CLIMBING BEHAVIOUR IN THREE AFRICAN RODENT SPECIES

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ABSTRACT

The climbing ability and propensity of *Thallomys paedulcus*, *Praomys natalensis* and *Saccostomus campestris* were studied in the laboratory. *Thallomys* was morphologically and psychologically best adapted to arboreal life, although *Praomys* had the highest climbing frequency, largely attributable to a greater exploratory tendency. All three species made use of the tail in a prehensile manner, and it was also used as a balancing organ by *Thallomys* and *Praomys*. These two species, but more noticeably *Thallomys*, made use of semi-opposable digits on the hind-feet whilst climbing. Only *Thallomys* scent-marked branches.

INTRODUCTION

When a number of animal species co-exist we assume that each utilizes environmental resources in a different way in order to lessen interspecific competition. Differences in arboreal tendencies would thus be advantageous, especially if the species concerned, for example a group of rodents, broadly overlap in their ecological requirements.

To test for behavioural and anatomical correlations between differential inclination to climb and climbing ability, the arboreal tree-rat *Thallomys paedulcus*, the scansorial multimammate mouse *Praomys* (*Mastomys*) *natalensis*, and the terrestrial pouched mouse *Saccostomus campestris* were chosen. These occur sympatrically in parts of their range (De Witt 1972).

MATERIALS AND METHODS

Test animals were seven *T. paedulcus*, six *P. natalensis* and three *S. campestris*. Two *Thallomys* came from the Transvaal lowveld and four from the Kalahari Gemsbok National Park. One was born in captivity. The *Praomys* were descendants of wild-caught stock from around Pretoria. Two *Saccostomus* came from the Kalahari Gemsbok National Park and one from the Transvaal lowveld. The testing apparatus was a box (93 × 88 × 59 cm) with three sides and base of wood and the remaining side of perspex to serve as a viewing area. The only opening, at the top, was covered by thin wire mesh. Three branches, two with rough bark and the third barkless, were placed inside. Twigs ranged from a minimum diameter of 0,4 cm to a maximum of 3,5 cm. Wooden bars 50 cm long with diameters of 2,5 cm, 1,25 cm and 0,63 cm, were placed almost horizontally between certain branches. A nest-box with one perspex side was provided. A wire,

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diameter 0,4 cm, connected the top of the nest-box with a branch. Water and sunflower seeds were provided *ad lib.*; greens were occasionally given. The temperature in the testing room was maintained at approximately 25°C, and relative humidity at 36 per cent.

Animals were tested during the dark phase of a reversed photoperiod (09h00–17h00 of the 8:16 dark-light cycle). A red light (40 watt) permitted viewing of the interior of the test box.

Each individual was allowed a minimum of seven days acclimatization to the reversed light cycle. During the testing period animals were subjected to as little disturbance as possible, with enough food and water provided to last throughout the whole period. Each animal was tested for one hour at 'dusk' (Period A: 09h00–10h00), one hour at approximately 'midnight' (Period B: 12h00–13h00), and one hour at 'dawn' (Period C: 16h00–17h00) over a three-day period. The total testing time for all animals combined was 144 hours – *Thallomys* 63 hours, *Praomys* 54 hours and *Saccostomus* 27 hours. Quantitative data on inclination to climb and climbing ability ere obtained with a stopwatch and were combined with observational data. Recorded were:

(i) Contact latency, being the elapsed time between an individual's exit from nest-box (sleep) at dusk, till time of first contact with the climbing apparatus (i.e., sniffing, placing feet on, etc.).
(ii) Time elapsed before climbing.
(iii) Number of visits to the climbing apparatus.
(iv) Number of times climbed.
(v) Total time spent actively climbing.
(vi) Total time spent motionless/inactive while aloft, excluding grooming. Combining (v) and (vi) gave the total time aloft. The frequency of climbing was the time spent aloft calculated as a percentage of the total testing time for each one-hour period.
(vii) The number of falls.

Characteristics of climbing were noted, as well as additional behavioural traits such as marking.

