REACTIONS OF *CRYPTOMYS HOTTENTOTUS* TO WATER
(RODENTIA: BATHYERGIDAE)

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ABSTRACT

Mortalities did not result from the escape of mole-rats from flooded burrows; and under laboratory testing, *Cryptomys hottentotus* was not hesitant to enter water. Swimming motions were coordinated and effective, enabling animals to swim for up to 14 minutes. Moderate current and aquatic vegetation aided movement in water; lowered water temperature adversely affected swimming ability. Water presents many ecological, zoogeographic, and behavioural problems which remain to be explored for small mammals.

INTRODUCTION

Except for their own urine, certain bathyergids in arid areas may never encounter quantities of free-standing water larger than a dewdrop. Water requirements are met by a diet of succulent vegetation. Nonetheless, it might be thought that flooding occurring once in several decades could drown every mole-rat in a local area, or promote dispersal over edaphic and aquatic barriers into uncolonized areas.

The literature on swimming ability of mammals is surprisingly sparse (Dagg & Windsor 1972) and is particularly poor on fossorial forms which are rarely seen on the surface even under dry conditions. Knowledge of swimming ability can be important in interpreting the zoogeography of specialized fossorial forms which are susceptible to even minimal flooding, of potential value in controlling fossorial rodents occurring in agricultural areas, and in understanding the total behavioural repertoire of a species.

Increasing aridity may have been the impetus for geomyids, the North American fossorial rodents ecologically equivalent to bathyergids, to evolve subterranean habits (Russell 1968). A wide range of individual and species performance in water has been found in comparing three genera of geomyids (Best & Hart 1976; Hickman 1977). There is little information on swimming ability of bathyergids. Roberts (in Shortridge 1934) noted that *Cryptomys hottentotus* often inhabits marshy ground, and Genelly (1965) noted three helpless mole-rats stranded on a termite mound surrounded by an inundated vlei. This study reports on the ability of *Cryptomys hottentotus* to swim, the manner in which mole-rats fail or succeed in swimming, and the factors involved in enhancing or inhibiting swimming ability.

METHODS AND RESULTS

Specimens of *C. hottentotus* were trapped in Pietermaritzburg with a plastic tube live trap (Hickman unpubl. ms.), and maintained in 122 × 50 × 43 cm high glass aquaria on a diet of potatoes and carrots. A 3 cm layer of soil on the bottom of the cage was kept moist, and ambient temperature maintained at 23°C. Two plastic tubes, each measuring 30 cm long and 63 cm in diameter, provided refuges for the mole-rats.

Reaction to flooding

The response of *C. hottentotus* to both sudden (water hose placed directly into the burrow) and gradual (sprinkling water on the surface) flooding was observed in two ways. Firstly, ten individuals were released in an outdoor enclosure, allowed to establish a burrow overnight, and then flooded the next day (five with sudden, and five with gradual flooding; one trial each). All these mole-rats were able to evacuate flooded burrows. As the surface mound became increasingly wet, the plug collapsed downwards and water gushed into the burrow. Mole-rats then appeared at one of the burrow openings, and delayed three to four seconds before abandoning the system. Some animals were wet from the neck down while others had only the tail and hind feet wet. Retreating three metres or so, the animals then began grooming.

Secondly, ten other animals released in a dirt-filled, glass-fronted observation cage measuring 505 × 102 × 7,5 cm, were allowed three days to establish and become familiar with a burrow, and were then flooded (five with sudden, and five with gradual flooding; one trial each). Mole-rats reacted by pushing dirt towards any water trickling into the system. The soft soil in the chamber often collapsed completely when wet; however, all animals reached the surface. One of them was able to force its way 15 cm through the mud to the surface when the burrow roof collapsed.

No mortalities occurred in any of the outdoor or indoor flooding tests.

Entering water

A 56 × 45 × 27 cm plastic container was filled with water 1,5 cm deep, and a round plastic platform 19 cm in diameter and 1,5 cm high (the top barely above water) was placed in the centre. Both ambient and water temperature were 23°C. Mole-rats were scooped out of their cages with a plastic container, the container inverted over the platform allowing 15 seconds for the mole-rat to settle, and the container then lifted and the reactions of the mole-rat noted (Table 1).

