

## Food deprivation and drinking in two African rodents, *Mastomys natalensis* and *Rhabdomys pumilio*

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*Mastomys natalensis* and *Rhabdomys pumilio* from the moist Natal Midlands, South Africa, were deprived of food in the laboratory. Both species exhibited hypodipsia while fasting and, in terms of a hypothesis proposed by Wright (1976), therefore appear to be primarily mesophilic. *R. pumilio* tolerated up to five days without food and *M. natalensis* up to three days. *R. pumilio* appears adapted to occupy drier microhabitats than *M. natalensis*, and pre-adapted to colonize arid regions.

*Mastomys natalensis* en *Rhabdomys pumilio* vanaf die vogtige Natalse Middellande, Suid-Afrika, is in die laboratorium van voedsel ontnem. Beide spesies het hipodipsia ondervind terwyl hulle gevas het, en skyn dus, in terme van 'n hipotese voorgestel deur Wright (1976), primêr mesofilies te wees. *R. pumilio* het 'n maksimum van vyf dae sonder voedsel verdra, en *M. natalensis* 'n maksimum van drie dae. *R. pumilio* is blykbaar daarby aangepas om 'n droër mikrohabitat as *M. natalensis* te bewoon, en is vooraf aangepas daarby om droër gebiede te koloniseer.

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The Natal multimammate mouse *Mastomys natalensis* (A. Smith, 1834)\* (\*see taxonomic note) and the four-striped mouse *Rhabdomys pumilio* (Sparman, 1784) coexist in many parts of southern Africa. The literature suggests, however, that gradients of water abundance may influence habitat selection in these species (*inter alia* Perrin 1981a; Willan 1982; Willan & Hickman 1986). This is evident in their patterns of geographic distribution in southern Africa, where annual rainfall generally declines from east to west: *R. pumilio* is widely distributed in the region, including in its range much of the South West Arid Zone (Davis 1974), while *M. natalensis* is restricted to the wetter eastern parts and, except for an isolated population in central Namibia, does not penetrate the S.W. Arid (Green, Keogh, Gordon, Pinto & Hartwig 1980; Meester, Rautenbach, Dippenaar & Baker 1986). On the basis of a literature survey, Perrin (1981a) described *R. pumilio* as having a xeric tendency, and *M. natalensis sensu lato*\* a xeric tolerance. Haim & Fourie (1980) have proposed that differences in the water metabolism of *M. natalensis sensu lato* and *R. pumilio* may determine their range.

Periodic water shortage in xeric habitats inhibits primary production (Caldwell 1975) which in turn directly or indirectly reduces availability of food to heterotrophs. In adaptive response to periodic scarcity of food, xerophilic species have lower metabolic rates, and are therefore able to survive for longer on a given energy intake, than similar species occurring in less arid environments (Schmidt-Nielsen 1972). An indication of relative mesic or xeric adaptation may therefore be obtained by assessing species-specific tolerance of food deprivation.

An additional theoretical framework within which to test coarsely for mesic or xeric adaptation in small rodents was provided by Wright (1976). In a study on

patterns of drinking during food deprivation of six northern hemisphere rodents, Wright demonstrated the occurrence in xerophilic species of absolute polydipsia (i.e. water consumption at least 50% above that under conditions of *ad libitum* food availability), with mesophilic species displaying hypodipsia (i.e. reduced drinking). No adaptive explanation was advanced regarding these trends, but a hypothesis was proposed which predicted similar responses in other mesophilic and xerophilic rodent species (Wright 1976).

Toward an understanding of the role of water abundance on habitat selection and niche separation in *M. natalensis* and *R. pumilio* in the Natal Midlands, South Africa, a laboratory study was accordingly undertaken on their tolerance of, and water consumption during, food deprivation.

