Original Investigation

Swimming performance in semiaquatic and terrestrial Oryzomyine rodents

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ABSTRACT

Semiaquatic and terrestrial mammals frequently have to cross or move along water bodies, both trying to remain on the water surface using one or two pairs of limbs, combining different gaits and stride lengths and frequencies. This is the case of the semiaquatic water rats Nectomys and the cursorial Cerradomys, sister genera of the Oryzomyini tribe, capable of swimming using similar gaits. They provide an opportunity to investigate performance specializations involving the semiaquatic habitat, our objective in this study. Rodents were filmed at 30 frames s^{-1} in lateral view, swimming in a glass aquarium. Video sequences were analyzed dividing the swimming cycle into power and recovery phases. Differences in swimming performance were detected between species of Nectomys and Cerradomys, but not between species of the same genus. Absolute mean speed did not differ between the semiaquatic and terrestrial groups, but the semiaquatic Nectomys had longer stride lengths with lower stride frequency, whereas the terrestrial Cerradomys had higher stride frequency and relative swimming speed. The widest behavior repertoire of Nectomys allowed more efficient, but not necessarily faster swimming than the terrestrial Cerradomys. Efficient aquatic locomotion in Nectomys is ultimately a result of improved buoyancy by hydrophobic fur and subtle morphological specializations, which allow this genus to perform more efficiently in water than the terrestrial Cerradomys without compromising locomotion in the terrestrial environment.

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Introduction

Locomotion takes part in practically all aspects of an animal life, affecting key tasks of their survival, such as catching prey, mate search and predator escape (Moermond, 1986; Bennett, 1989; Bock, 1994; Van Damme and Van Dooren, 1999). Many animal species, including most mammals, frequently have to move across or along water bodies and are thus able to swim (Fish, 1996a). Several terrestrial and semiaquatic mammals swim trying to remain on the water surface using one or two pairs of limbs (Dagg and Windsor, 1972; Hickman and Machiné, 1986; Fish and Baudinette, 1999; Lodé, 1999; Santori et al., 2005, 2008). However, in spite of the

degree of maneuverability on water surface, these swimming gaits have low performance, even if swimming bipedally. A more effective swimming mode is bipedal paddling, where bipedal swimming is associated with the use of propulsors (tail, limb, or flippers) to generate maximum power with minimum drag, considered an adaptation to aquatic or semiaquatic locomotion (Webb, 1988; Fish, 1992).

Semiaquatic habit evolved at least twice in the rodent tribe Oryzomyini, one of them in the genus Nectomys (Weksler, 2006). This tribe is the most diverse of the sigmodontine radiation, mainly composed of medium-sized, unspecialized, forest-dwelling, omnivorous rodents, with nocturnal and cursorial habits (Weksler, 2006). The semiaquatic habit of the genus Nectomys is well known, and comparisons of locomotor behavior with other terrestrial genera in the family provide a rare opportunity to investigate the evolution of behavioral adaptations to a semiaquatic lifestyle. The swimming of Nectomys was first compared with the terrestrial Cerradomys by Santori et al. (2008), which focused on swimming behavior and water buoyancy, but not on swimming performance.

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The most common swimming behavior of *Nectomys* was described as a fast bipedal paddling, with a hydrodynamic body posture and a short gliding phase during the gait cycle (Santori et al., 2008). *Cerradomys* is primarily terrestrial (Alho and Villela, 1984), capable of swimming using bipedal gaits, but do not maintain a hydrodynamic body posture as efficient as *Nectomys* because of its less hydrophobic fur (Santori et al., 2008). Therefore, even if *Cerradomys* species use the same gait as semiaquatic species, it is likely to have a less effective swimming performance than *Nectomys*.

We investigated to what extent and in what aspects the swimming performance of the semiaquatic *Nectomys* is more effective than the terrestrial *Cerradomys*. If semiterrestrial species swim faster, what performance variables allow them to do so. To investigate these questions we compared swimming performance between four species of these genera.

