

Swimming Ability of 5 Species of African Rainforest Murid Rodents in Relation to Their Habitat Preferences

Violaine Nicolas^{1,*} and Marc Colyn²

¹Muséum National d'Histoire Naturelle, Département de Systématique et Evolution, USM 601, Laboratoire Mammifères et Oiseaux, 55 rue Buffon, 75005 Paris, France. Tel: 33-1-40793505. Fax: 33-1-40793063. E-mail: vnicolas@mnhn.fr

²Unité Mixte de Recherche CNRS 6553, Université de Rennes 1, Station Biologique, 35380 Paimpont, France
Tel: 33-2-99618188. E-mail: marc.colyn@univ-rennes1.fr

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Violaine Nicolas and Marc Colyn (2006) Swimming ability of 5 species of African rainforest murid rodents in relation to their habitat preferences. *Zoological Studies* 45(2): 264-268. The swimming abilities of 5 species of rainforest rodents (*Heimyscus fumosus* (Brosset et al.), *Hybomys univittatus* (Peters), *Hylomyscus stella* (Thomas), *Malacomys longipes* Milne-Edwards, and *Praomys* cf. *misonnei* Van der Straeten and Dieterlen) are described in order to discuss the relation between the ability of these species to escape flooding by swimming, and their preference for upland or flooded forest habitats. The 5 species exhibited a gradient of swimming abilities: the 2 upland species (*H. univittatus* and *H. fumosus*) were poor swimmers; the 2 habitat generalists (*P. cf. misonnei* and *H. stella*) were better swimmers but did not use the underwater medium; and the species which preferentially inhabits flooded forest (*M. longipes*) could swim well on and below the water surface. These differences in swimming ability may be related to differences in the resistance of the fur to absorb water, tail and hind foot lengths, and the use of either continuous or intermittent swimming among these species.
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The undisturbed lowland forest (110 m elevation) of the eastern part (02°09'S, 10°30'E) of the Monts Doudou "Aire d'Exploitation Rationnelle de Faune" (Gabon), is mainly covered by upland forest, but swamp and riparian forests are also present (see Sosef et al. 2004). Both the swamp and riparian forests are subject to flooding. The swamp forests are flooded seasonally or semi-permanently due to the presence of poorly drained soils. Numerous small rivers (3-7 m in breadth) originating in the adjacent mountains drain the lowland forest. The water can rise rapidly after heavy rains, and the flood may persist for a relatively short period of time (a few hours to a few days). In the last 2 decades, riparian habitats have been recognized by ecologists as being a priority area for conservation of terrestrial wildlife,

because they generally contain more species of birds and mammals than upland habitats, provide critical habitats for wildlife, and function as corridors (Darveau et al. 2001). The murid rodent fauna of the Mont Doudou lowland forest is well known (Nicolas 2003, Nicolas and Colyn 2003, Nicolas et al. 2004). Even if no species seems to be restricted to upland, swamp, or riparian forest, certain species are more habitat-specialized than others. For example, *Malacomys longipes* Milne-Edwards is more abundant in flooded than in upland forests (Delany 1964, Rham 1967, Dudu 1991, Granjon 1991, Nicolas 2003), which is reflected in its vernacular name ("big-eared swamp rat"). It belongs to the "semi-aquatic carnivore" guild, and uses its narrow stilt-like hind feet to wade in shallow water (Kerbis Peterhans

*To whom correspondence and reprint requests should be addressed.

and Patterson 1995). *Hybomys univittatus* (Peters) and *Heimyscus fumosus* (Brosset et al.) are more abundant in the upland than in the flooded forest, while *Praomys cf. misonnei* Van der Straeten and Dieterlen and *Hylomyscus stella* (Thomas) are more catholic in their habitat choices (Nicolas 2003, Nicolas et al. 2004). Rodent species' habitat preferences can, at least partially, be explained by their ability to escape flooding by swimming to dry ground. Two studies were previously performed on the swimming abilities of African rodents (Hickman and Machiné 1986, Duplantier and Ba 2001), but neither of them examined rainforest species. In this study, we compared the swimming abilities of 5 common rodent species of the Mont Doudou lowland forest, in order to test the hypothesis that species which have greater swimming abilities preferentially inhabit wetter areas (Hickman and Machiné 1986).