RESULTS

Exploration and inclination to climb

Individuals of all three species, when placed in the testing apparatus, showed the usual brief period of hesitancy or freezing while sniffing the air. Subsequent movements had the body in a tense and elongated posture, belly close to the ground and the tail held stiffly, although occasionally *Thallomys* or *Praomys* individuals would stand on their hind-legs to test the air. *Thallomys* maintained the most rigid tail and proved to be the most tense of the species tested; in contrast *Saccostomus* began to explore almost immediately and had the shortest contact latency time (Table 1). *Praomys*, although timid, was inquisitive and generally more active and explorative than *Thallomys*, as partly indicated by the number of visits to the climbing apparatus (Table 1).

Interspecific differences in inclination to climb can be deduced from the variation shown in

the time elapsed before climbing, the number of visits to the climbing apparatus and the number of times climbed (Table 1).

Thallomys had the longest contact latency time and paid the least number of visits to the climbing apparatus (except during Period A) yet little time passed before this species actually started climbing. This reflects the cautious nature of *Thallomys*, but also points to a high climbing tendency.

TABLE 1

Mean contact latency (MCL) and mean time elapsed (MTE) before climbing, number of visits to the climbing apparatus and number of times climbed in each testing period for *Thallomys*, *Praomys* and *Saccostomus*.

Kal.: Kalahari Gemsbok National Park. Tvl: Transvaal Lowveld.

			Number of visits				*Number of times climbed*			
	MCL	*MTE*	*Period*				*Period*			
Species	*(minutes)*	*(minutes)*	*A*	*B*	*C*	*Mean*	*A*	*B*	*C*	*Mean*
Thallomys										
Kal.	—	—	—	—	—	—	11,5	6,0	11,0	9,5
Tvl	—	—	—	—	—	—	7,3	2,3	3,5	4,4
Mean	7,6	8,5	2,3	0,6	0,6	1,2	9,4	4,2	7,3	7,0
Praomys	6,0	12,6	7,3	2,0	2,5	4,0	13,2	9,0	6,0	9,4
Saccostomus	2,4	—	1,3	1,3	4,3	2,3	0	1,0	8,3	3,1

Climbing activity

Praomys was the most active of the species tested. Veenstra (1958) observed a 24-hour activity cycle in *Praomys*, with a marked increase in activity occurring at night with a peak at dawn. *Thallomys* was inactive during daylight hours but *Saccostomus*, although predominantly nocturnal, was active in cages during daylight hours. *Saccostomus* activity was negligible during Period A, and reached its maximum at dawn as shown by the increase in climbing activity (Figure 1). Both *Thallomys* and *Praomys* had activity peaks at dusk, the mean number of climbs coinciding with the maximum time aloft (Table 1 and Figure 2: I). Towards dawn climbing

activity decreased. The *Praomys* tested were most active on the ground (Table 2) and while climbing at dusk (Period A), with activity decreasing towards Period C. Ground activity of *Praomys* coincided with the total time aloft (Figure 2: I).

The total time Aloft/Active/Inactive of each individual shows wide variation within a species. *Thallomys* spent the highest maximum amount of time aloft during each climb, and showed the highest mean (Figure 2: I) during all three periods. The Kalahari *Thallomys* spent more time aloft, but percentage activity was lower than that of Transvaal *Thallomys*. This probably indicates a greater propensity for climbing, as opposed to the shorter range in climbing times of *Praomys* and *Saccostomus* which seems to be indicative of a greater tendency towards exploration.

Praomys and especially *Saccostomus* spent the greater part of the time aloft in being active (Figure 2: II), as opposed to *Thallomys*, which was inactive for approximately half the total time aloft (Figure 2: III). The greater inactivity of *Thallomys* while aloft is again a possible indication of a greater climbing propensity, as it may feel more secure and relaxed whilst aloft than the other two species.

Thallomys and *Praomys* showed a similar pattern of climbing activity (Figure 2: I) with a decrease in total time aloft from Period A to Period C, with the highest maximum range and mean occurring during Period B. *Saccostomus* showed a linear increase from Period A through to Period C, quite different to the situation found in the other species. Application of a Students *t*-test showed no significant difference ($p \leqslant 0{,}05$) between the climbing frequency of *Thallomys* and *Praomys*, *Saccostomus*, however, differed significantly from both *Praomys* and *Thallomys*.