Material and methods

Study species and experimental subjects

We used adult rodents maintained in a breeding colony at the Laboratory of Biology and Parasitology of Wild Reservoir Mammals (Fundação Oswaldo Cruz, Brazil). Individuals of *Nectomys squamipes* were wild-caught at the municipality of Sumidouro, Rio de Janeiro State, while *N. rattus* came from the municipality of Teresina de Goiás, Goiás State, Brazil. Individuals of *Cerradomys scotti* came from the municipalities of Alto Paraíso and Cavalcanti, Goiás State, whereas *C. vivoi* were from the municipality of Juramento, Minas Gerais State, Brazil.

Procedures of rodent breeding colony are further detailed in D'Andrea et al. (1986). Room temperature was maintained at 27 °C ($SD = 6$) and relative humidity between 60 and 90%. Light–dark cycle was 12:12 with light starting at 06:00 h. Water and food were offered *ad libitum* and the diet consisted of NUVILAB CR1 mouse pellets (Nuvital Nutrients Ltd., Colombo, Brazil). Animals were housed individually in polypropylene cages (41 cm × 34 cm × 17 cm). Our procedures conformed to guidelines approved by the Animal Use and Ethics Committee of the Fundação Oswaldo Cruz (CEUA-FIOCRUZ, number P-0076-01). Body size of adult *Cerradomys vivoi* (143.3 mm) and *C. scotti* (148.2 mm) are smaller than *Nectomys rattus* (210.8 mm) and *N. squamipes* (200.7 mm) (Bonvicino et al. 2008; Percequillo et al. 2008).

The *Nectomys* genus is composed of semiaquatic rodent species and display interdigital webbing, as well as natatory fringes (Ernest and Mares, 1986; Weksler, 2006). The genus is widely distributed in South America (Reis et al., 2011), and in Brazil occurs in forested areas in the Atlantic Forest and Amazon biomes, gallery forests of Cerrado and Caatinga (Reis et al., 2011). Their habitats are always associated with streams, rivers and flooded areas, feeding on arthropods, fruits and fungi (Bergallo, 1994; Ernest and Mares, 1986; Reis et al., 2011). In an area of mangrove habitat in the Atlantic Forest biome, *N. squamipes* made a disproportional large use of stream habitat for displacement, foraging and resting (Prevedello et al., 2010).

The *Cerradomys* genus (n. gen. Cricetidae, Sigmodontinae) (Weksler et al., 2006) include terrestrial and omnivore species, distributed in open and dry vegetation, or mesic areas of dry regions formed mainly by the Chaco, Cerrado, Pantanal, and Caatinga biomes, from northeastern Brazil to eastern Paraguay and central Bolivia (Fonseca and Kierulff, 1989; Stallings, 1989; Vieira, 1997, 1999; Percequillo et al., 2008). *Cerradomys scotti* is found in most open habitats of Cerrado, but also in gallery forests, being observed in the Cerrado physiognomies of "campo sujo", "campo cerrado", "cerrado sensu stricto" (Percequillo et al., 2008), and in "veredas" (Langguth and Bonvicino, 2002). *Cerradomys vivoi* inhabits secondary semideciduous and gallery forests on transitional areas
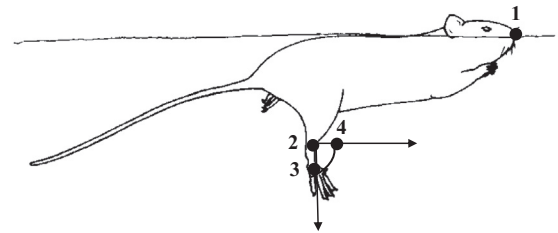
Fig. 1. Points digitized on the image to collect data on swimming performance of the rodents: 1 – tip of the nose to measure horizontal displacement of the body; 4-2-3 – hind foot angle variation during power phase of bipedal swimming.

between Cerrado and Caatinga, including arboreal areas of Caatinga (Percequillo et al., 2008).

Swimming performance

Measurements of animal performance in laboratory can be used to determine the effect of morphological variation on the real or potential ability of animals to carry out tasks that are relevant to individual fitness (Wainwright, 1991), establishing the relationship between the phenotype and ecology of animals (Arnold, 1983; Wainwright, 1991; Bock, 1994; Ricklefs and Miles, 1994). In locomotor studies, maximal speed is frequently used to evaluate performance (Arnold, 1983; Bennett, 1989; Ricklefs and Miles 1994; Delciellos and Vieira, 2006, 2007, 2009).

