Short communications

Do *Mastomys natalensis* pups develop more quickly than *M. coucha* pups?

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The multi-mammate mice *Mastomys natalensis* and *M. coucha* occur allopatrically through much of their ranges, suggesting some measure of ecological or competitive separation. In this study we examined pup growth and development to weaning in *M. natalensis* and *M. coucha*. Despite faster development by *M. natalensis* in the first week *post partum*, behavioural and physical development demonstrated no further differences. Therefore, it appears neither species exhibits a significant advantage in behavioural development at weaning. However, *M. natalensis* pups showed faster growth rates and heavier weaning mass than *M. coucha* pups. Differences in the growth and weaning masses of pups suggest a disparity in food intake, food quality, energy expenditure or energy assimilation rates that may be important in understanding social or ecological differences between these two cryptic rodents.

Key words: growth, ontogeny, rainfall, competition, exclusion.

Multi-mammate mice occur through most of sub-Saharan Africa, with two cryptic species *Mastomys natalensis* and *M. coucha* occurring extensively within southern Africa. Whereas *M. coucha* is endemic to the region, *M. natalensis* has the widest distribution of any African rodent (Fiedler 1988). Compared to *M. natalensis,* that primarily occupies savanna woodland (Gordon 1984), the distribution of *M. coucha* extends into grasslands and marginally into the South West Arid and South West Cape zones (Green *et al.* 1980; Gordon 1984). Rainfall is of considerable consequence to the distribution and ecology of these two *Mastomys* species as Venturi (2001) demonstrated the most important predictors describing their ranges were the coefficient of variation in precipitation (CVP), mean annual precipitation (MAP), mean primary productivity (MPP) and potential evaporation (PE). Significantly, Venturi (2001) predicted that *M. coucha* should occur in areas with greater PE and CVP and lower MPP and MAP than *M. natalensis.* Indeed, *M. natalensis* generally occurs in the wetter eastern areas of southern Africa receiving >600 mm annual rainfall and *M. coucha* in the drier western areas, with an annual precipitation of <700 mm (Gordon 1984; Venturi 2001), the two species being recorded sympatrically within the 600–700 mm rainfall isohyets.

These data suggest some measure of ecological divergence, with *M. natalensis* unable to tolerate the less mesic areas of the region. The absence, however, of *M. coucha* from more mesic regions remains unclear, though interspecific competition, either past or present, may have led to its competitive exclusion by *M. natalensis.* Certainly the widespread occurrence of *M. natalensis* suggests it may be able to out-compete *M. coucha* through a variety of habitats. Similarly, in West Africa Duplantier *et al.* (1996) proposed that the more extensive distribution of *M. erythroleucus,* compared to *M. natalensis,* could be explained by its greater reproductive performance, allowing it to colonize newer habitats more rapidly.

In this study we provide new data examining differences in the pre-weaning growth and development of *M. coucha* and *M. natalensis,* factors that could provide some insight into species-specific differences in their behaviour and ecology.

Ten breeding pairs of both *M. coucha* and *M. natalensis* were maintained in the experimental holding facilities (25°C, 14L:10D) of the University of Pretoria. The ethical committee of the Faculty of Natural and Agricultural Sciences of the University sanctioned all holding and handling procedures.

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Water was provided *ad libitum* to all individuals. To control for maximum energy and protein intake, each adult received 10 g of a diet formulated to contain a digestible protein content of 15 % and energy value of approximately 123 kJ a day (following the methods of Lamb & van Aarde 2001), which provided sufficient energy for growth and reproduction (Perrin & Clarke 1987).

Captive breeding pairs of *M. natalensis* were established from individuals captured at Richards Bay (28°43′S, 32°12′E), KwaZulu/Natal, and *M. coucha* from Pretoria (25°45′S, 28°14′E), Gauteng, South Africa. The species status of these founder populations was confirmed by starch gel protein electrophoresis (G. Campbell, in litt.). Only data from multiparous females were used from the first or second litters, which were kept with their parents until weaning at 21 days *post partum* (Meester 1960). Two males and two females from each litter were left with the breeding pair to be raised, in order to control for the possible effect of litter size on pup growth rates from birth to weaning.

The development of pups was monitored using the methods of Brooks (1972) and Baker & Meester (1977). These are briefly described below.

Righting behaviour: pups were turned on to their backs on a flat, level surface to measure righting behaviour. From this test the number of individuals able to right themselves, as well the time taken to right (seconds) were recorded for each litter. If a pup failed to right itself within 30 s the test was terminated.

'Cliff drop' avoidance: to test for 'cliff drop' avoidance, pups were placed on the edge of a flat wooden plank 1 cm deep that was placed directly on top of a laboratory bench. Their front legs and heads were positioned perpendicularly off the plank, while their torso, tail and back legs remained on the plank. Animals were recorded as (1) falling off the plank or; (2) crawling back from the edge of the plank and avoiding a 'cliff-drop'.

