of the population sample. This variability may be related to the high density presented by *M. huberti* during our study, which was twice that in Betanti (a trend also shown during a long term study of the two populations, Granjon et al., unpubl.). High density in a small area with no possibility for dispersal, leads to a hierarchical social organization in rodents[25–27]. This social organization implies that some groups of individuals have access to the best resources while the others do not. Social constraints might result, in Terema, in the best resources being monopolized by a very small number of individuals who alone would ensure the persistence of the species in this island. Behavioral tests should help to investigate the above-described phenomenon. In Betanti, the very low rate of recapture may be partly attributed to dispersal and lower density, but also to very low survival after the perturbation of capture.

The case of *Mastomys huberti* represents a complex situation since many factors appear to differentiate between the populations (table 4). However, this study clearly allows competition (inter or intra- species) to be rejected as the proximal factor influencing body size variation in *Mastomys*. When mainland and island habitats of the species are compared, water availability appears to be the major factor distinguishing them (table 4).

Ecophysiological characteristics and their relation to body size variation. Whatever habitats the populations were sampled from, their water turnover rates in the field were not different on average. This means that *M. huberti* can cope with water-scarce habitats as well as with humid habitats. The similarity of water turnover rates in mainland and island populations of *M. huberti* may signify that the species has not evolved specific adaptations to dry islands, and that its water requirements have not changed. The only trait which has changed is body size, and thus the quantity of water necessary to maintain a similar level of water turnover rate when water becomes less available.

Body weight variability under experimental conditions of different water availability reveals that the species is capable of varying its body weight without changing its relative body water content, in response either to constraints or to better conditions. This pattern suggests a relative plasticity of these populations for this biological trait. The limited loss of body weight in deprived conditions displayed by the Betanti sample as compared to the two others can be interpreted as a lack of plasticity, and may also indicate a higher resistance to water scarcity.

Juveniles of *Aethomys namaquensis* and *Tatera leucogaster*, reared in the absence of water, gained very little weight when compared to less deprived juveniles[28]. The same trend was found when *Meriones shawi* was water-deprived during its growth period: its body weight increased regularly but the levels reached were always lower than when it was not deprived[29]. Thus, small size during the dry season in island populations of *M.huberti* might be the result of environmental constraints during the growth period, at the beginning of the dry season, and/or of selection in favor of individuals tolerating such constraints. Laboratory experiments limiting water availability during the growth period should help to test the relevance of such factors to body size variation in *Mastomys*.

MacMillen and Hinds[14] proposed a model for the evolution of the Heteromyidae rodent family, concluding that selection may have initially favored a decrease in mass with a concomitant increase in the efficiency of water regulation and a reduction in absolute energy need. Richmond et al.[30] have indicated that a positive correlation exists between body weight and water loss, in 7 mammalian species. Additionally, different authors have shown that chronic water deprivation resulted in renal hypertrophy, and an increase in the thickness of the inner stripe zone of the outer medulla when compared to control animals[29,31]. These quantitative and qualitative adaptive changes resulted in a more efficient water conservation. We did not test this in the present study, but the two island populations showed a high kidney-size to body-weight ratio which might have resulted from the phenomenon described above.

Evolutionary implications. Laboratory studies of the progeny of island and mainland *M. huberti* reveal that even though body size differences between animals of the two origins are not as important as those observed in the field, the difference is still significant, which suggests that island dwarfism in *M. huberti* might have a genetic component as well as an environmental one[11]. The laboratory experiments presented here were aimed at obtaining preliminary information on how the different populations adjust their water exchanges to water availability. Terema and Niayes animals show an apparent physiological plasticity. While Betanti animals do not adjust their water consumption to water availability, they succeed in maintaining a water balance, while the two former populations show a water deficit under water-deprived conditions. This may be interpreted as the consequence of a loss of physiological plasticity in animals from Betanti and might be the result of strong selection pressures in favor of a relatively constant but low need for water. This assumption can be tested by measuring water consumption in laboratory conditions. Future research should focus on the study of the Betanti population, the particular behavior of which under laboratory conditions suggests that this population has evolved special adaptations and/or requirements as far as water is concerned.

Lawlor[5] has hypothesized that large body size should be favored among food generalists on islands because they would be exploiting a homogeneous environment, while a reduction of size should favor food specialists since their food supply is distributed heterogeneously. This hypothesis is supported by observations of *Mastomys erythroleucus*, a generalist species found in Senegal, in which an island population composed of large-sized individuals was studied[19]. However, for *M. huberti* Lawlor's hypothesis is not valid, since the species, which is a generalist too, is represented on islands by dwarf individuals. The difference between the two examples is that one of the species occurs on relatively humid islands while the other (*M. huberti*) is found only on dry islands.

In conclusion, the case of *M. huberti* in Senegal agrees with Angerbjörn's[7] suggestion that different selective forces can influence island features such as dwarfism, and that each case has to be considered according to the species' biological characteristics and the environmental conditions it encounters.

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