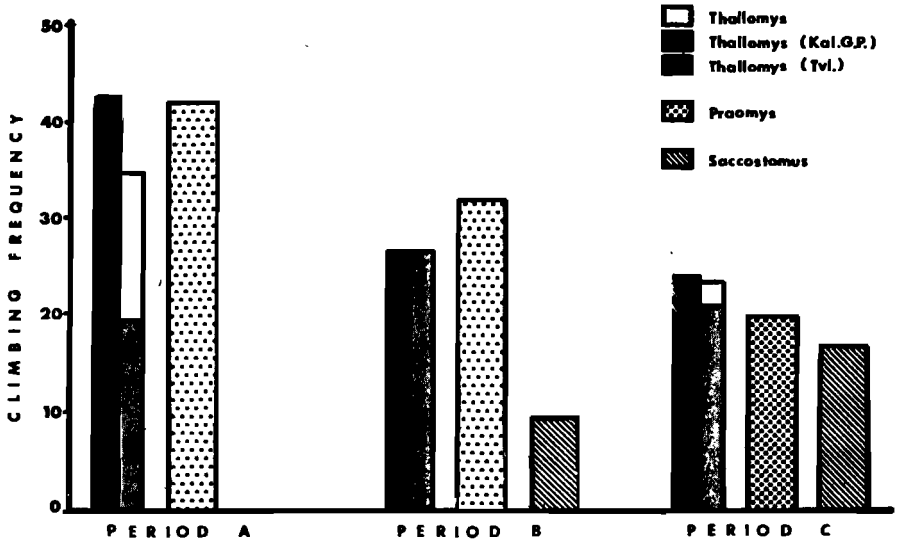

FIGURE 1

Climbing frequency of *Thallomys*, *Praomys* and *Saccostomus*.