MATERIALS AND METHODS

Swimming ability

Tests of swimming ability were carried out in a 40 cm diameter, 40 cm high plastic bucket, filled with fresh water. The water temperature was 22°C. Animals were individually tested for 10 min (Duplantier and Ba 2001). The resistance of the fur to absorbing water is usually an important factor affecting swimming ability (Stock 1972, Hickman 1988, Giannoni et al. 1994, 2001). Thus, the quantity of water retained by the fur was measured by weighing the animals before and after the test, and also after 1, 3, and 5 min in the water. At the end of each minute, animal activity (swimming, floating, sinking, or diving) was noted (Duplantier and Ba 2001). When a rodent showed difficulty in surfacing again after sinking and we had the impression that it could drown, it was taken out of water and the test was ended. The swimming ability of 6-14 animals per species was tested: 6 males and 7 females of *H. fumosus*, 7 males and 5 females of *H. univittatus*, 7 males and 4 females of *H. stella*, 6 males of *M. longipes*, and 8 males and 6 females of *P. cf. misonnei*. All were healthy adults trapped in the forest and then kept in individual cages and provided with a diet of manioc and palm nuts for several days prior to the tests. Specimens were weighed (body weight (BW), to the nearest gram) and measured (head + body length (HB), tail length (TL), and hind-foot length (HF), to the nearest 0.1 mm), because these mor-

phological features have been proposed as important parameters affecting swimming ability (Hickman and Machiné 1986, Giannoni et al. 1993, Williams 1998).

Species identification

Due to the existence of sibling species, all animals were euthanized by cervical dislocation for further species identification. Species identification was based on both external and cranio-dental examinations. For the genera *Hylomyscus* and *Praomys*, the validity of our identification at the species level was tested by comparing the 16S rDNA sequence of several specimens to those of specimens previously identified by (Nicolas 2003).

Data analysis

TL and HF were expressed as a percentage of the HB. Water uptake by the fur after 1, 3, 5, and 10 min in the water was expressed as a percentage of the initial weight. All comparisons among species and between sexes were analyzed with one-way analysis of variance (ANOVA). Where the ANOVA resulted in significant *F* ratios ($p < 0.05$), we used Tukey's multiple comparison test to determine which pairs of habitats or species significantly differed. Spearman rank correlation coefficients were used to test for correlations between the initial weights of individuals and the magnitude of water uptake by the fur at the end of the test.

We tested the existence of sex-related differences in morphological measurements and swimming ability within each species. As no significant difference was recorded, only data for both sexes combined are presented in this paper.

RESULTS

There was a gradient of body weights and sizes among the various species (Table 1). *Hylomyscus stella* and *H. fumosus* had similar body weights and sizes, and they were the lightest and smallest species. *Hybomys univittatus* and *M. longipes* also had similar body weights and sizes, and were the heaviest and largest species. *Praomys cf. misonnei* had an intermediate body weight and size compared to the 4 other species. Great variations existed among species in the length of the tail relative to the body size (Table 1). The species with the relatively smallest tail was *H.*

univittatus, followed by *H. fumosus* and *M. longipes*. *Malacomys longipes* and *P. cf misonnei* had similar tail lengths relative to their body sizes. Finally, *H. stella* had the relatively longest tail. Significant differences in the length of the hind foot relative to the body size also existed among species (Table 1). *Hylomyscus stella* had the relatively smallest hind foot length, while *M. longipes* had the greatest one. *Heimyscus fumosus*, *P. cf misonnei*, and *H. univittatus* had intermediate hind foot lengths, and differences among these species were not significant. None of the studied species had a flattened tail or webbed feet.