### Methods

*M. natalensis* and *R. pumilio* were livetrapped during April–May 1977 near Pietermaritzburg, Natal (29°37'S / 30°26'E). *Mastomys* from the study area were karyotyped as *M. natalensis* (2N=32; J.M. Hallett, *in litt.* 1977). Before experimentation, animals were maintained for four weeks under partially controlled conditions (14L:10D; 18–25°C) with Epol mouse cubes and water provided *ad libitum*.

The response of 16 adults (eight males, eight females) of each species to food deprivation was studied in a Conviron controlled environment cabinet set to cycle at 14L (at 25°C and 50% rH) and 10D (15°C and 70% rH), which approximated field (runway) conditions when the animals were collected (Willan 1982). Animals were individually housed in cages 50 × 25 × 21 cm fitted with feeding dishes and steel-spouted drinking bottles calibrated to read to the nearest 0,1 ml. No litter or nesting

material were provided. Two replications per species were run, one for each sex. A seven-day acclimation period preceded each trial, during which mouse cubes and water were provided *ad libitum*. Acclimation was followed by three experimental periods, during which body mass and water consumption were recorded every 24 h: a further *ad libitum* period of five days, a food deprivation period which varied in length according to species-specific tolerances, and a five-day *ad libitum* recovery period.

In order to bring the experiment to a suitably objective endpoint without starving animals to death, the subjects were kept under regular observation (2–8 hourly, depending on the stage of the experiment) and, except in one case, deprivation was terminated before mortality occurred, at a stage when individuals were so weakened as to be incapable of sustained activity. In the absence of food, free-living animals in such condition would not live for more than a few hours.

Depending on whether or not data fulfilled the requirements for parametric statistical analysis (Sokal & Rohlf 1969), sample means were compared using the parametric *z* test or the nonparametric Mann-Whitney *U* test.

## Results

There was no significant sexual difference in response to food deprivation in either species (*U* test for differences in mean tolerances) and data for the two sexes are therefore combined.

*R. pumilio* was the more tolerant of fasting: 14 of the 16 individuals survived five days without food and two were withdrawn before reaching five days. Eight *M. natalensis* survived three days of fasting; seven individuals were withdrawn and one died before reaching three days.

Mean duration of fasting was significantly greater in *R. pumilio*, and this species tolerated significantly greater mass loss than *M. natalensis* (Table 1). Post-deprivation mass recovery was slower in *R. pumilio* (Table 1), but had this species fasted for only three days, its recovery rate would probably have been at least as rapid as that of *M. natalensis*.

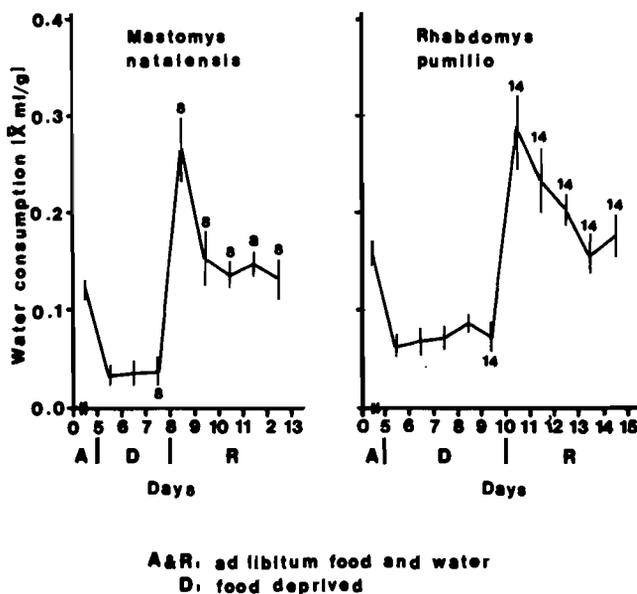
Patterns of drinking are illustrated in Figure 1, in which water consumption (ml/g) was calculated using the mean baseline mass of individuals (Period A). Water consumption during the baseline period was significantly higher in *R. pumilio* than in *M. natalensis* ( $z = 2,12$ ;  $P < 0,05$ ). Both *M. natalensis* and *R. pumilio* depressed drinking during food deprivation, by daily means of 72% and 50% respectively. By the second day of the recovery period, water consumption in *M. natalensis* was approximately normal, but this did not occur until the fourth day in *R. pumilio*. As in the case of mass recovery after fasting (above), drinking in *R. pumilio* would presumably have normalized more rapidly had it fasted for only three days.