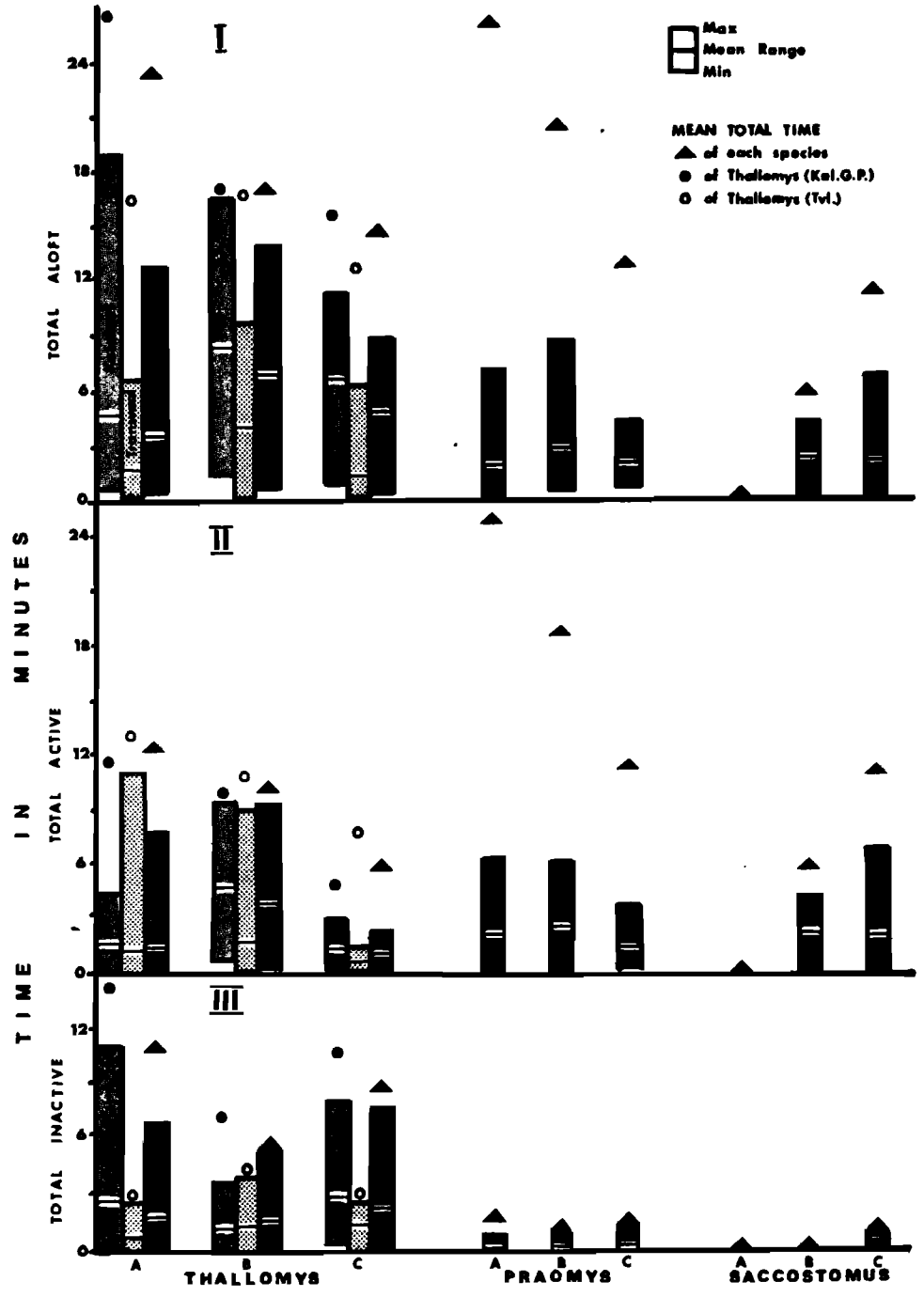

FIGURE 2 (I–III)

Total time aloft, active and inactive of each species, with the corresponding range in duration and mean time of each climb. A–C, test periods.

Intraspecific variation in climbing activity of *Thallomys* from the Kalahari and Transvaal was not significant.

King (1968) observed that the semi-arboreal *Peromyscus* (*e.g. P. leucopus*) climbed more boxes than the terrestrial forms (*e.g. P. polionotus*). If climbing on to the nest-box is taken as an indication of climbing propensity, then *Thallomys* has the greatest and *Saccostomus* the least propensity for climbing (Table 3). Activity on top of the nesting box coincides with the activity peaks of all three species.

Climbing ability

Horner (in Layne 1970) emphasized that tail length is the principal structural adaptation for climbing in *Peromyscus*. This also seems to be the case in the three species studied, as the climbing frequency correlates well with the tail to body length ratio (Table 4 and Figure 1).

Thallomys had the highest mean tail to total body length ratio of the species tested (Table 4), with individuals from the Kalahari having relatively higher tail to body length ratios than those from the Transvaal, for whom this ratio was very similar to that of *Praomys*. Likewise, *Thallomys* from the Kalahari showed a higher climbing frequency than those from the Transvaal. *Saccostomus*, with the shortest tail, had the lowest climbing frequency, although the frequency

TABLE 2

Mean time (minutes) spent on ground by *Thallomys*, *Praomys* and *Saccostomus*, excluding grooming, eating and drinking activities.

Kal. and Tvl as in Table 1.

	Period A			*Period B*			*Period C*		
Species	*Act.**	*Inact.*	*Total*	*Act.**	*Inact.*	*Total*	*Act.**	*Inact.*	*Total*
Thallomys									
Kal.	5,3	0,3	5,6	4,1	0,2	4,2	4,4	1,0	5,4
Tvl	17,4	6,3	24,03	20,2	9,5	30,1	28,4	21,5	50,3
Mean	11,3	3,3	14,6	12,2	5,0	17,2	16,4	11,3	27,7
Praomys	18,5	1,5	20,0	16,3	2,2	18,5	11,4	0,3	11,7
Saccostomus	5,3	0	5,3	9,4	0	9,4	8,1	8,1	16,2

*Act. = active.
Inact. = inactive.

