

Swimming Behaviour in Six Species of African Rodents (Cricetidae, Muridae)

Graham C. HICKMAN & Carla MACHINÉ

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The swimming ability of six species of African rodents is described: the pouched mouse (*Saccostomus campestris*), the white-tailed rat (*Mystromys albicaudatus*), the multimammate mouse (*Praomys (Mastomys) natalensis*), the bushveld gerbil (*Tatera leucogaster*), the striped mouse (*Rhodomys pumilio*), and the single-striped mouse (*Lemniscomys griselda*). Buoyancy was positively correlated to swimming time; mass was negatively correlated to swimming time. Maintenance of body temperature did not differ significantly between species, so that the negative effect of poor insulation on swimming performance was not a factor in interspecific comparisons. Distribution and habitat of the six species are discussed; species tested which preferentially inhabit damp or wet areas demonstrated greater swimming ability.

[Department of Zoology, University of Natal, Pietermaritzburg, South Africa].

1. INTRODUCTION

Many small mammals encounter large expanses of water, either voluntarily or involuntarily, during their life. Whether or not water acts as a distributional barrier or dispersal mechanism may depend largely on the ability of the animal to swim. Most terrestrial mammals are believed capable of swimming or at least remaining afloat should the need arise.

The actual knowledge on the swimming ability of mammals has been based largely on incidental or casual observations (Aldrich & Quilliam, 1966; Stock, 1972), although recently more detailed studies have been conducted. Dagg & Windsor (1972) and Getz (1967) studied swimming behaviour in some North American small mammals. In particular, comparative behavioural studies on rodents have been conducted by Schmidly & Packard (1967), Starrett & Fisler (1970), Hickman (1977), Esher, Wolfe & Layne (1978) and Harris & Petersen (1979), with some studies examining ecological and distributional aspects of swimming ability (Fisler, 1961; Hafner & Hafner, 1975; Carter & Merritt, 1981;

Hickman, Nevo & Heth, 1983). Other studies have considered phylogenetic, morphological, and external factors affecting swimming ability such as temperature (Wilber, 1959, 1963; Wilber & Hunn, 1960), genetics (Kennerly, 1963), hormones (Schapiro, Salas & Vukovitch, 1970) and use of vibrissae (Ahl, 1982).

Descriptions of any aspect of swimming behaviour in African rodents are few (Hickman, 1978, 1983a, b;). The present paper compares swimming ability in six common indigenous species of terrestrial African rodents. General behavioural patterns are described noting the effect of buoyancy, mass, and temperature.

2. MATERIAL AND METHODS

Five of the six species of animals tested were trapped in the vicinity of Pietermaritzburg, Natal, South Africa: the pouched mouse (*Saccostomus campestris*), white-tailed rat (*Mysstromys albicaudatus*), multimammate mouse *Praomys (Mastomys) natalensis*, single-striped mouse (*Lemniscomys griselda*) and bushveld gerbil (*Tatera leucogaster*). Four striped mice (*Rhabdomys pumilio*) were trapped at Cathedral Peak in the Drakensberg Mountains of Natal. Animals were housed separately in 450 mm × 280 mm × 120 mm cages with *ad libitum* water and commercial food cubes, and testing was initiated after a minimum acclimatisation time of two weeks.

General swimming performance (five trials per individual) was observed in an all-glass aquarium (900 mm long × 400 mm wide × 240 mm high) filled with water at 24°C to a depth of 22 cm. A black plastic sheet with white stripes demarcating 10 cm intervals was affixed to the back of the aquarium for measuring swimming speeds during trials. The water was replaced daily. Animals were lowered slowly into the water in a 270 mm long × 160 mm wide × 90 mm high, perforated plastic box and removed from the water quickly when showing signs of fatigue (*i.e.* the nose dipping below the surface with the animal experiencing difficulty in resurfacing). Behaviour was documented with a video recorder and 35 mm photographs.

The effect of buoyancy on swimming ability was determined by recording the mass of the animal before placement in the water and at minute intervals during trials (the increase in mass noted during the trial representing the rate of water uptake by the fur). Addition of concentrated detergent (commercial dishwashing fluid) to the water eliminated the buoyancy resulting from the air-trapping capacity of the fur.

Maintenance of body temperature was measured by taking the core body temperatures of animals rectally with a thermocouple thermometer

Table 1
Swimming posture and behaviour of six South African rodent species arranged from left to right with increasing swimming proficiency.

Swimming parameter	<i>S. campestris</i>	<i>M. albicaudatus</i>	<i>T. leucogaster</i>	<i>L. griselda</i>	<i>R. pumilio</i>	<i>P. natalensis</i>
Position of body in water	horizontal; dorsal surface, eyes and ears exposed	horizontal; posterior sinking slightly; eyes & ears exposed	$\pm 30^\circ$ angle; dorsal surface submerged to just posterior to the eyes	$\pm 30^\circ$ angle; dorsal surface submerged; ears may/may not be exposed	$\pm 30^\circ$ angle; dorsal surface submerged; ears may/may not be exposed	$\pm 45^\circ$ angle; ears usually submerged
Eyes	Open	Open	Open	Open	Open	Open
Tail	Sometimes arched vertically above surface, otherwise horizontal	Limp or slight sideways movement due to kicking of hind limbs	Slight sculling due to movement of hind limbs	Slight sculling due to movement of hind limbs	"flicked" for turning — used with fore limbs	Vigorous "wagging" used for balance when floating; flicked for turning
Gait	Dog-paddle with all four limbs	Predominantly alternate kicking of hind limbs, fore limbs tucked up under chin	Predominantly alternate kicking of hind limbs, fore limbs tucked up under chin	Predominantly alternate kicking of hind limbs, fore limbs tucked up under chin	Predominantly alternate kicking of hind limbs, fore limbs tucked up under chin	Predominantly alternate kicking of hind limbs, fore limbs tucked up under chin
Splashing	None	When vertical in a corner	When vertical in a corner	None	When vertical in a corner	None
Defecation	0—5 pellets	1—3 pellets	None	None	2—5 pellets	1—2 pellets
Floating	None	None	None	+30—65 secs	None	Several minutes