Rodents were filmed at 30 frames s^{-1} in lateral view, swimming in a 150 cm × 20 cm × 30 cm glass aquarium. The first 50 cm of the aquarium allowed rodents to accelerate. Rodent steady swimming was obtained by including in the camera field of vision only the region after the initial acceleration section of the aquarium. We encouraged individuals to swim at their maximal speed by gently touching their back. A 150 cm long reference grid with a 50 cm scale was set at the back wall of the aquarium, crossing the camera field of vision, to provide a frame of reference for the distances traveled by the rodents (Fish, 1996b).

Each rodent was filmed at least three times, and the best video sequence of each individual was selected. The best sequences were those where individuals swam on a straight line without interference of lateral walls or the bottom of the aquarium, and where we could observe at least one complete locomotor cycle (Fish, 1996b; Santori et al., 2005, 2008). To a more detailed methodology see Santori et al. (2008).

Frame by frame analysis of the video was done at the Laboratório de Zoologia de Vertebrados – Tetrapoda/Universidade do Estado do Rio de Janeiro. Video sequences were analyzed with the software APAS (Ariel Performance Analysis System, Ariel Dynamics, CA, USA). Based on limb movements, we divided the swimming locomotor cycle into power and recovery phases. The beginning of the power phase was indicated by the protraction of a foot, whereas the end of power phase was indicated by the farthest posterior extension of that foot before it was retracted (Fish, 1993a; Santori et al., 2008).

To measure performance during a locomotor cycle we marked reference points on the video of swimming rodents (Santori et al., 2005, 2010), placed at the tip of the nose and at the hindfeet (Fig. 1). Hindfeed angle width, the angle formed by hindfeet with a horizontal line was calculated as the difference between maximum value of the angle, measured at the end of power phase, and minimum value, measured at the start of the power phase during a locomotor cycle. Other performance variables measured during a locomotor cycle were (a) stride length (cm) – horizontal displacement of the reference point placed at the tip of the nose (Pennycuick, 1975), (b) power stroke duration (s) – time the limb remains protracted,

Table 1
Descriptive statistics (mean ± SD) of bipedal swimming performance variables of the four species of rodent studied and results of ANOVA testing for significant differences in species. Degrees of freedom = 3.

Variable	*N. rattus* $n = 14$	*N. squamipes* $n = 15$	*C. vivoi* $n = 4$	*C. scotti* $n = 6$	F	P
Total stride duration (s)	0.28 ± 0.04	0.28 ± 0.02	0.21 ± 0.02	0.22 ± 0.03	9.54	<0.01
Power phase duration (s)	0.10 ± 0.01	0.10 ± 0.01	0.08 ± 0.01	0.08 ± 0.01	6.14	<0.01
Recovery phase duration (s)	0.18 ± 0.04	0.18 ± 0.02	0.13 ± 0.01	0.14 ± 0.03	6.57	<0.01
Stride length (cm)	13.03 ± 2.25	11.89 ± 2.44	9.37 ± 2.50	7.95 ± 1.25	8.54	<0.01
Swimming speed (cm s^{-1})	47.18 ± 7.92	42.77 ± 7.41	44.68 ± 9.80	36.58 ± 6.59	2.74	0.06
Relative swimming speed	0.23 ± 0.04	0.22 ± 0.04 ($n = 14$)	0.31 ± 0.06	0.25 ± 0.05 ($n = 4$)	3.87	0.02
Stride frequency (Hz)	3.66 ± 0.52	3.63 ± 0.33	4.83 ± 0.42	4.62 ± 0.59	13.45	<0.01

(c) recovery duration (s) – time the limb is in forward acceleration movement, (d) stride duration (s) – time lag between two identical limb positions, (e) swimming speed (cm s^{-1}) – the horizontal displacement of the reference point at the nose divided by stride duration, (f) frequency (Hz) – number of locomotor cycles per second (1/stride duration), (g) relative swimming speed – stride length divided by head–body length, and (h) duration of the locomotor cycle (Pennycuick, 1975; Renous, 1994; Santori et al., 2008). At high swimming speeds and stride frequencies, at 30 frames s^{-1} or higher, individuals changed from bipedal paddling to swimming bound, or quadruped submerged swimming gaits, when it was not possible to measure all the performance variables in bipedal paddling.