Bar-drop avoidance: to monitor bar-drop avoidance, individuals were placed on a thin wooden beam, 1 cm wide, in order to determine at what age they could balance for at least 30 s without falling off. This test was only performed once pups could avoid a 'cliff drop'. For both tests, the day at which individuals consistently avoided a fall was recorded.

Grasp reflex: the strength of an individual's grasp reflex was determined by pressing a thin blunt-ended object into the palm of its front paw. Three categories of grasp reflex were recorded, (1) none: no flexing/curling of the digits in response; (2) weak: the individual responded by weakly curling the digits, though the object was not actually gripped; (3) strong: the pup responded by curling the digits sufficiently to grip on to the object.

Locomotory ability: the locomotory ability of pups was recorded by placing them on a flat, horizontal surface and observing their movements. Three phases of locomotory ability were classified (1) crawling: in which an individual moved feebly with its legs, the head always dragging on the ground during locomotion; (2) crawl-walk, in which the individual was inconsistently able to lift its head clear of the ground while moving, though not to keep its head constantly up; and (3) walking, in which individuals could walk or run strongly and never dragged their heads along the ground.

Geotaxic response: pups were placed, with their heads facing downwards, on a sloping wooden beam, positioned at an angle of approximately 30°. The age was recorded at which individuals were first able to elicit a positive geotaxic response by successfully turning themselves around on the beam and crawling.

Rooting behaviour: to determine the preponderance for pups to exhibit an instinctive rooting response a finger of a gloved hand was pressed lightly to the side of their face. A positive rooting response was recorded if the individual turned its head consistently towards the direction of the stimulus. In addition, the day on which the eyes opened and upper incisors erupted were noted.

To assess potential differences in growth rate, pups were weighed daily (Ohaus Precision Advanced Balance) from birth to weaning. From these data, pup masses were compared between the two species shortly after birth on day 1, and thereafter on a daily basis until day 21. Using these data it was possible to assess differences in pup mass, for both species and sex, at birth and weaning (21 days).

For each species, male–female comparisons were made for the time taken (days) for the development of different behavioural and anatomical features to develop. For each litter, the average time taken for this development was recorded for each sex and compared between the sexes of each litter ($n = 10$) using a Wilcoxon matched-pairs test (Zar 1996). However, as the rate of growth and the timing of aspects of the behavioural development of littermates did not differ significantly by sex,

Table 1. Comparative development times (days) of specific behavioural and physical characteristics of *Mastomys natalensis* (n = 10) and *M. coucha* (n = 10) litters. Results of interspecific statistical comparisons provided using Mann-Whitney U-tests.

	Mastomys natalensis	*Mastomys coucha*	U	P*
Ability to right	1.6 ± 0.2	6.1 ± 0.6	2.5	***
Strong grasp reflex	4.3 ± 0.3	7.9 ± 1.2	12.5	**
Exhibit positive geotaxis	6.1 ± 0.5	4.4 ± 0.6	25	NS
Cliff-drop response	8.9 ± 0.5	7.2 ± 1.0	28	NS
No longer rooting	10.0 ± 1.0	12.7 ± 1.0	34	NS
Upper incisors erupted	12.4 ± 0.3	12.3 ± 0.3	47.5	NS
Avoid fall in bar test	13.4 ± 0.4	13.0 ± 0.5	47.5	NS
Eyes open	16.0 ± 0.3	17.1 ± 0.6	32	NS

*Significance of statistical analyses: NS, not significant; *P < 0.05; **P < 005; ***P < 0.0005.

mean values were calculated for each litter for consideration in the final analyses, which therefore compares data for the 10 litters of each species. All values are expressed as means ± S.E.

In addition least-squares linear regression equations (Zar 1996) were used to calculate the daily growth rate of individual litters, as pre-weaning growth can be considered near-linear (*cf.* Sikes 1995). Differences in growth rates for individual litters could then be compared for the two species.

Pup ontogeny

Mastomys natalensis pups were able to right themselves considerably sooner than *M. coucha* pups (Table 1). A strong grasp reflex also developed more quickly for *M. natalensis* pups, compared to *M. coucha* individuals (Table 1). These early ontogenetic traits were the only ones to differ significantly between species (Table 1).