probe prior to placement of animals in a narrow glass jar (100 mm diameter, 240 mm deep) containing water at 16°C. Depth of water in the jar was regulated so that animals were able to keep one hind foot touching the bottom of the container, so that swimming was not required to keep the head above water; animals were thus kept relatively stationary and increases in body temperature due to muscle activity during swimming minimised. Temperatures were taken at minute intervals until the animal showed signs of cold exposure and distress.

3. RESULTS

3.1. General Swimming Performance

Qualitative aspects of the swimming behaviour of the six species are summarised in Table 1. The initial swimming posture of *S. campestris* and *M. albicaudatus* was horizontal, with the entire dorsal surface (including nose, eyes and ears) above the surface (Fig. 1a, b). In *T. leucogaster*, *L. griselda* and *R. pumilio*, the angle of the body with the water surface was greater (approximately 30°) once the initial "frantic" swimming had subsided (Fig. 1c, d, e). The ears were often submerged with the water level just posterior to the eyes.

P. natalensis displayed various swimming postures. One 71 g male remained horizontal with the entire dorsal surface above the water, but *P. natalensis* generally swam with the body at a 30°–45° angle to the surface (Fig. 1f), with the eyes and snout above, and ears just below, the water level.

In all species, the hind quarters sank gradually, forcing the animals into a vertical swimming posture with only the tip of the snout protruding from the water. Animals often swam vertically before tiring, particularly when attempting to cling to the walls or to climb out in the corners of the tank. Eyes were kept open throughout trials even when submerged.

The tail in *M. albicaudatus*, *T. leucogaster* and *L. griselda* hung limply behind the body during swimming, and although slight lateral motion was noted, sculling appeared to be as a result of the kicking of the hind limbs rather than as an independent motion. *S. campestris* sometimes held the tail out of the water in a vertical arc, particularly when the back was arched when elevating the anterior and posterior extremities above the water. In most instances, however, the tail was horizontally positioned. *P. natalensis* used the tail during swimming more than any other species tested by vigorous "wagging" or "sculling"; balance was maintained when floating by holding the tail still in the water, with slow and deliberate curling when the animal began to roll

or sink. The tail of *P. natalensis* and of *R. pumilio* also assisted turning while swimming, with a distinctive "flick" of the tail in conjunction with fore and hind limbs allowing precise turning.

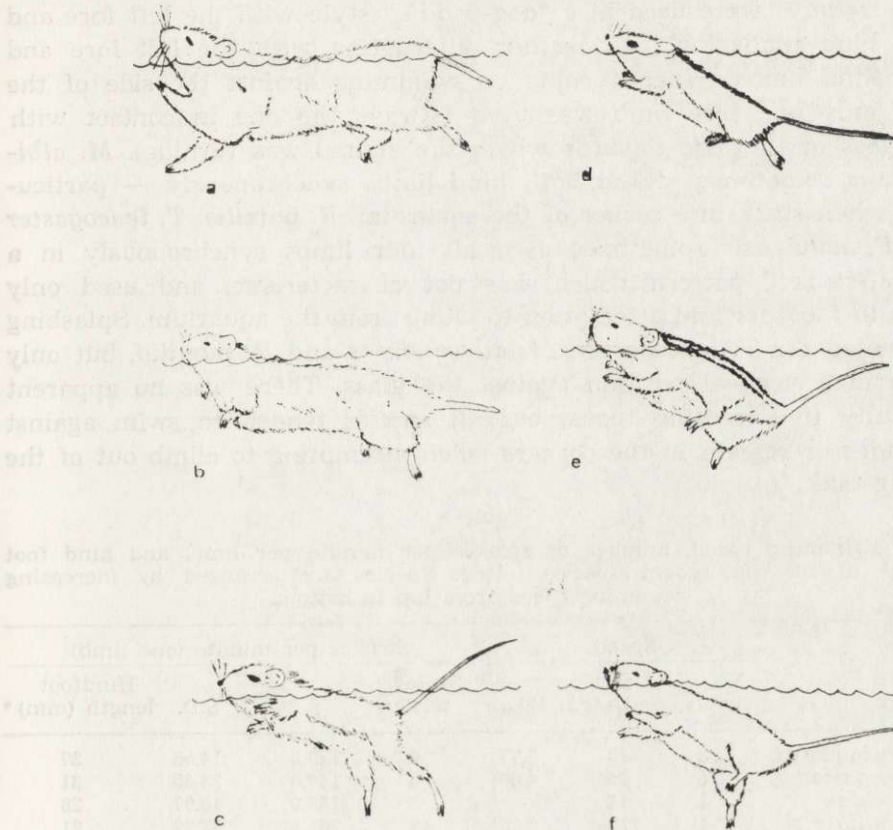


Fig. 1. Typical swimming postures of six rodent species, arranged from weakest to strongest swimmers (drawn from photographs).