Seven mole-rats released individually on a platform surrounded by water showed little difference in exploratory time between first and second trials (15 seconds against 10 seconds in a 36 g mole-rat), or between the time when first contact was made with water and the time when all four legs were submerged (0 to 40 seconds) in a 36 g mole-rat, but 208 seconds in a 51 g mole-rat). Most animals did not hesitate to enter the water (only one 51 g individual stayed on the platform for as long as ten minutes). Most of the time in the water was spent in a leisurely plod along the walls. Animals often walked across the dry platform for a second or

TABLE 1.

Platform experiment for seven individuals entering water, two trials each. "Contact" is the time elapsed between lifting the container and the first contact with the water of the snout or paw, while "completion" is the time until all four feet are in water. Time is indicated in seconds.

	♂ 36 g		♀ 43 g		♀ 50 g		♀ 51 g		♂ 67 g		♀ 72 g		♂ 104 g	
Trials	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Contact	15	10	8	35	35	25	15	600	1	5	1	1	1	3
Interval	0	40	0	35	20	55	208	0	0	0	9	4	0	0
Completion	15	50	8	70	55	30	223	600	1	5	10	5	1	3

TABLE 2.

Reaction of mole-rats released into a tilted aquarium partially filled with water. "Contact" is time until first contact is made with water, while "completion" is further time until animal starts paddling with all four legs. Time in seconds.

Weight	Sex	Contact	Completion
34 g	♂	34	5
*84 g	♀	5	1 200+
99 g	♀	15	45
111 g	♂	10	225

* It took this animal 50 seconds to stand with all four legs in water, but it never actually swam during 1 200 seconds of observation.

two, and then plunged back into the water on the other side.

A second test of propensity towards entering water (also at 23°C) involved tilting 15° from the horizontal one end of a 122×50×43 cm aquarium so that the water was at a depth of nine cm at the deep end. At the opposite end where a 12×30 cm dry area remained, four mole-rats were released, and the time which elapsed before contact with water and commencement of swimming recorded (Table 2).

The four mole-rats entered the deeper water in the aquarium with little hesitation; contact with the water occurred after 5 to 34 seconds, and swimming commenced 5 to 225 seconds after contact with water. Mole-rats remained aggressive throughout the trials, clicking their teeth and attempting to bite when removed.

Swimming

Swimming style, speed, and endurance were observed in a 122×50×43 cm glass aquarium filled with water at 23°C to a depth of 23 cm. Eight mole-rats were lowered slowly into the water on a platform and swimming behaviour was photographed with super-eight mm cine film at 50 frames/second and analysed in slow motion on an editing machine. Animals were removed (five trials per animal) once the nose became submerged.

The basic body posture of swimming mole-rats was rigid from initial introduction to the water until removal; even so, turns were executed with ease (Figure 1). The water level, when
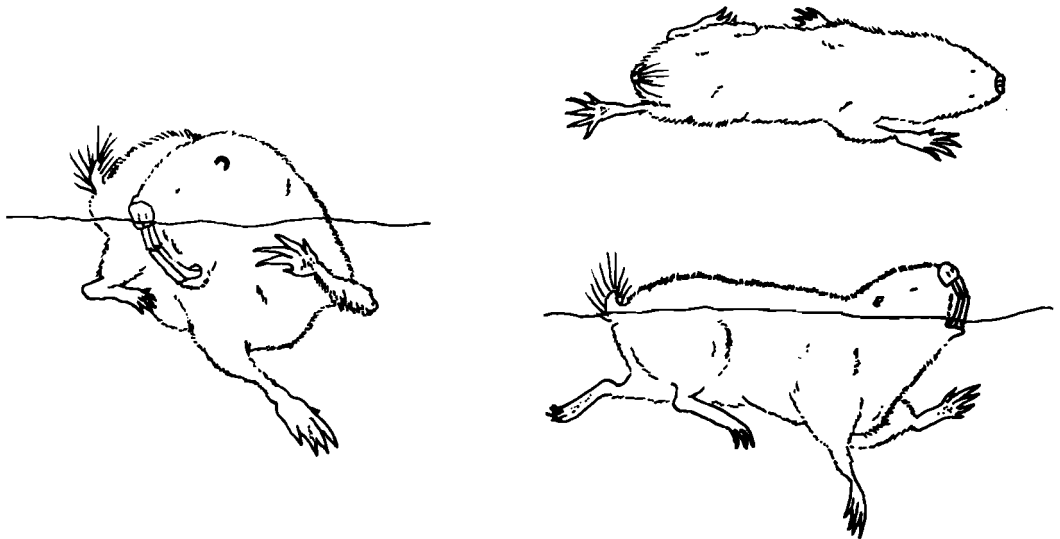

FIGURE 1.