Statistical methods

Data normality was tested using Kolmogorov–Smirnov tests. Relative swimming speed was arcsine transformed (Zar, 1984). Homogeneity of variance was tested using Levene's test. Sample size was sufficient to make intersexual comparisons only for *N. squamipes*.

Student's *t*-test was used to test differences in performance variables between semiaquatic and terrestrial groups (Zar, 1984). To test differences between the duration of recovery and power phases, we used *t*-test for paired samples (Zar, 1984). All means are reported ± standard deviation (*SD*). We considered results statistically significant at *P* < 0.05.

Results

Fifteen individuals of *N. squamipes* (10 females, 5 males), fourteen individuals of *N. rattus* (3 females, 11 males), four individuals of *C. vivoi* (1 female, 3 males), and six individuals of *C. scotti* (3 females, 3 males) were tested. Mean ± *SD* head–body length (mm) of these individuals was 203.4 ± 11.0 for *N. rattus*, 195.2 ± 10.2 for *N. squamipes*, 143.8 ± 11.1 for *C. vivoi*, and 141.8 ± 6.3 for *C. scotti*.

Swimming performance

Data of males and females of *N. squamipes* were pooled because no significantly differences in swimming performance were detected between sexes (all *P* > 0.74). Total stride duration, power phase duration, recovery phase duration, stride length, relative swimming speed, and stride frequency differed significantly between species, but not swimming speed (Table 1). Significance in power phase duration was caused by the difference between *C. vivoi* and *N. rattus* (Tukey *HSD* = 13.03, *P* = 0.04). Significant difference in total stride duration was caused by the differences between each species of *Cerradomys* and species of *Nectomys* (*C. vivoi* and *N. rattus*: Tukey *HSD* = 13.03, *P* = 0.02; *C. vivoi* and *N. squamipes*: Tukey *HSD* = 11.89, *P* = 0.02; *C. scotti* and *N. rattus*: Tukey *HSD* = 13.03, *P* = 0.02; *C. scotti* and *N. squamipes*: Tukey *HSD* = 11.89, *P* = 0.02). In stride frequency, significant difference was found between *C. vivoi* and *N. rattus* (Tukey *HSD* = 13.03, *P* < 0.01), *C. vivoi* and *N. squamipes* (Tukey *HSD* = 11.89, *P* < 0.01), *C. scotti* and *N. rattus* (Tukey *HSD* = 13.03, *P* < 0.01), and between *C. scotti* and *N. squamipes* (Tukey *HSD* = 11.89, *P* < 0.01). Significance in relative speed was caused by the difference between *C. vivoi* and *N. squamipes* (Tukey *HSD* = 0.22, *P* = 0.02). Stride length differed significantly between *C. scotti* and *N. rattus* (Tukey *HSD* = 13.03, *P* < 0.01), and between *C. scotti* and *N. squamipes* (Tukey *HSD* = 11.89, *P* = 0.02). Recovery phase duration differed significantly between *C. scotti* and *N. squamipes* (Tukey *HSD* = 11.89, *P* = 0.04).

In all species power phase was significantly shorter than recovery phase duration in paired *t*-tests (*N. rattus* – *t* = −7.74, *d.f.* = 13, *P* < 0.01; *N. squamipes* – *t* = −13.56, *d.f.* = 14, *P* < 0.01; *C. vivoi* – *t* = −103.92, *d.f.* = 3, *P* < 0.01; *C. scotti* – *t* = −4.81, *d.f.* = 5, *P* < 0.01).

Because significant differences in performance variables occurred only among species of *Nectomys* and *Cerradomys*, we pooled data from species of each genus, forming two groups according to their habits, semiaquatic (*N. rattus* and *N. squamipes*) and terrestrial (*C. scotti* and *C. vivoi*). The terrestrial group had significantly higher relative swimming speed and stride frequency, while the semiaquatic group had higher means in the other variables (Table 2).

Stride frequency decreased significantly with increase in body size when all individuals of the four species were analyzed together (*r* = −0.63, *n* = 39, *F* = 22.50, *d.f.* = 1, *P* < 0.01). In both groups, semiaquatic and terrestrial, relationship between duration of power and recovery phases were significant and inversely correlated with stride frequency (Table 3).