- (a) *S. campestris*. Horizontal position of body with dorsal surface exposed; tail hanging limply; use of all four limbs in dog-paddle stroke.
- (b) *M. albicaudatus*. Horizontal position of body but with posterior slightly submerged; eyes and ears exposed; tail hanging limply; front limbs tucked up into chest; hind limbs alternating stroking.
- (c) *T. leucogaster*. Long, strong hind limbs alternating; body at a slight ($\pm 30^\circ$) angle to the water surface; position of tail usually below surface.
- (d) *L. griselda*. Same gaits as (b) and (c); ears partly submerged due to angle of body to the water surface.
- (e) *R. pumilio*. Same gait as (b) and (c); ears occasionally out of the water; tail and forelimbs used for turning.
- (f) *P. natalensis*. Same gait as (b) and (c); greater angle between body and water surface than in *R. pumilio*; tail used for balance when floating and turning

The swimming gait used by all species (except *S. campestris*) was predominantly an alternate kicking of the hind limbs with the fore limbs tucked under the chin (and only used when turning, attempting to climb out of the tank, or when tiring). When front limbs were used, all four limbs were used in a "dog-paddle" style with the left fore and right hind limbs kicking together, alternating with the left fore and right hind limbs. When turning or swimming against the side of the tank, only one fore limb was used (always the one in contact with the glass or the side towards which the animal was turning). *M. albicaudatus* sometimes kicked both hind limbs synchronously — particularly when stuck in a corner of the aquarium. *R. pumilio*, *T. leucogaster* and *P. natalensis* sometimes used all four limbs synchronously in a "breast-stroke" pattern which was not characteristic, and used only when in a corner and attempting to climb from the aquarium. Splashing was noted for *T. leucogaster*, *M. albicaudatus* and *R. pumilio*, but only when in a vertical position against the glass. There was no apparent difficulty in executing turns, but all species tended to swim against the sides or remain in the corners when attempting to climb out of the testing tank.

Table 2

Mean swimming speed, number of strokes per minute per limb, and hind foot lengths of the six rodent species tested. Species are arranged by increasing swimming speed from top to bottom.

Species	Speed			Strokes per minute (one limb)			
	No. of trials	\bar{x} (cm/sec.)	S.D.	No. of trials	\bar{x}	S.D.	Hindfoot length (mm) *
<i>M. albicaudatus</i>	3	13	5.77	6	139.2	14.58	27
<i>T. leucogaster</i>	5	15	4.00	8	147.0	25.85	31
<i>L. griselda</i>	1	17	—	2	188.0	16.97	28
<i>R. pumilio</i>	4	17	0.00	12	261.4	33.22	21
<i>S. campestris</i>	2	19	1.41	2	273.5	37.48	20
<i>P. natalensis</i>	8	27	8.40	11	155.2	21.31	23

* measurements from De Graaf (1981)

Swimming speed and number of strokes per leg per minute in each of the six species are noted in Table 2. *M. albicaudatus* was the slowest swimmer and *P. natalensis* the fastest; *S. campestris* and *R. pumilio* had relatively fast strokes while *M. albicaudatus* and *T. leucogaster* paddled slowly.

Swimming endurance for each species is listed in Table 3. No distinction is made between male and female performances, since there was no significant difference in swim times between sexes (*t*-test, $p > 0.05$) for all species (except *M. albicaudatus* and *L. griselda* of which only males were sampled).

For individual performances *P. natalensis* was able to "swim" (maintain the nostrils out of the water by actively kicking or floating) for the longest periods of time; however, mean swimming time for all individuals tested was higher for *R. pumilio*. *S. campestris* swam for

Table 3

Mean mass and swimming time of six rodent species, five trials per individual, arranged in order of increasing swimming time (which is with the exception of *S. campestris* and *L. griselda*, also the order of decreasing mass).

Species	n indiv	n trials	Mean Mass (g)	Mean Time (secs)	S.E.	Range (secs)
<i>S. campestris</i>	7	35	101	138	31.90	17—776
<i>M. albicaudatus</i>	3	15	116	185	20.30	50—350
<i>T. leucogaster</i>	4	20	101	211	15.78	89—331
<i>L. griselda</i>	1	5	63	275	6.78	247—291
<i>P. natalensis</i>	4	20	67	536	111.28	85—1620
<i>R. pumilio</i>	4	20	43	608	65.06	263—1165

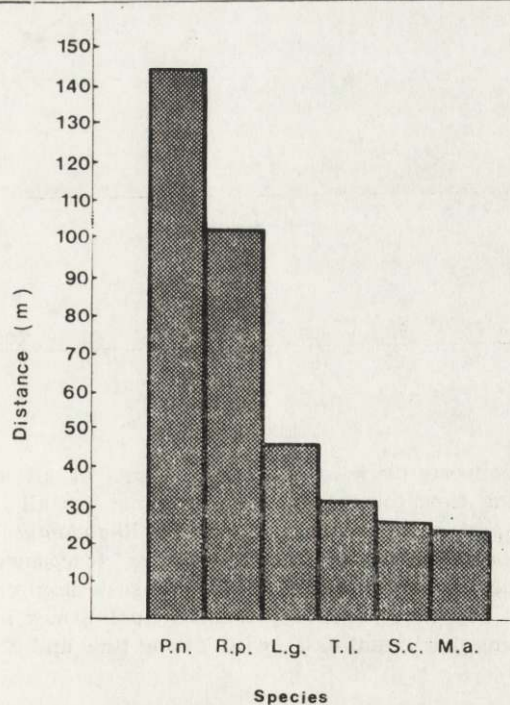


Fig. 2. Projected distances traversable by swimming cricetid and murid rodents tested in the present study. Distances calculated by multiplying mean speed (Table 2) by mean time (Table 3) for each species. P.n.=*Praomys natalensis*, R.p.=*Rhabdomys pumilio*, L.g.=*Lemniscomys griselda*, T.l.=*Tatera leucogaster*, S.c.=*Saccostomus campestris*, M.a.=*Mystromys albicaudatus*.