Three views of swimming mole-rats. In anterior view, the mole-rat is beginning to turn to the right (note the massive head and medially pointed legs). The dorsal view emphasizes the well-spread digits and stroking pattern (front left and rear right are at the furthest extent of stroking, while the front right and rear left are about to begin their downward stroke). In lateral view, the back of the mole-rat is still dry so that the body is floating high in the water. Water eventually covers the scapular area. (Note the large chest and vertically directed tail).

the fur was dry, extended to below the nose and ears, and along the flank to the base of the tail. Initially, the grey-brown fur of swimming mole-rats appeared to have a silver sheen because of trapped air. As the fur gradually became water-logged bare patches of skin became evident, particularly along the ventral portion of the mandible and the upper forearm. The back was arched, allowing water to eventually cover the scapular region. The tail curved out of the water and for the most part remained stationary throughout. Individual mole-rats did not swim consistently with the eyes open or shut.

The stroke pattern involved two diagonal legs moving simultaneously, the diagonal pairs stroking alternately. Except for one individual which, after swimming for seven minutes, floated motionless for 20 seconds and then resumed swimming, there was no alteration in this sequence (such as synchronous kicks with the hind legs). The cupped forelegs stroked vertically and inwards. The hind legs were further apart in stroking, and appeared to produce a stronger forward thrust. The hind feet sometimes left the water at the end of the posterior stroke. The digits of both front and hind limbs were widespread when stroking, and bunched on return. Paddling became increasingly deliberate as the animal tired. However, there was no splashing even when individuals were first introduced into the aquarium. Equilibratory problems only occurred when the fur became soaked and the posterior end of the animal tended to sink, or when swimming into the sides of the aquarium occasionally caused momentary instability.

Swimming speed ranged from 0 to 122 mm per second, while endurance in six out of eight animals which completed all five trials (Table 3) ranged from 80 to 845 seconds. None of the animals displayed distinctive behaviour such as defecation while swimming. Upon removal from the water (i.e. when the nose first became submerged) some individuals emitted a short, high-pitched squeak. Even though exhausted, mole-rats generally remained very aggressive, biting anything within reach.

Physical factors

The specific gravity was investigated in three mole-rats which had died in captivity. When these animals were tested with all air expressed from the lungs but with the fur dry and therefore containing trapped air, the specific gravity proved to be marginally less than one (0,99 for 104 g body mass; 0,98 for 67 g; 0,94 for 111 g; each animal tested once). Such animals when placed in water floated for a while as expected, but as soon as the trapped air escaped and the fur became soaked, they sank to the bottom head first. The massive cranium, adapted for digging, dragged down the anterior end, while air in the gut (typical of many herbivores) tended to raise the hindquarters.

The lungs of the same three mole-rats were then filled with air. Once again they floated in water until the fur became saturated and then sank. The floating times were: eight minutes for 104 g body mass; ten minutes for 67 g; seven minutes for 111 g.

Facial vibrissae were cut at the base with scissors after anaesthetizing four animals with ether. Stiff hairs of the tail and feet were also clipped, and comparison made between clipped and non-clipped swimming individuals. Despite the highly thigmotactic nature of mole-rats, there was little effect on swimming motion or endurance.

TABLE 3.

Swimming endurance times for eight individuals, five trials each.

Sex and mass (g)	Time (seconds)					$\overline{Y}$
♂ 29	235	155	253	190	190	205
♂ 41	589	555	535	295	80	411
♀ 46	435	460	385	250	345	375
♀ 50	248	175	255	206	308	238
♀ 56	268	61	2			110
♀ 65	45	63	15			41
♂ 67	845	605	307	548	395	540
♀ 70	240	335	475	340	368	316
$\overline{Y}$	364	300	278	305	251	$\overline{\overline{Y}}$ 280

$$\overline{\overline{Y}} = 300$$

TABLE 4.

Rheotaxis test for six mole-rats when lowered into the water (L) and swimming (S) either with (W) or against (A) the current.
*Change from original direction of swimming.