TABLE 3

Mean time (minutes) spent on nesting box by *Thallomys*, *Praomys* and *Saccostomus*. Kal. and Tvl as in Table 1.

	Period A			*Period B*			*Period C*		
Species	*Act.**	*Inact.*	*Total*	*Act.**	*Inact.*	*Total*	*Act.**	*Inact.*	*Total*
Thallomys									
Kal.	2,5	1,1	4,0	7,1	4,2	11,2	3,4	2,2	5,7
Tvl	10,3	3,2	13,4	2,5	0,6	3,5	3,4	1,4	4,8
Mean	6,4	2,2	8,6	4,8	2,4	7,2	3,4	1,8	5,2
Praomys	3,6	1,1	5,1	2,4	0,2	0	0	0	0
Saccostomus	0	0	0	0,04	0	0,04	0,14	0	0,14

*Act. = active.
Inact. = inactive.

TABLE 4

Measurements (mm) of *Thallomys*, *Praomys* and *Saccostomus*, with tail to total body length ratio and hind-foot to body length ratio. Kal. and Tvl as in Table 1.

Species	*Total length*	*Tail length*	*Tail: Total per cent*	*Hind-foot length*	*Hind foot: Body length per cent*
Thallomys					
Kal.	296	143	48,3	26	16,6
Tvl	283	124	43,8	26	16,0
Mean	290	134	46,2	26	16,6
Praomys	221	96	43,4	23	18,4
Saccostomus	179	44	24,6	20	13,3

of the Kalahari individuals, with a noticeably longer tail, was higher than the mean of the species.

It is possible that the hairs on the tail serve as tactile organs. In *Praomys* the tail is covered with short rigid hair. *Thallomys* from the Kalahari had long hairs on the tail, whereas those of the other individuals were slightly shorter. The tail of *Saccostomus* is short, almost naked, and thickened towards the base. Herskovitz (1969) states that tails of arboreal species are covered, at least terminally, with long, tactile hairs.

It has been observed (Dice in Klingener 1968) that forest forms tend to have longer tails and larger feet than their prairie relations, and Dice suggested a possible correlation of these features with semi-arboreal habits. *Praomys* had the highest percentage hind-foot to total body length (Table 4) and *Saccostomus* the lowest, indicating that it is the least arboreal in its habits.

Layne (1970) states that the number and development of the plantar tubercles are structural adaptations for climbing, the higher, more sharply pointed and enlarged tubercles (Herskovitz 1969) being adapted for clutching slender branches and twigs. The fore-feet of all the species tested had five pads and the hind-feet six.

The tubercles of *Saccostomus* were the flattest, and no prominent pads were present on the toe tips. The tubercles of the fore-feet were more developed than those of the hind-feet, especially the two furthest from the fingers. The tubercles of the hind-feet of *Praomys* were the highest and most sharply pointed of all three species, though smaller in diameter than those of *Thallomys*.

The feet of semi-arboreal species are broad, with long and partially opposable outer digits (Herskovitz 1969), as observed in *Thallomys* and to a lesser degree in *Praomys*. The claws are recurved, as in *Thallomys* and *Praomys*, while those of *Saccostomus* are larger and straighter.

The feet of *Thallomys* are especially adapted to arboreal habits with the fifth digit of the hind-foot being elongated. The hind-feet of *Thallomys* also have the largest round tubercles of all three species. The tips of the toes have pronounced, pointed pads, again making the feet of this species best adapted for climbing, with *Praomys* a close second.

Thallomys appeared to be the best adapted to climbing, having no difficulty climbing up or down vertical branches, generally by hopping or galloping. This occurred both in the laboratory and in the field *e.g.* up trunks of *Acacia* trees. It climbed with agility, jumping from branch to branch, or climbed upside-down, and was the only species observed to climb on the thinnest branches. Whilst climbing, the toes of the hind-feet were spread, the outer digits encircling the branch or bar to oppose each other. The fore-feet were placed flat on the branch, and did not encircle it. *Praomys* used its feet in a similar manner.