the shortest mean time. Although five of the seven pouched mice swam for ± 30 –80 seconds, one female (91 g) swam for a maximum of 12 minutes and one male (85 g) swam for a maximum of four minutes. The mean time of 138 seconds shown in Table 3 for this species is, therefore, higher than expected for the species. Figure 2 illustrates the mean

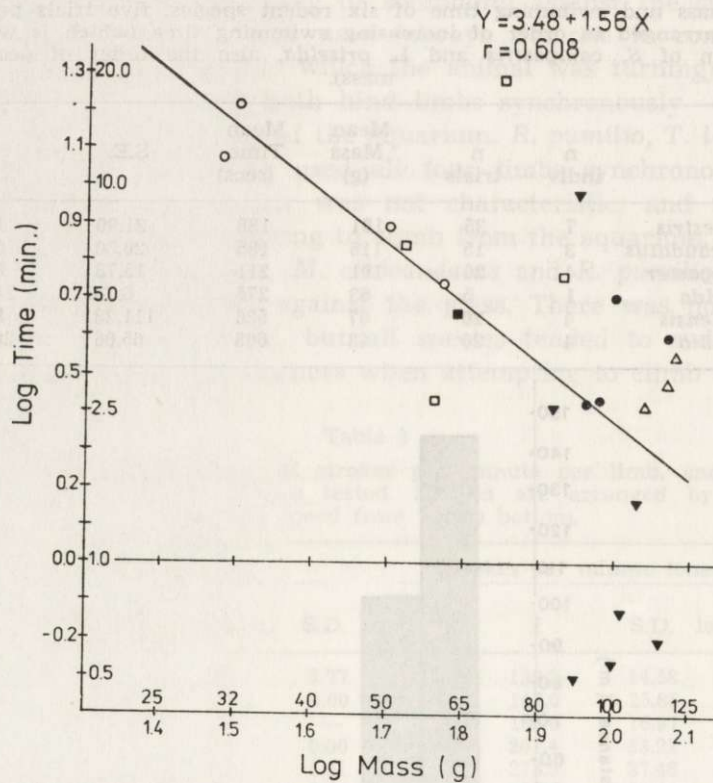


Fig. 3. Correlation between body mass (mean weights of all individuals in each species) and swimming time (means of all swim times for all individuals in each species) for cricetid and murid rodents tested. \circ = *Rhodomys pumilio*, \square = *Praomys natalensis*, \blacksquare = *Lemniscomys griselda*, \bullet = *Tatera lencogaster*, \triangle = *Myodomys albicaudatus*, \blacktriangledown = *Saccostomus campestris*. Double scale used on axes: Outer scale represents log values and inner scale represents actual values in minutes (vertical axis) and grams (horizontal axis), with Y = log time and X = log mass.

distance that each species can be expected capable of swimming. Although only one male of *L. griselda* was available for testing, the mean values are taken for five trials of this one individual. Wilbur (1958) proposed that when the logarithm of swimming time in minutes

is plotted against the logarithm of body weight in grams, a straight line is obtained; Figure 3 shows that for the six species in this study, a significant negative correlation between body mass and swimming time was obtained ($p < 0.05$).

Defecation during swimming did not occur in *T. leucogaster* or *L. griselda*. All three *M. albicaudatus* defecated one to three pellets. Two of four *P. natalensis* and *R. pumilio* defecated one to two pellets, and two to five pellets, respectively. Five of the seven *S. campestris* defecated up to five pellets during swimming trials.

3.2. Effect of Buoyancy

Buoyancy increased swimming times greatly, particularly for *P. natalensis*. One male (71 g) spent approximately 70% of the trial floating motionlessly with all four limbs hanging limply with the tail alone maintaining balance. The other three *P. natalensis* floated without paddling, but for only short periods of time. *L. griselda* was also motionless in the water for ± 30 –65 seconds. Floating was less evident for *R. pumilio*, *T. leucogaster*, *M. albicaudatus* and *S. campestris*, although several

Table 4

Water uptake by the pelage of six rodent species, expressed as an increase in mass. The values shown in columns A–C are mean values for all individuals of each species. The calculation $\frac{A \cdot 100}{B \cdot C}$ eliminates two other variables, namely the length of the trial (which differed between species) and the mean body mass. The latter was assumed to be correlated to surface area of the body and would therefore influence the water uptake values in different sized animals. The values obtained were multiplied by 100 for more manageable results. Species are arranged by decreasing degree of water uptake.

Species	A: Mass (Wet) — Mass (dry) (gms)	B: Duration (mins)	C: Body Mass (gms)	Water uptake $\left(\frac{A \cdot 100}{B \cdot C}\right)$
<i>S. campestris</i>	9.8	1	101	9.7
<i>M. albicaudatus</i>	22.0	3	116	6.3
<i>T. leucogaster</i>	14.0	4	101	3.5
<i>L. griselda</i>	11.5	10	63	1.8
<i>R. pumilio</i>	6.7	10	43	1.6
<i>P. natalensis</i>	9.8	10	67	1.5

animals only moved the limbs weakly or stopped paddling completely for a few seconds. The effect of water uptake by fur on swimming time was quantitatively determined and shown to be negatively correlated

(Table 4). The correlation was significant ($p < 0.05$) as shown in Figure 4. *S. campestris*, *M. albicaudatus*, and *T. leucogaster* have soft, water-absorbent fur which becomes quickly water-logged. *L. griselda*, *R. pumilio* and *P. natalensis* have water-resistant pelages which increase buoyancy.