	♂ 36 g		♀ 43 g		♂ 64 g		♂ 67 g		♀ 73 g		♂ 104 g	
Trials	L	S	L	S	L	S	L	S	L	S	L	S
1	W	W	A	A	W	W	A	A	A	A	A	A
2	A *	W	W *	A	A	A	A	A	W	W	W	W
3	W	W	W	W	W *	A	W	W	A	A	W *	A
4			W	W	W	W	W	W	W	W	W	W
5			A *	W	W	W			A	A	W	W
6					A *	W						

Environmental factors

The effects of current and rheotaxis were tested in a cement trough measuring 27,5 cm wide, 17 cm high and 3,5 m long. Water at 21 °C was maintained at a level of 14 cm, and flowing at a rate sufficient to move a wooden matchstick floating on the surface 1 metre every 20 seconds. Mole-rats were slowly lowered into the water on a platform facing either upstream or downstream until swimming commenced. Trials were repeated until the animal appeared exhausted and in danger of sinking (Table 4).

In 28 trials, there were six changes in direction (three to swim upstream and three to downstream). Animals were highly thigmotactic, and continued to swim in the direction they were facing once having touched the side of the trough. Attempts to climb up the wall of the trough sometimes resulted in a shift of direction.

Debris and vegetation in the water (10 sticks measuring 10 × 4 cm; five lily pads 8 × 5 cm; and a handful of grass) were added to the water under the same conditions described under "swimming". Animals were also released on a windless day into a lily pond with air and water temperature at 24°C. Floating objects had no discernible inhibitory effect on swimming mole-rats. Mole-rats appeared to glide over and under lily pads with no reduction in speed, and were able to climb out of the water in areas of thick vegetation and travel several metres over the surface. In the aquarium, debris was pushed away; there were no attempts to cling to sticks or other debris.

Water temperature tests were conducted at 8°C and 23°C (ambient temperature at 23°C). The number of strokes of the right forelimb was counted for each trial, and the time each individual swam before having the nose submerged was recorded (Table 5). A 15°C decrease

TABLE 5.

Swimming trials at water temperatures of 8°C and 23°C, indicating number of strokes with the right forepaw and rate expressed as strokes per second. Note that the average swimming time of 316 seconds compares favourably with the average for 25 swimming trials at 23°C in Table 3.

		♂ 34 g	♀ 43 g	♀ 64 g	♂ 67 g	♂ 74 g	♂ 111 g	= Y
8°C	Strokes	219	350	475	152	496	285	330
	Time (secs)	68	85	145	55	145	105	101
	Strokes/second	3,22	4,12	3,28	2,76	3,42	2,74	3,26
23°C	Strokes	670	520	1 904	452	1 179	540	878
	Time (secs)	320	155	710	147	400	165	316
	Strokes/second	2,09	3,36	2,68	3,08	2,95	3,27	2,91

in water temperature generally caused a reduction in swimming time, and an increase in the number of strokes per second. The mean for six individuals at 8° C was 330 strokes of the right forepaw in 101 seconds (3,26 strokes per second), as compared to the 23° C trial: 878 strokes in 316 seconds (2,91 strokes per second). Larger animals such as an 111 g individual might be expected to be less affected by low temperatures than a small one, since there is a smaller ratio of surface area to body mass. A tiring phase characterized by a noticeable slowing down of strokes per second was not as evident in the 8° C trials. Instead, an increase in stroking resulted in a decrease in endurance. Animals appeared panicky in the colder water and in danger of sinking, even though they retained enough energy to maintain stroking. Stroking motions at lower temperatures appeared more deliberate.