Table 2
Descriptive statistics (mean ± SD) of bipedal swimming performance variables for rodents species grouped according to their habits and results of Student's *t*-test comparing semiaquatic and terrestrial means. Degrees of freedom = 37 for all variables, except relative speed (*d.f.* = 34).

Variable	*Nectomys* (semiaquatic) $n = 29$	*Cerradomys* (terrestrial) $n = 10$	t	P
Total stride duration (s)	0.29 ± 0.03	0.22 ± 0.03	5.45	<0.01
Power phase duration (s)	0.10 ± 0.01	0.08 ± 0.01	4.15	<0.01
Recovery phase duration (s)	0.18 ± 0.03	0.13 ± 0.02	4.52	<0.01
Stride length (cm)	12.44 ± 2.38	8.52 ± 1.86	4.72	<0.01
Swimming speed (cm s^{-1})	44.89 ± 7.85	39.82 ± 8.58	1.72	0.09
Relative swimming speed	0.23 ± 0.04 ($n = 28$)	0.28 ± 0.06 ($n = 8$)	−2.68	0.01
Stride frequency (Hz)	3.64 ± 0.43	4.71 ± 0.51	−6.44	<0.01

Table 3
Summary of linear correlation analysis between stride frequency and duration of the two phases in bipedal swimming: power and recovery. Degrees of freedom = 1.

Groups	Gait phase	n	F	P	r
Semiaquatic	Power	29	7.71	<0.01	−0.47
Terrestrial	Power	10	6.96	0.03	−0.68
Semiaquatic	Recovery	29	162.16	<0.01	−0.93
Terrestrial	Recovery	10	36.90	<0.01	−0.91

Table 4
Summary of linear correlation analysis between swimming speed and stride length, and between swimming speed and stride frequency during bipedal swimming. Degrees of freedom = 1.

Groups	Variable	n	F	P	R
Semiaquatic	Stride length	29	45.22	<0.01	0.79
Terrestrial		10	30.34	<0.01	0.89
Semiaquatic	Stride frequency	29	0.92	0.35	0.18
Terrestrial		10	0.18	0.68	0.15

Swimming speed was positively and significantly correlated with stride length in semiaquatic and terrestrial groups (Table 4), but not with stride frequency (Table 4).

Mean hindfeet angle width in bipedal swimming (Table 5) was significantly larger in semiaquatic than in terrestrial group (ANOVA – $F = 31.96$, $P < 0.01$, $d.f. = 1$). Correlations of hindfeet angle with stride length, stride frequency and swimming speed were not significant in both groups (Table 6).

Swimming bound and quadruped submerged swimming

In swimming bound, the rodents of genus *Nectomys* developed propulsion on the water surface using an asymmetrical gait like the bound used in terrestrial locomotion of small mammals. *Nectomys rattus* ($n = 3$) presented mean total stride duration of 0.14 s (± 0.02), mean power phase duration of 0.09 s (± 0.04), mean recovery phase duration of 0.06 s (± 0.02), mean stride length of 13.73 cm (± 2.14), mean swimming speed of 95.77 cm s^{-1} (± 18.45), and mean stride frequency of 6.99 Hz (± 0.87). In this kind of swimming gait, *N. squamipes* ($n = 1$) presented total stride duration of 0.12 s, power phase duration of 0.07 s, recovery phase duration of 0.05 s, stride length of 16.30 cm, swimming speed of 139.32 cm s^{-1} and stride frequency of 8.55 Hz. Individuals of *Cerradomys* did not present this swimming behavior.

At the submerged swimming, rodents used a quadrupedal symmetric gait with limbs forming diagonal couplets, i.e., the power phase of a forelimb occurred synchronically with the power phase of a hind limb of the opposite side of the body. Using this kind of gait, mean swimming speed of *N. rattus* ($n = 7$) was 56.26 cm s^{-1} (± 8.13), while the two individuals of *C. vivoi* presented swimming speed of 54.53 and 60.02 cm s^{-1}.

Discussion

Longer and less frequent strides are expected if mammals more specialized to aquatic locomotion are more efficient swimmers, i.e., move longer distances per stride and unit effort. The higher values of *Nectomys* in performance variables (stride length, total

Table 6
Summary of linear correlation analysis between mean width hindfeet angle during power phase and other performance variables in bipedal swimming. Degrees of freedom = 1 for all. Semiaquatic group: $n = 11$, except for stride length ($n = 10$). Terrestrial group: $n = 8$.