Detergent in the water produced a significant decrease (Mann-Whitney *U*-test, $p < 0.05$) in the swimming times of all species (Fig. 5). When the swim times of all individuals (irrespective of species) were compared,

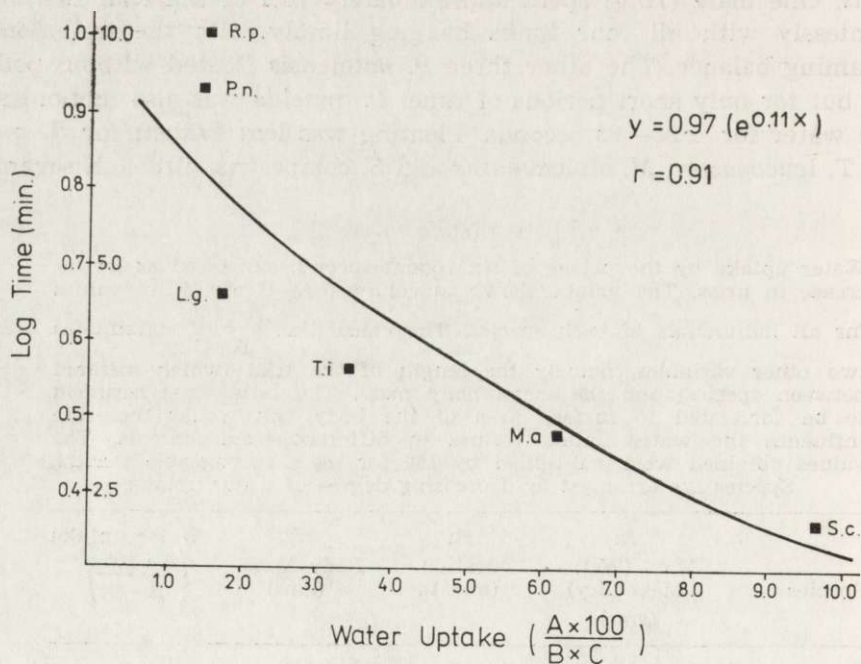


Fig. 4. Correlation between water uptake by the fur and swimming time. Parameters of water intake are: A=Mass in grams (wet) — Mass in grams (dry); B=Duration of trial to nearest minute; C=Mean body mass for a species. Double scale on vertical axis indicates actual time (minutes) on inner scale and log time (Y) on outer scale. Species tested were R.p.=*Rhabdomys pumilio*; P.n.=*Praomys natalensis*; L.g.=*Lemniscomys griselda*; T.l.=*Tatera leucogaster*; M.a.=*Myodomys albicaudatus*; S.c.=*Saccostomus campestris*.

the decrease in time caused by detergent was also significant (t -test, $p < 0.05$). Animals sank quickly in comparison to the non-detergent performances as the fur quickly became soaked to the skin.

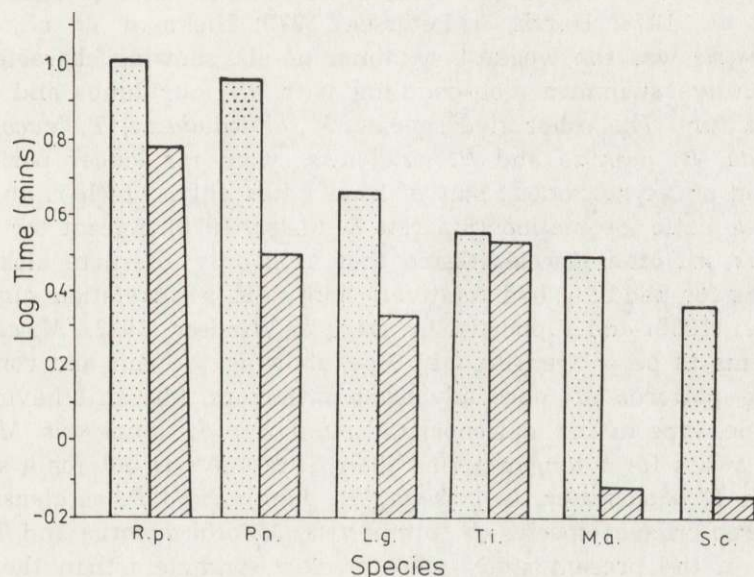


Fig. 5. Effect of the addition of detergent to the water on swimming time for six species of rodents. The swimming time for "non-detergent" trials (dotted) is higher than those with detergent (lined) for all species. R.p.=*R. pumilio*; P.n.=*P. natalensis*; L.g.=*L. griselda*; T.l.=*T. leucogaster*; M.a.=*M. albicaudatus*; S.c.=*S. campestris*.

3.3. Maintenance of Body Temperature

Body core temperatures for the six species ranged from 32.7° for *M. albicaudatus* to 36.0°C in *R. pumilio*; temperature differences can be accounted for by the activity of the animal prior to examination. *M. albicaudatus*, being nocturnal, had been sleeping at the time when temperatures were taken, whereas *R. pumilio*, being diurnal, was highly active and excitable when handled, which perhaps accounts in part for the higher body temperature. The drop in temperature per minute when the animals were placed in cold water was exponential in all species, and no significant difference was evident ($p < 0.05$). Core body temperatures dropped to 17–18°C within seven to nine minutes in all species during testing.