DISCUSSION

Considering that a fossorial mammal must move through an environment much denser than water, its body may be expected to be very heavy, rugged, muscular, and prone to sink in water. The massive skull and incisors of *Cryptomys* appear to be a handicap. Nonetheless, other fossorial anatomical modifications (such as streamlining) which resemble those of most aquatic mammals (Howell 1930) preadapt mole-rats to swimming. The most important factor contributing to the swimming ability of mole-rats is the mass of air trapped by the pelage. However, there is no heavy oily pelage secretion as found in kangaroo rats to aid flotation (Stock 1972). The size range of the mole-rats tested corresponded most closely to that of *Thomomys bottae*, smallest of the three geomyid species tested by Hickman (1977). Both *Thomomys* and *Cryptomys* conform to the general principle that larger animals are not necessarily faster than small (Dagg & Windsor 1972). The claws are very short in both *Thomomys* and *Cryptomys*. Unlike *Thomomys*, *Cryptomys* is totally blind (Eloff 1958), but this seemed to have little effect on swimming ability. *Cryptomys* was notably thigmotactic; nonetheless, even the shortening of facial vibrissae and stiff fringe hairs on the tail and feet had little effect on swimming ability. Geomyids do not utilize the distinctive fur-lined external cheek pouches for swimming (they are not present in bathyergids), and the longer tail does not contribute to propulsion in water (Hickman 1977). The basic body posture in geomyids and *Cryptomys* in swimming is rigid with no undulation. The cup-like feet of *Cryptomys* used for pushing dirt appeared very functional for stroking.

The basic stroking sequence used by *Cryptomys* is common to that used by most small mammals (Dagg & Windsor 1972). The front legs stroke vertically, and the hind legs are more spread apart and propulsive in both *Cryptomys* and the geomyids, reflecting the bracing of the hind feet on the burrow walls and the motion of the foreclaws when pushing loosened dirt under the body. The effect of changes in physical appearance of neonates and concurrent changes in swimming behaviour during maturation which has been reported for some surface dwellers and casual burrowers (Dagg & Windsor 1972) needs investigation in fossorial forms.

It would be interesting to determine if the swimming ability of a population from an arid

area differs appreciably from that of populations from areas where flooding occurs regularly. Many burrows are located in areas that rarely flood, even with abundant rain. Eloff (1953) flooded one burrow with 2 718 litres of water in three and a half hours before any seepage was detected; another burrow absorbed 4 372 litres of water (16,6 litres per minute) without overflow. Other burrow systems may flood regularly, but some tunnels may be located above normal flood levels. Tunnels leading to high ground have been reported for the geomyid, *Thomomys bottae*, in Texas (Williams 1976). Genelly (1965) reported this circumstance in Rhodesia where termite mounds provided a sanctuary from rising waters for *Cryptomys*. In the present study a mole-rat drowned in a trap after being submerged in an overnight rainfall. With access to higher ground via burrows, swimming need not be employed. However, in situations where burrows are completely inundated or where there is prolongation of high water conditions (as frequently occurs during rainy seasons), those individuals which are able to swim and are motivated so to do would be selected for.

The uninhibited manner in which mole-rats entered water may have been either a reflection of total unfamiliarity with a standing body of water, or total familiarity with moisture in the form of damp burrow walls and high humidity in the burrow system. Some mole-rats stumbled into the water during testing. Pit-fall type traps which depend on an animal stumbling into the trap have long been used for the capture of fossorial mammals, so that accidents may be more important than motivation in introducing an animal to water.

Cryptomys hottentotus was proficient at swimming, and compared well with smaller and less fossorial forms like the heteromyid *Perognathus* (Schmidly & Packard 1967), where swimming endurance trials ranged from 79,1 to 126,5 seconds. Although poor thermoregulators are normally protected against large temperature fluctuations by burrows, it is still surprising that lower water temperature adversely affected swimming endurance of *Cryptomys* while the smaller heteromyid *Microdipodops* was not so affected (Hafner & Hafner 1975). The wide range in individual performance times in the present study is, in part, an artifact of the subjective determination of when an animal is drowning. Activities prior to swimming (such as sleeping, eating, or grooming) are also likely to affect swimming ability during trials by affecting mass, condition of pelage, and available expendable energy. Large time differences in swimming due to the effect of currents, temperature, vegetation and debris probably occur also under natural conditions. Field studies of the effect of environmental factors on swimming ability should be undertaken. Marking populations and regular retrapping along a river or at the edge of a frequently flooded marsh would be particularly enlightening as to distance of movements and mortalities involved.

Any benefit from swimming ability would probably occur only after long periods of time, for a short-term study on *Peromyscus* (Savage 1973) indicates that a stream can be a very effective barrier even to surface forms. As noted for the Geomyidae (Hickman 1977), water may actually have a beneficial effect on distribution of the species, forcing animals to emigrate from an established burrow and providing friable soil for colonization.

Swimming ability may directly affect behaviour patterns involved in burrow construction and food gathering.

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