At birth, pups of both species were only able to crawl, though the age at which they were able to lift their heads intermittently in a walk-crawl (*M. coucha* = 9.0 ± 0.5 days, *M. natalensis* = 9.5 ± 0.7 days; Mann-Whitney U-test: $U_{10,10}$ = 37.5, P = 0.34) or could walk strongly (*M. coucha* = 15.1 ± 0.5 days, *M. natalensis* = 15.2 ± 0.4 days; Mann-Whitney U-test: $U_{10,10}$ = 45.5, P = 0.73) did not differ significantly between species. Other locomotor abilities included development of a 'cliff drop' avoidance at a similar age for both species (Table 1), some 4–6 days before developing an avoidance to falling off a bar (Table 1). A positive geotaxis response developed after a similar period for both *M. natalensis* and *M. coucha* (Table 1). A cessation to rooting behaviour occurred at approximately the same time as the eruption of the upper incisors (Table 1). Finally, pups opened their eyes, on average from 16–17 days of age (Table 1). No inter-specific differences were recorded for any of these variables (Table 1).

Pup growth

At one day of age *M. coucha* pups weighed, on average, 2.0 ± 0.1 g while *M. natalensis* pups weighed 2.1 ± 0.1 g, with no significant interspecific difference in pup mass (Mann-Whitney U; $U_{10,10}$ = 42, P = 0.55; Fig. 1). However, linear regression analysis showed that *M. natalensis* pups gained mass at 0.40 ± 0.01 g/day, while *M. coucha*

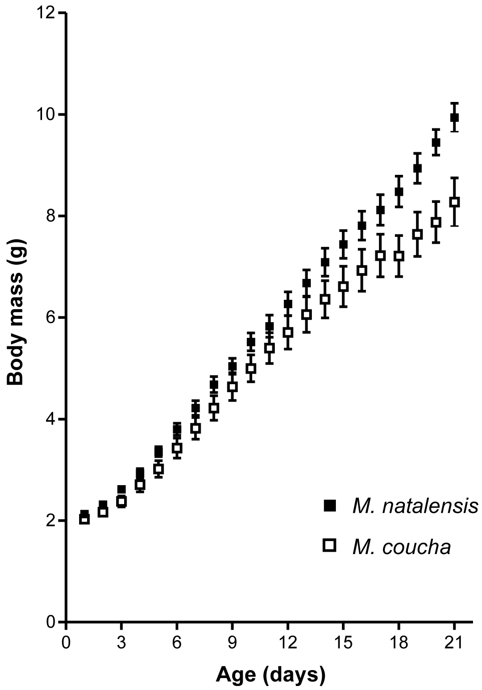

Fig. 1. Comparative mean (±S.E.) body mass of *Mastomys natalensis* (n = 10) and *M. coucha* (n = 10) litters from birth until weaning at 21 days of age.

pups increased mass at 0.33 ±0.01 g/day, the rate of body mass increase being significantly greater for *M. natalensis* than *M. coucha* (Mann-Whitney *U*; $U_{10,10} = 19.5$, $P = 0.019$; Fig. 1). Therefore, by weaning at 21 days of age, *M. natalensis* pups, weighing on average 9.9 ±0.3 g, were significantly heavier than *M. coucha* pups that averaged 8.3 ± 0.5 g (Mann-Whitney *U*; $U_{10,10} = 15$, $P = 0.014$; Fig. 1).

The birth mass and behavioural development in our study are largely in accordance with those recorded for *M. natalensis* (*sensu lato*) by Meester (1960) and Baker & Meester (1977). However, our data represent the first quantitative comparison of pre-weaning growth and development between *M. coucha* and *M. natalensis.* While we demonstrate the advanced development of post-natal attributes such as a strong grasp reflex and righting ability of *M. natalensis* within the first week of birth in comparison to *M. coucha,* our results suggest no differences in the development of important behavioural of physical characteristics in the second and third weeks following birth, implying a similar degree of development should have been reached by both species at weaning. Therefore, it appears neither species exhibits a significant advantage in behavioural development at weaning.

We did record, however, a difference in growth rates and mass at weaning between the species. *Mastomys natalensis* (*sensu lato*) may reach sexual maturity from 54 days of age (Meester 1960), well before the age of full physical development. If female body mass is correlated to litter size, as it is for *M. natalensis* as well as *M. erythroleucus* and *M. huberti* (Duplantier *et al.* 1996), this suggests the faster-growing female *M. natalensis* should produce larger litters than *M. coucha,* certainly during the period prior to full physical development. Unfortunately, owing to large variation in the mean litter size of *M. natalensis* reported in the literature (e.g. 6.0, Duplantier *et al.* 1996; 11.0, Leirs *et al.* 1993), it is difficult to make meaningful comparisons with the data available for *M. coucha,* for which an average litter size of 7.9 pups has been recorded under laboratory conditions (Lamb & van Aarde 2001). In fact, these discrepancies suggest that variation in local environmental conditions are more important than species distinctions in determining litter sizes.

Differences in the growth and weaning masses of pups do, however, suggest a disparity in daily food (milk) intake, energy expenditure or energy assimilation rates. At present, we can only speculate on such energetic constraints on growth or metabolism, or the possible influence of body mass on dominance and competitive ability, though these problems warrant future investigation.

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