DISCUSSION

Intraspecific swim times varied greatly for all six species. No significant differences were found between males and females of any species in accordance with other studies on rodents (Best & Hart, 1976; Evans *et al.*, 1978; Harris & Petersen, 1979; Hickman *et al.*, 1983). *S. campestris* was the weakest swimmer of all, showing characteristics of a primitive swimmer (dog-paddling with all four limbs and highly absorbent fur). The other five species, *M. albicaudatus*, *T. leucogaster*, *L. griselda*, *R. pumilio* and *P. natalensis* swam for longer periods of time using an asynchronous gait of hind limbs only, which is an adaptation to aquatic locomotion (Starrett & Fisler, 1970). Except for *M. albicaudatus*, all other species tested that used only alternate kicking of hind limbs for paddling had relatively long tails, a correlation suggested by Howell (1930) and supported by Dagg & Windsor (1972). *M. albicaudatus* seems to be a "transitional" type, showing the gait and confident swimming patterns of more advanced swimmers, but still having the body shape, type of fur and short tail similar to *S. campestris*. *M. albicaudatus* swam for a longer period than *S. campestris* but for a shorter time than *T. leucogaster*, *L. griselda*, *R. pumilio* and *P. natalensis*.

The three cricetid species (*S. campestris*, *M. albicaudatus* and *T. leucogaster*) in the present study were weaker swimmers than the three murid species (*L. griselda*, *R. pumilio* and *P. natalensis*), although more extensive testing under field conditions with a greater variety of species must be undertaken to elucidate general trends in swimming ability. Carter & Merritt (1981), for example, record swimming times of approximately 26 minutes for *Peromyscus leucopus* (*Cricetidae*) at 20°C (well above the murid performances of the present study), while Evans *et al.* (1978) record times of less than two minutes for the same species at 29°C. Factors affecting swimming ability are not clearly understood, and King *et al.* (1968) propose no definite relationship between behavioural responses and taxonomic status for the genus *Peromyscus*, one of the very few genera which have been tested for swimming ability to any extent at all.

Best & Hart (1976) proposed that the tail of pocket gophers may function as a "water-depth probe" since the tail contacting the bottom of the trough prompted exhausted and sinking animals to immediately begin stroking again. Hickman (1984) noted the importance of the tail for orientation to geomyids during digging. Tail probing might explain in part why the species with long tails (*T. leucogaster*, *R. pumilio*, *L. griselda* and *P. natalensis*) swam for longer periods than the other two species (*M. albicaudatus* and *S. campestris*). The tail was, however, also used to a greater extent in these "long-tailed" species for turning and

maintaining balance when floating (neither function was evident in *M. albicaudatus* or *S. campestris*).

A correlation between body mass and swimming speed was not apparent in accordance with Dagg & Windsor (1972), although there was a negative correlation between number of strokes per minute and body mass. With the exception of *S. campestris*, the heaviest species (*M. albicaudatus*) had the slowest stroke, while the smallest species (*R. pumilio*) stroked most rapidly. The other three species, *T. leucogaster*, *L. griselda*, and *P. natalensis* also followed the trend of slower strokes with increasing body size. No correlation was found between hind foot length and speed, nor between hind foot length and the number of strokes per minute. Dagg & Windsor (1972) suggest that the stroking speed of a leg is not a function of leg length, but rather the power of the muscles which increases with the growth of the animal.

There was a definite correlation between body mass and swimming time for the six species tested in the present study. The smallest species (*R. pumilio*) swam for the longest period of time and the heaviest species (*M. albicaudatus*) swam for less time than all species except *S. campestris*. This inverse relationship between body mass and endurance is contrary to the findings of Wilber (1958, 1963) and Getz (1967) who found a positive correlation when plotting log time in minutes against log mass in grams. The negative correlation in the present study is not, however, unexpected, since smaller animals have a greater surface area to body mass which increased the effect of buoyancy (Hickman, 1986). It is also generally accepted that metabolic rate and activity are relatively higher in a smaller animals, and these animals would therefore make a more active and "energetic" attempt to remain afloat. Moreover, increased heat production would somewhat offset the drastic loss of heat to the water, although in the present study the water was relatively warm (24°C), and no significant difference was found between species in tests for decreases in body temperatures in cold water (16°C).

It may also be significant that the three heaviest species (*M. albicaudatus*, *S. campestris* and *T. leucogaster*) all have soft, water-absorbent fur (Table 4) which acts as an anchor when water-logged (Hickman, 1983a). The water-resistant property and reflective appearance of the fur are both due to air trapped in the pelage. Perhaps the discrepancy over the correlation between swimming time and body mass was partly due to the three heaviest species having the most absorbent fur and the lighter species having water-repellent fur, although correlation need not be explained by this single factor alone.

Stock (1972) proposed that oil secretion by dermal glands is of importance in making the fur water-resistant; the effect of oils was

explored in the present study. Detergent in the water decreased swimming time in all species and increased the difficulty in maintaining equilibrium (Dagg & Windsor, 1972). Hickman (1977) suggested that since fecal pellets have a negative buoyancy, defecation while swimming may inadvertently reduce mass, but more important, may have a detergent effect on the air trapping capacity of pelage in confined situations. Since *S. campestris* and *R. pumilio* had totally different swimming abilities, and yet both defecated more than any other species, defecation appears to be of minor importance to swimming ability, especially in open areas of water which would typify natural conditions.