Horner (in Layne 1970) stated that the long tail of semi-arboreal forms was more effective as a balancer, prop and tactile organ than the shorter tail of more terrestrial taxa. Ewer (1971) observed that *Rattus rattus*, while running on a wire, swings its tail constantly from side to side. This occurred in both *Thallomys* and *Praomys* where the tail was kept fairly rigid and swung from side to side when walking horizontally on a branch, thus helping to balance the animal. During vertical climbing the tail was curled around the branch to act as a prehensile organ. Occasionally, while sitting sideways on a branch, the tail would hang down vertically on the opposite side of the branch to the head, thus helping to maintain balance. At other times, and especially during grooming, the tail was curled around a suitable branch. *Saccostomus* encountered difficulty on downward climbs, the tail being too short to curl around the thicker branches, and generally fell. Whilst climbing horizontally it made considerable use of the tail for balancing.

While climbing the animals bent their legs so that the ventral surface was close to the branch. This was especially noticeable in *Saccostomus*, and to a lesser degree in *Praomys*, while negotiating a difficult climb. On thin branches, *Saccostomus* interlocked the hind-legs around the twig, and was pulled forward by the fore-feet.

Saccostomus generally climbed very slowly, seeming to ponder where to place its feet, although of all three species, it took the biggest steps between branches with the aid of the strong fore-feet. The hind-foot was placed flat on the branch as opposed to the use of the semi-opposing first (big) toe of *Thallomys* and *Praomys*.

Behaviour of semi-arboreal forms during climbing suggests caution or deliberation as though they were aware of being in a precarious position (King 1968). King also observed that terrestrial forms appeared to be more reckless and inclined to fall more often. *Thallomys* appeared to take few risks while climbing, suggesting caution; the reason why a few individuals fell was that they tried to jump from the branches up to the mesh above. Application of a χ^2-test showed no significant difference ($p = 5$ per cent) between the number of falls of the three species tested, although *Saccostomus* fell the most and *Thallomys* the least.

All three species appeared to better their climbing with experience, this, however, being the least noticeable in *Thallomys* adults. The *Thallomys* subadult was noticeably hesitant during the first few climbs, becoming more self-assured as time progressed.

A few individuals of all three species would repeatedly follow approximately the same route through the branches, only gradually expanding their routes as they became accustomed to the new environment. The above behaviour could possibly be the result of scent-marking by other individuals along the branches.

Climbing on the barkless branch was noticeably avoided. *Saccostomus* failed even to sniff at it, but *Praomys* did attempt to climb, though rather more cautiously than on the other branches. All three species preferred to climb the branches provided, and not the bars, although this avoidance behaviour was the least noticeable in *Thallomys*.

Marking

On the test apparatus specimens of *Thallomys* occasionally rubbed their cheeks against a branch after a bout of gnawing, and also marked by means of perineal dragging against branches. It was also the only species to urinate while aloft. Marking behaviour would be important to *Thallomys* and facilitate finding a way along branches during darkness by means of scent.

DISCUSSION

Of the three species tested, *Thallomys* shows the best psychological and anatomical adaptations to an arboreal existence. Individuals from the north-western Cape (Kalahari Gemsbok National Park) had relatively longer tails than those from the Transvaal, and also showed a higher frequency in climbing. This probably reflects adaptations to local conditions in the Kalahari. *Thallomys* is adapted to living in isolated trees, whereas in the Transvaal more use is made of ground surface (De Witt 1972). *Thallomys* from the Transvaal is usually referred to *T. p.*

paedulcus, while those from the Kalahari Gemsbok National Park are regarded as being intermediate between *T. p. kalaharicus* and *T. p. nigricauda* (Smithers 1971). Although not the most active, *Thallomys* spent most time aloft, and was also the most active when doing so. Although the arboreal tendencies of *Praomys* may, on first appraisal, be surprising, we know very little of the vertical utilization of the habitat by co-existing species. Very few field studies on rodents, apart from Delany (1971), examined differential arboreal tendencies of co-occurring species and Delany's study did not include the species we tested. Although, on the strength of our results and those of Veenstra (1958), *Praomys* can be considered an important user of the vertical component in a habitat, off-the-ground trapping at different levels would provide more conclusive evidence.

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