## Discussion

It is apparent that under the conditions of the present

**Table 1** Maximum and mean tolerances ( $\pm 2$ SEM) of food deprivation of *Mastomys natalensis* and *Rhabdomys pumilio*; sample size: 16 animals of each species, except as indicated in brackets

Parameters	Species		Statistics (Mann-Whitney <i>U</i> test)
	<i>Mastomys natalensis</i>	<i>Rhabdomys pumilio</i>	
Time			
Maximum tolerance (h)	72	120	–
$\bar{X}$ tolerance (h)	60,3 $\pm$ 6,0	118,5 $\pm$ 2,2	$U = 0$ ; $P < ,001$
Mass			
$\bar{X}$ baseline (g)	58,7 $\pm$ 7,0	43,9 $\pm$ 1,9	–
$\bar{X}$ post-deprivation (%)	78,4 $\pm$ 2,0 (8)	75,2 $\pm$ 1,6 (14)	$U = 19$ ; $P < ,01$
$\bar{X}$ post-recovery (%)	99,6 $\pm$ 2,2 (8)	93,6 $\pm$ 2,4 (14)	$U = 11$ ; $P < ,001$



**Figure 1** Effect of food deprivation on mean daily water consumption ( $\pm 2$ SEM) of *Mastomys natalensis* and *Rhabdomys pumilio*. Sample size: 16 animals of each species, except as indicated in the body of the figure.

study *R. pumilio* was markedly more tolerant of food deprivation than was *M. natalensis*. This conclusion is reinforced by consideration of the following additional factors.

First, the mean baseline mass of *R. pumilio* used in the experiment was 25% lower than that of *M. natalensis*, which therefore enjoyed a more favourable surface/volume ratio and associated energy conservation advantages.

Second, locomotor activity of food-deprived *R. pumilio* is almost twice as high as that of *M. natalensis*, with *R. pumilio* significantly increasing and *M. natalensis* significantly decreasing activity relative to that during *ad libitum* food and water availability (Willan & Hickman 1986). This implies a considerable disparity between the species in energy expended on locomotion in the present

experiment. Moreover, reduced locomotor activity in starving laboratory rats is accompanied by a lowering of energy expenditure per unit of activity (Westerterp 1976) — starvation induces slower movement, and the energy cost of moving a given distance declines with declining speed (Taylor, Schmidt-Nielsen & Raab 1970). The disparity in energy loss between *R. pumilio* and *M. natalensis* (which, like the laboratory rat, reduces locomotor activity when fasting; Willan & Hickman 1986) may therefore have been even greater than indicated by their different activity levels.

Third, Haim & Fourie (1980) have shown that *R. pumilio* has a significantly higher thermal conductance and, at temperatures below the thermoneutral zone ( $T_a = 32^\circ\text{C}$  for both species), a higher food intake and significantly higher metabolic rate than *M. natalensis sensu lato*. (It is unlikely that *M. natalensis* and *M. coucha* would differ significantly in terms of these parameters, so that the question of which species was the subject of Haim & Fourie's study is probably immaterial.) In the present study, where the maximum and minimum ambient temperatures were  $25^\circ\text{C}$  and  $15^\circ\text{C}$  respectively, and where potentially insulative nesting material was not available, *R. pumilio* was thus further disadvantaged relative to *M. natalensis* in respect of energy expenditure during food deprivation.