It was expected that when immersed in cold water, those species with more water resistant pelages would maintain body temperatures constant for longer periods than those with absorbent pelages; this was not the case. Core body temperatures in all species dropped rapidly within the first ten minutes of animals being placed in the cold water. In another study (Esher *et al.*, 1978), cotton rats and rice rats were very sluggish when removed from a water bath. Although swimming performances of animals in the present study were not timed at low temperatures, it is expected (Wilber, 1958; Wilber & Hunn, 1960; Esher *et al.*, 1978; Hickman, 1978) that swimming performances would be greatly reduced. Hafner & Hafner (1975), however, found no significant difference in the swimming ability of kangaroo mice (*Microdipodops pallidus*) at 10°, 20° and 30°C.

The possibility that swimming ability has been a determining factor in the distribution of small terrestrial mammals, or that distribution may be correlated to the quantity of water present in a specific habitat, has been considered by several authors, and has resulted in varying opinions. Hickman (1978) suggested that the flooding of *Cryptomys* burrows may select for populations with better swimming abilities in certain areas, and Getz (1967) demonstrated that habitat preferences and niche segregation appear to be influenced by inclination to enter water and swimming ability. Schmidly & Packard (1967) found some correlation between geographic distribution and swimming ability in pocket mice (*Perognathus*) as did Hafner & Hafner (1975) in a study on *Microdipodops*. Evans *et al.* (1978), however, found no conclusive correlation between swimming and distributional patterns in a study of eight muroid species of rodents.

Although there seems to be a correlation between the type of habitat and the swimming ability in the six species tested in the present study, a wet habitat/positive swimming performance hypothesis is still not conclusive. Distribution and habitats of the six species tested for in the present study are described by several authors, namely Short-

ridge (1934), Smithers (1971), De Graaf (1981), Willan (1982) and Smithers (1983). *R. pumilio* and *P. natalensis* prefer damp or wet habitats and are often found in the vicinity of water, although *R. pumilio* may be found in dry habitats. *L. griselda* and *T. leucogaster* are also often found in wet regions, the latter not being tolerant of dry areas with a rainfall of less than 250 mm per year. *S. campestris* inhabits open veld, dense bush, or dry riverbeds, while *M. albicaudatus* is reported to inhabit montane grassvelds. The general trend, therefore, indicates that species which demonstrated greater swimming ability, both in the water-resistance of the pelage and in the use of a hind-limb gait, are also those species which inhabit areas close to water. Species that do not reveal any particular preference to dry or wet habitats are, on the whole, weaker swimmers. The Southern African distributions of the six species in this study as described by De Graaf (1981), show no correlation between swimming ability and extent of distribution; *S. campestris* and *P. natalensis* for example, both have very wide distributions and yet their swimming ability is very different, as has already been discussed.

The swimming performance of the six South African species tested in the present study compares favourably with the results of other authors for other species of rodents in various areas. Although *Microtus* are excellent swimmers, capable of swimming for approximately half an hour and of diving and swimming below the water surface (Fisler, 1961; Carter & Merritt, 1981), most other rodents which have been tested are capable of swimming for less than ten minutes, including *Microdipodops* (Hafner & Hafner, 1975), *Geomys* (Best & Hart, 1976; Hickman, 1977), *Thomomys* and *Pappogeomys* (Hickman, 1978) and *Tachyoryctes* (Hickman, 1983a). Many of the above species are fossorial, but similar swimming times have also been reported for eight non-fossorial muroid rodents (Evans *et al.*, 1978). This extreme variation of swimming ability in the eight muroid rodents was also evident in the six South African species tested in this study.

Many questions concerning the factors which affect swimming ability and the influence it may have on the distribution of different species still remain unanswered. The scope for further study on the species tested in the present study and the rodents and other small terrestrial mammals of every continent is therefore unlimited, whether one chooses to examine physiological and morphological aspects (*e.g.* effect of oil secreting glands and defecation on buoyancy, ability to learn and improve swimming performance, development of muscles and use of limbs with age); the psychological aspects (propensity to enter water); or the

environmental aspects (effect of water temperature, debris in the water, currents, and crowding).