All individuals of *M. longipes* completed the 10 min test. In contrast, one of 11 *H. stella* and three of 14 *P. cf. misonnei* had to be removed before the end of the test, while all *H. fumosus* and *H. univittatus* had to be removed before 6.5 min (depending on the individual, the test was ended after 1.25-6.5 min for *H. fumosus* and after 1.5-5.5 min for *H. univittatus*). Thus, the mean duration of the test was significantly lower for *H. fumosus* and *H. univittatus* than for the other species (Table 1).

Malacomys longipes, *H. stella*, and *P. cf. misonnei* occasionally ceased actively swimming and floated passively, whereas neither *H. fumosus* nor *H. univittatus* floated passively (Table 1). A diving sequence of a few seconds was observed for 1 specimen of *M. longipes*. This diving sequence

did not occur during a scan (1 scan/min) and therefore was not included in the data of table 1.

For *H. univittatus*, *P. cf misonnei*, and *M. longipes*, the increase in body weight (due to water absorption by the pelage) peaked after 1 min in the water and then did not vary significantly until the end of the test (Table 1). For *H. fumosus* and *H. stella*, it was significantly greater at the end of the test than after 1 min in the water. For a given species, there was great individual variation in water uptake. After 1, 3, and 5 min in the water, the average increase in body weight was greater for *H. fumosus* than for *M. longipes* and *H. stella*, and it was greater for *H. univittatus* than for *M. longipes* (Table 1). Regardless of the species, we detected no correlation between the initial weight of individuals and the magnitude of water uptake at the end of the test ($0.028 < r_s < 0.750$, $p > 0.05$). Finally, individuals that had to be removed from the water before the end of the test did not display the highest water uptake: the individual of *H. stella* that was pulled early from the bucket ranked 9th highest in water uptake, while those individuals of *P. cf. misonnei* ranked 4th, 10th, and 13th.

DISCUSSION

The 5 studied species exhibited a gradient of

Table 1. Comparison of external measurements and swimming abilities among species. Hf, *Heimyscus fumosus*; Hs, *Hylomyscus stella*; Hu, *Hybomys univittatus*; MI, *Malacomys longipes*; Pm, *Praomys cf misonnei*. Differences between species were considered significant at $p < 0.05$ (Tukey's test). Body weight (BW) is in grams (g), head+body length (HB) in millimeters (mm), and the test duration in minutes (min)

	<i>H. univittatus</i>	<i>H. fumosus</i>	<i>P. cf misonnei</i>	<i>H. stella</i>	<i>M. longipes</i>	Results of ANOVA (Tukey's test)
External measurements (mean \pm SD)						
BW	46.3 \pm 17.3	18.2 \pm 2.7	29.7 \pm 6.5	17.5 \pm 2.5	65.4 \pm 18.8	Hf = Hs < Pm < Hu = MI
HB	118 \pm 18	91 \pm 6	104 \pm 7	87 \pm 4	132 \pm 21	Hf = Hs < Pm < Hu = MI
(TL*100)/HB	90 \pm 7	106 \pm 6	127 \pm 7	149 \pm 3	122 \pm 8	Hu < Hf < MI = Pm < Hs
(HF*100)/HB	23.4 \pm 2.6	21.6 \pm 1.8	21.8 \pm 1.9	20.2 \pm 0.9	27.5 \pm 6.6	Hs < Hf = Pm = Hu < MI
Test duration (mean \pm SD)	3.09 \pm 1.23	3.32 \pm 1.31	7.57 \pm 2.20	9.35 \pm 1.15	10.00 \pm 0.00	Hu = Hf < Pm = Hs = MI
Activity (% of scan)						
Swimming	69	90	77	87	50	-
Floating	0	0	21	12	50	-
Sinking	31	10	2	1	0	-
Water uptake by fur (% of initial weight; mean \pm SD)						
after 1 min in water	11.6 \pm 5.6	11.4 \pm 5.1	10.2 \pm 4.0	7.8 \pm 3.8	6.4 \pm 2.3	MI = Hs < Hf; MI < Hu
after 3 min in water	13.9 \pm 6.0	13.8 \pm 3.4	12.2 \pm 4.5	10.2 \pm 3.7	8.5 \pm 2.1	MI = Hs < Hf; MI < Hu
after 5 min in water	17.7 \pm 7.5	15.0 \pm 6.7	10.0 \pm 5.7	11.1 \pm 3.7	8.5 \pm 2.1	MI = Hs < Hf; MI < Hu
after 10 min in water	-	-	10.1 \pm 6.9	13.2 \pm 4.5	8.9 \pm 3.4	MI = Pm = Hs