Extrapolation from the results of this study to a field situation must be tempered by the probability that the present experiment, in which food was totally withdrawn, did not accurately reflect starvation in nature. Sudden elimination of the food supply of free-living animals would be an unlikely event, and starvation would therefore tend to be slower in the field than in the laboratory. In addition, the relative tolerances of ketoacidosis (resulting from a total lack of dietary carbohydrates during laboratory food deprivation) are unknown for the two species. Nonetheless, good reasons exist for believing that free-living *R. pumilio* are more tolerant of food shortage than are *M. natalensis*, as set out below.

*R. pumilio* accumulates large fat reserves when food is plentiful (Brooks 1974; Perrin 1981b; Willan 1982), and the comparatively high tolerance of food deprivation of this species may be partially explained in terms of fat mobilization during periods of shortfall in energy intake. *R. pumilio* is an opportunistic omnivore (Perrin 1980) and its ability to store fat appears to be an adaptation to the exploitation of nutritious but ephemeral food resources (Perrin 1981b), or to surviving prolonged periods of food shortage, for example after fire (Willan & Hickman 1986). The poor performance of *M. natalensis*, which is a primarily graminivorous omnivore (De Graaff 1981; Smithers 1983) and is not potentially a fat species (Willan 1982), is possibly explained by its adaptation to degraded habitats in which interspecific competition is slight (Meester, Rowe-Rowe & Lloyd 1979) and food resources may be comparatively plentiful (Willan 1982). This species may therefore be adapted to a more or less continuous food supply, and would not have evolved mechanisms permitting prolonged survival of food shortage in the field.

The significant difference in daily baseline water consumption of the two species may have been partially the result of their different patterns of diel activity. Free-living *M. natalensis* are nocturnal, while *R. pumilio* is diurnal with crepuscular activity peaks (De Graaff 1981; Smithers 1983). In captivity, *M. natalensis* remains strictly nocturnal, and *R. pumilio* mainly diurnal (Perrin 1981a; Willan 1982). Mouse cubes contained respectively 10,8% and 14,4% water during the light and dark parts of the experimental cycle (Willan 1982), and *M. natalensis* thus had 33% more preformed water available in its food, possibly therefore requiring less drinking water than *R. pumilio*. Assuming a similar trend in the moisture content of dry seeds in the field, and although extremes of hydration of this type of food are probably less pronounced under natural conditions than in the laboratory, free-living *R. pumilio* may obtain less water than *M. natalensis* from this source.

Differences in the feeding habits of the two species in the field (above) would be expected to further influence their drinking requirements. Free-living *R. pumilio* consume much highly hydrated food, namely green plant material and insects (Perrin 1980), from which large amounts of preformed water would be obtained. Morphologically, *R. pumilio* is better adapted for herbivory than is *M. natalensis* (Perrin & Curtis 1980). In addition, *R. pumilio* thrives and gains weight on a laboratory diet comprising only insects, but *M. natalensis* does not (Willan 1982). It is therefore possible that free-living *R. pumilio* are generally independent of drinking water, as is the case in many rodent species, including some xerophilic forms (*inter alia* Schmidt-Nielsen 1964).

Green & Rowe-Rowe (1987) concluded that *M. natalensis* are unlikely to drink when the vegetation is lush. This idea is supported by the fact that the total water intake of free-living *M. natalensis*, as measured under moist summer conditions at a Natal Midlands site (Green & Rowe-Rowe 1987), was almost twice as high as that during the baseline period in the present study, where the food was comparatively poorly hydrated and water was available *ad libitum*. In addition, the primarily graminivorous diet of *M. natalensis* (De Graaff 1981; Smithers 1983) suggests that this species may be an obligate drinker under drier environmental conditions than exist in the Natal Midlands.

The level of adaptation to shortage of free water displayed by *R. pumilio* would place this species in a category of arid-adapted rodents termed 'moist' species by Schmidt-Nielsen (1964, p. 182). Based on Wright's (1976) hypothesis, however, the hypodipsic response of both *M. natalensis* and *R. pumilio* to fasting suggests that the populations from which laboratory stocks were drawn are primarily mesophilic. The present study was not designed to test Wright's hypothesis, but the findings lend it a measure of support. The terms mesic and xeric are relative ones, but in the moist Natal Midlands, where mean annual rainfall is generally in excess of 800 mm (Weather Bureau 1960), truly xeric habitats do not exist. The performance of the two species was therefore entirely predictable.