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REFERENCES

1. Ahl A. S., 1982: Evidence of use of vibrissae in swimming in *Sigmodon fulviventer*. *Anim. Behav.*, 30: 1203—1206.
2. Aldrich A. & Quilliam T. A., 1966: Some aspects of mole behaviour. *J. Zool. Lond.*, 149: 112—114.
3. Best L. & Hart E. B., 1976: Swimming ability of pocket gophers (*Geomyidae*). *Tex. J. Sci.*, 27: 361—366.
4. Carter J. L. & Merritt P. F., 1981: Evaluation of swimming ability as a means of island invasion by small mammals in coastal Virginia. *Ann. Carnegie Mus.*, 50: 31—46.
5. Dagg A. I. & Windsor D. E., 1972: Swimming in northern terrestrial mammals. *Can. J. Zool.*, 50: 117—130.
6. De Graaf G., 1981: The rodents of Southern Africa. Durban, Pretoria: Butterworths.
7. Esher R. J., Wolfe J. L., & Layne J. N., 1978: Swimming behavior of rice rats (*Oryzomys palustris*) and cotton rats (*Sigmodon hispidus*). *J. Mammal.*, 59: 551—558.
8. Evans R. L., Katz E. M., Olson N. L. & Dewsbury D. A., 1978: A comparative study of swimming behaviour in eight species of muroid rodents. *Bull. Psychon. Soc.*, 11: 168—170.
9. Fislser G. F., 1961: Behaviour of salt-marsh *Microtus* during winter high tides. *J. Mammal.*, 42: 37—43.
10. Getz L. L., 1967: Responses of selected small mammals to water. *Univ. Conn. Occas. Pap. Biol., Sci. Ser.*, 1: 71—81.
11. Hafner J. C., & Hafner M. S., 1975: Water as a potential barrier to dispersal in *Microdipodops*. *J. Mammal.*, 56: 911—914.
12. Harris C. E. & Petersen M. K., 1979: Comparative swimming performances in selected cricetid and heteromyid rodents. *Occas. Pap. Zool.*, 3: 1—16.
13. Hickman G. C., 1977: Swimming behavior in representative species of the three genera of North American geomyids. *Southwest Nat.*, 21: 553—558.
14. Hickman G. C., 1978: Reactions of *Cryptomys hottentotus* to water (*Rodentia: Bathyergidae*). *Zool. Afr.*, 13: 319—328.
15. Hickman G. C., 1983a: Burrows, surface movement and swimming of *Tachyoryctes splendens* (*Rodentia: Rhizomyidae*) during flood conditions in Kenya. *J. Zool. Lond.*, 200: 71—82.
16. Hickman G. C., 1983b: Swimming ability of a naked mole-rat, *Heterocephalus glaber*. *Mammalia*, 47: 267—269.
17. Hickman G. C., 1984: Behavior of North American geomyids during surface movement and construction of earth mounds. *Special Publ. Mus. Texas Tech Univ.*, 22: 165—186.
18. Hickman G. C., 1986: Swimming of *Amblysomus hottentotus* (*Insectivora: Chry-*

- sochloridae*) with notes on *Chrysoxalax* and *Eremitalpa*. IV International Colloquium on Ecology and Taxonomy of African Small Mammals, SWA/Namibia, Cimbebasia, Ser. A, 8: 55—61.
19. Hickman G. C., Nevo E. & Heth G., 1983: Geographic variation in the swimming ability of *Spalax ehrenbergi* (Rodentia: Spalacidae) in Israel. *J. Biogeog.*, 10: 29—36.
 20. Howell A. B., 1930: Aquatic mammals — their adaptations to life in water. Baltimore: Charles C. Thomas.
 21. Kennerly T. E., Jr., 1963: Gene flow pattern and swimming ability of the pocket gopher. *Southwest. Nat.*, 8: 85—88.
 22. King J. A., Price E. O. & Weber P. G., 1968: Behavioral comparisons within the genus *Peromyscus*. *Pap. Mich. Acad. Sci. Arts. Lett.*, 53: 113—136.
 23. Schapiro S. M., Salas M. & Vukovitch K., 1970: Hormonal effects on ontogeny of swimming ability in the rat: assessment of the central nervous system development. *Science*, 168: 147—151.
 24. Schmidly D. J. & Packard R. L., 1967: Swimming ability in pocket mice. *Southwest. Nat.*, 12: 469—487.
 25. Shortridge G. C., 1934: The mammals of South West Africa. (Vol. 1). London: Heinemann.
 26. Smithers R. H. N., 1971: The mammals of Botswana. Museum Memoir No. 4. The Trustees of the National Museum of Salisbury, Rhodesia.
 27. Smithers R. H. N., 1983: The mammals of the Southern African subregion. Pretoria: University of Pretoria.
 28. Starrett A. & Fisler G. F., 1970: Aquatic adaptations of the water-mouse, *Rheomys underwoodi*. *Contrib. Sci. (Los Ang.)*, 182: 1—4.
 29. Stock A. D., 1972: Swimming ability in kangaroo rats. *Southwest. Nat.*, 17: 98—99.
 30. Wilber C. G., 1958: Biological similarity and swimming time in rodents. *Anat. Rec.*, 131: 608—609.
 31. Wilber C. G., 1959: Some factors which are correlated with swimming capacity in guinea pigs. *J. Appl. Physiol.*, 14: 199—203.
 32. Wilber C. G. & Hunn J. B., 1960: Swimming of albino mice. *J. Appl. Physiol.*, 15: 704—705.
 33. Wilber C. G., 1963: The swimming capacity of the golden hamster. *J. Mammal.*, 44: 265—267.
 34. Willan K. B. R., 1982: Social ecology of *Otomys irroratus*, *Rhabdomys pumilio* and *Praomys natalensis*. Doctoral Dissertation; University of Natal, Pietermaritzburg, South Africa.

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Graham C. HICKMAN i Carla MACHINÉ

ZDOLNOŚĆ PŁYWANIA U SZESĆCIU GATUNKÓW AFRYKAŃSKICH GRYZONI
(CRICETIDAE, MURIDAE)

Streszczenie

Opisano zdolność pływania u sześciu gatunków afrykańskich gryzoni: *Saccostomus campestris*, *Mystromys albicaudatus*, *Praomys (Mastomys) natalensis*, *Tatera leucogaster*, *Rhabdomys pumilio* i *Lemniscomys griselda*. Zdolność utrzymywania się na powierzchni wody była dodatnio skorelowana z czasem pływania, a ciężar ciała — ujemnie. Utrzymywanie temperatury ciała nie różniło się istotnie u badanych gatunków, a więc negatywny wpływ złej izolacji na zdolność pływania pominięto w porównaniach międzygatunkowych. Dyskutowane jest rozmieszczenie i typy środowisk użytkowanych przez badane gatunki. Te z nich, które zamieszkiwały wilgotne lub mokre tereny wykazywały większą umiejętność pływania.