Variable	Semiaquatic			Terrestrial		
	F	r	P	F	r	P
Stride length	0.13	−0.12	0.72	3.90	0.63	0.10
Stride frequency	0.08	0.09	0.79	0.35	−0.23	0.58
Swimming speed	0.004	−0.02	0.95	3.80	0.62	0.10

stride duration, power and recovery phase duration), reaching similar or faster swimming speeds than *Cerradomys* (Table 2), indicate more efficient swimming. When the whole range of mammalian body sizes is considered, involving 3 orders of magnitude, stride frequency is inversely related to body size (Williams, 1983; Heglund and Taylor, 1988), and speed increases with body size (Peters, 1983). Accordingly, stride frequencies of *Nectomys* and *Cerradomys* were higher and speed lower than the larger *Ondatra zibethicus* (2.5 Hz, 58 cm s^{-1}) and *Hydromys chrysogaster* (1.28 Hz, 25–177 cm s^{-1}) (Fish, 1984, 1993a; Fish and Baudinette, 1999). As *Nectomys* is slightly larger than *Cerradomys*, on average 50 g, an allometric effect could also be considered, but body size effects on metabolic rates and performance disappear at smaller scales, such as in the 50 g difference between *Cerradomys* and *Nectomys*. Therefore, differences in stride frequency between *Nectomys* and *Cerradomys* probably reflect mostly adaptation to different lifestyles (semiaquatic vs. terrestrial), but may also include an allometric component due to the higher body size of *Nectomys*.

The asymmetry in the power stroke of bipedal paddling by the rodents studied may be an intrinsic characteristic of all four-limb mammals when swimming. *Nectomys* and *Cerradomys* swimming was characterized by a recovery phase longer than the power phase. This asymmetry in the stroke cycle was also observed in other semiaquatic mammals, bipedal paddlers such as the rodents *O. zibethicus* and *H. chrysogaster*, the water opossum *Chironectes minimus*, and in a quadrupedal swimmer, *Mustela vison* (Williams, 1983; Fish, 1984, 1993a; Fish and Baudinette, 1999). Terrestrial mammals when swimming also showed an asymmetry in the stroke cycle, such as the virginia opossum, *Didelphis virginiana*, and the thick-tailed opossum, *Lutreolina crassicaudata*, which swim using quadrupedal gaits with a recovery phase longer than the power phase (Fish, 1993a; Santori et al., 2005). In aquatic locomotion, the reduced power phase generates propulsive forces and, at the same time, minimizes drag produced by limbs in motion (Fish, 1984, 1993a). This principle may be applied to any four-limbed swimming mammal, whether semiaquatic or terrestrial. Terrestrial mammals also have some buoyancy capacity when swimming, more limited compared to semiaquatic mammals, but still providing body stability and a longer recovery phase (Hildebrand, 1987; Fish and Stein, 1991).

Swimming speed in units of body size (relative speed) in the terrestrial group (*Cerradomys*) was significantly higher than the semiaquatic group (*Nectomys*), and absolute swimming speed of *Nectomys* was higher, but not significantly, than *Cerradomys*. The results must be viewed with caution because of the small samples sizes involved, but are in accordance with the hypothesis of less efficient swimming by terrestrial rodents. The waterproofed

Table 5
Descriptive statistics (mean ± SD) of width of hindfeet angle (degree) during the power phase of bipedal swimming.

Variable	N. rattus n = 6	N. squamipes n = 5	C. vivoi n = 3	C. scotti n = 5	Semiaquatic n = 11	Terrestrial n = 8
Minimum mean angle	19.64 ± 13.13	14.72 ± 8.41	26.03 ± 3.83	17.97 ± 9.87	17.40 ± 11.0	21.00 ± 8.79
Maximum mean angle	139.26 ± 11.27	134.23 ± 10.40	137.39 ± 4.48	125.05 ± 20.05	136.97 ± 10.66	129.68 ± 16.62
Mean angle width	119.62 ± 18.69	119.52 ± 12.15	111.36 ± 5.49	107.08 ± 13.89	119.57 ± 15.29	108.68 ± 11.13

fur of *Nectomys* provides higher buoyancy ability than *Cerradomys* (Santori et al., 2008), hence it is probable that a lower buoyancy ability forced *Cerradomys* to swim at higher stroke frequencies to compensate, reaching their maximal speed. This floating effort was not necessary for *Nectomys*, which were able to float at lower speeds.