*R. pumilio* is morphologically variable, and numerous

subspecies have been recognized (*inter alia* Roberts 1951) whose status is currently regarded as uncertain (Meester *et al.* 1986). Marked regional variation does nevertheless exist in *R. pumilio*, suggesting that several valid subspecies may occur in southern Africa (Meester *et al.* 1986). Body size and relative tail length are apparently determined by the combined effects of temperature and rainfall (Coetzee 1970), while differences in colouration suggest that there may be taxonomically distinct eastern and western forms of *R. pumilio* (Rautenbach 1982). It would not be surprising if, correlated with these and other possible morphological differences, discrete physiological races of *R. pumilio* exist which are respectively more fully mesic- and xeric-adapted in the wetter (eastern) and drier (western) parts of its range, as hypothesized by D.P. Christian (*in litt.* 1979). As a test of this idea, it would be useful to compare the tolerance of food deprivation of eastern and western *R. pumilio*. It would be of interest to similarly compare *M. natalensis* and *M. coucha* — on the basis of the available distributional data (Green *et al.* 1980) *M. coucha* appears to have a generally more westerly range, and would therefore be expected to better tolerate food shortage than *M. natalensis*.

*R. pumilio* is essentially a savanna species, although ranging extensively in the S.W. Arid Zone (Davis 1962). The presence of xerophilic features in mesophilic (Natal Midlands) *R. pumilio* has interesting implications in respect of both the local and regional distribution of this species. The capacity of mesophilic *R. pumilio* to store and mobilize fat, and to capitalize on preformed water available in its food, may adapt this species to exploit drier microhabitats than *M. natalensis* and possibly pre-adapt it to colonize and survive in arid environments.

#### \*Taxonomic note

*M. natalensis* (A. Smith, 1834) with karyotype  $2N = 32$ , and *M. coucha* (A. Smith, 1836) with  $2N = 36$  were classified together as *Praomys natalensis* (A. Smith, 1847) until recently (Green *et al.* 1980), although the existence of sibling species within *P. natalensis* was recognized earlier (*inter alia* Green, Gordon & Lyons 1978; Hallett 1979). Meester *et al.* (1986) and others now formally treat *Mastomys* as a separate genus comprising three species, *coucha*, *natalensis* and *shortridgei* (St Leger, 1933). *M. natalensis* and *M. coucha* are indistinguishable on external morphology but their chromosomal and haemoglobin patterns are dissimilar and, despite broad sympatry, there is no evidence of hybridization in the field (Green *et al.* 1980); there are significant behavioural (Gordon 1984) and pheromonal differences between them (D. Gordon & P. Apps, unpubl.). The exact range limits of the two species are not yet fully known, but their broad distribution is given by Meester *et al.* (1986) as follows: *M. natalensis* — southern and eastern Cape Province, Transkei, Natal, eastern Transvaal, Zimbabwe, and central and north-eastern Namibia; *M. coucha* — eastern and northern Cape Province, Zululand, Lesotho, Orange Free State, southern and western Transvaal, southern and western

Zimbabwe, and central Namibia; both species probably occur more widely in southern Africa, while their range elsewhere in Africa is unknown. The formerly confused taxonomic status of *M. natalensis* has resulted in a situation where the identity of the particular *Mastomys* species referred to in many publications cannot be established with certainty as being *M. natalensis* or *M. coucha*. Based on distributional data, Bronner (1986) has distinguished as far as possible those studies which could reliably be assigned to one or the other species, while studies which could not be so assigned were referred to *M. natalensis sensu lato*. This convention and Bronner's categories are followed here.

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