swimming abilities: the 2 upland species (*H. univittatus* and *H. fumosus*) were poor swimmers, the 2 generalist species (*P. cf. misonnei* and *H. stella*) were better swimmers but did not go under the water, and the species which preferentially inhabits flooded areas (*M. longipes*) could swim both on and below the water surface. All studied species lack the interdigital webbing or the laterally compressed tail present in many semi-aquatic or aquatic animals (Dunstone 1998, Fish 2000). Differences in swimming abilities among species could have been due to several factors. 1) Body mass: Smaller species have a greater surface area to body mass ratio, which increases the effect of buoyancy (Wilber 1958, Hickman and Machiné 1986, Hickman 1988). However, the 2 heaviest species in our study (*M. longipes* and *H. univittatus*) had contrasting swimming abilities. 2) Tail length: Species with long tails usually swim for longer periods than others, because the tail can function as a “water-depth probe” and is used for turning and maintaining balance while floating (Hickman and Machiné 1986). In agreement with this observation, the 2 studied species with the smaller tail length/body length ratios (*H. univittatus* and *H. fumosus*) were the worst swimmers. 3) Hind foot length: The elongated hind foot of *M. longipes*, compared to the other species, may enhance its swimming ability by constituting a better propulsor (Williams 1998). 4) Water absorption: Resistance of the fur to water absorption is considered to be an important factor affecting swimming ability (Stock 1972, Hickman 1988, Giannoni et al. 1994 2001). Water uptake by fur was greater for the 2 worst swimmers (*H. univittatus* and *H. fumosus*) than for the best swimmer (*M. longipes*). 5) Swimming: The 2 species that had to be removed before the end of the 10 min test (*H. univittatus* and *H. fumosus*) swam continuously until exhaustion, whereas the other species occasionally stopped actively swimming and passively floated for a short time. In some circumstances, intermittent swimming can decrease energetic costs of moving compared to continuously swimming. Moreover, pauses during intermittent swimming can assist the recovery from fatigue and thereby increase the total amount of work completed in a bout (Kramer and McLaughlin 2001). This might explain why *P. cf. misonnei*, *H. stella*, and *M. longipes* could swim longer than *H. univittatus* and *H. fumosus*. To conclude, the observed differences in species' swimming abilities might be explained by differences among species in the resistance of the fur to water absorption, tail

length, hind foot length, and the use of either continuous or intermittent swimming.

Our results possibly support the relation between the ability to escape flooding by swimming and the preference for a certain forest habitat type. Only simple swimming tests were carried out in our study, and they are merely sufficient to understand the ability of species to escape accidental flooding by swimming. To better understand the swimming ability of these species, e.g., their ability to cross streams and small rivers, swimming tests should be carried out in larger containers, and additional information on swimming posture, pausing and moving durations, propulsive velocity, thrust production, and locomotive energetics is necessary (Hickman and Machiné 1986, Hickman 1988, Williams 1998, Fish 2000, Cook et al. 2001, Kramer and McLaughlin 2001).

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