In tetrapods, speed is the product of stride frequency and length, hence high speed is obtained by increasing either one, or both (Walker and Liem, 1994). In terrestrial locomotion, stride frequency increases linearly with speed (Heglund and Taylor, 1988) but, in swimming, the relationship between swimming speed and stride frequency is controversial (Fish, 1984). In the two genera studied swimming speed increased by longer rather than more frequent strides, similarly to observed in tetrapods such as *M. vison*, *H. chrysogaster*, *O. zibethicus* and sea otters, which swim using alternated movement of propulsor limbs, and increase swimming speed frequently without change in stride frequency (Fish, 1982; Williams, 1983, 1989; Fish and Baudinette, 1999). Conversely, in the semiaquatic bipedal swimmers *C. minimus* and *Mustela lutreola*, and the terrestrial *D. virginiana* and *Mustela putorius*, swimming speed increases with stride frequency – above $28 \, cm \, s^{-1}$ for the opossums (Fish, 1993b; Lodé, 1999). The arc formed by the hind feet in a horizontal plane may be used to increase speed in *C. minimus* and *O. zibethicus* (Fish, 1984, 1993b), but the same was not observed in *Nectomys* and *Cerradomys*. Therefore, the relative importance of stride length and frequency in swimming speed may vary depending on the species. At this point, no general pattern emerges.

Submerged swimming speeds recorded for *N. rattus* and *C. vivoi* were intermediate between the bipedal paddling and the swimming bound, and similar among the few individuals that used it. The evidence is limited, but it favors no difference between terrestrial and semiaquatic species in submerged swimming. Submerged swimming was not observed in the individuals of *N. squamipes* and *C. scotti* tested, but it was observed in the field and laboratory for other individuals of *N. squamipes* (R.T. Santori, personal observation). Efficiency is higher in submerged compared to surface swimming because wave drag is reduced when animals swim underwater (Fish, 1992), but terrestrial and semiaquatic animals have limited ability to sustain long submerged displacements without breathing, which may impose similar constraints on both.

Contrary to bipedal paddling, swimming bound is a quadruped gait where both limbs move simultaneously, first described in this group of rodents by Santori et al. (2008). This gait is similar to that exhibited by hopping mammals in terrestrial locomotion, where animals take advantage of limbs touching the ground to generate propulsion (Phillipson, 1905; Alexander, 2003). Despite the high speed of swimming bound, stride length was lower than bipedal paddling, hence its high speed is provided mostly by more frequent strides. The swimming bound in this group of rodents was first described by Santori et al. (2008). Only three individuals of *N. rattus* and one of *N. squamipes* presented this swimming gait, hence it is probably rarely used, when high stride frequency and speed are necessary, such as to escape from predators.

The changes in locomotor behavior observed in both genera during swimming are analogous to those found in terrestrial mammals to increase speed, but *Nectomys* were able to use three kinds of swimming gaits, and achieved bipedal paddling using lower stride frequencies and longer stride lengths. This wider behavioral repertoire of *Nectomys* is related to a more efficient swimming than the terrestrial *Cerradomys*. Efficiency, however, does not mean necessarily faster, as the maximum speeds of the two groups were similar. Efficiency of *Nectomys* is ultimately a combination of its improved buoyancy and agility (i.e. comparative higher values of stride length, total stride duration, power and recovery phase duration). Along the gradient formed by terrestrial, semiaquatic, and aquatic mammals, *Nectomys* seems better adapted

than *Cerradomys*, although not as specialized as other semiaquatic mammals. Water efficient locomotion and performance was ultimately a result of improved buoyancy by hydrophobic fur and subtle morphological specializations (tail fringe hairs, webbed hindfeet, more dorsally positioned eyes and nose), which allows *Nectomys* to perform more efficiently in water than the terrestrial *Cerradomys*, and at the same time being able of locomotion in the terrestrial environment.

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