

## POSTURAL BEHAVIOR OF THE SEMIAQUATIC *NECTOMYS* (RODENTIA, SIGMODONTINAE) IN SWIMMING BOUND

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### ABSTRACT

Oryzomyine rodents of *Nectomys* have a repertoire of swimming postural behaviors used in different ecological aspects of its life, affecting key tasks of their survival. These species present three swimming behaviors: bipedal surface swimming, quadruped symmetric submerged swimming, and swimming bound, with correspondent differences in performance. Here we describe and measure the postural behavior in the swimming bound of *Nectomys squamipes* and *N. rattus*. Rodents were filmed at 30 frames s<sup>-1</sup> in lateral view, swimming in a glass aquarium. Video sequences were analyzed dividing the swimming cycle into power and recovery phases. The two species did not differ in swimming behavior. Both species presented displacement of the head at vertical axis during impulsion, reaching its maximum displacement at the end of the phase. The power phase of the hindlimbs was primarily responsible for the animal propulsion. The flexion and extension of the head relative to the neck occurred in the impulsion and the recovery phase, respectively. During the hindlimbs power phase occurred the extension of the spine, raising the body of the animal above the water surface. The swimming bound allows a burst of speed and likely escape predation, hence involving specific postural behavior described here for the first time. These specific behaviors are related to morphological adaptations of spine, hindlimbs and feet, that allow spine extension and hindlimb thrust in an aquatic environment beyond the abilities of terrestrial rodents.

**Keywords:** forelimbs; hindlimbs; locomotion; spine extension; water rat.

### INTRODUCTION

Swimming in mammals evolved from primitive changes in the pattern of terrestrial quadruped locomotion with symmetrical movements (Gingerich 1994, Fish 1996b, Thewissen *et al.* 2009). The quadrupedal drag-based swimming on the surface would be the most primitive type of swimming in mammals, showing the same neuromotor pattern of terrestrial locomotion with diagonal gaits (trot, walking and running) (Williams 1983, 2001, Fish 1996b - but see Rivera *et al.* 2011). The bipedal swimming is a step in the transition to a more specialized form of swimming, where there is suppression of the activity of the forelimbs, leaving them available for other functions

as well as reducing interference between ipsolateral members (Fish 1996b, Santori *et al.* 2008). More derived swimming modes are those based on lift and body oscillation, as in cetaceans and pinnipeds, for example (Fish 1996b, Fish *et al.* 2008, Iosilevskii & Weihs 2008, Gleiss *et al.* 2011). The lift-based swimming mode probably evolved from asymmetric gaits such as the bound and half-bound of terrestrial mammals (Fish 1993, 1996b). In these types of terrestrial locomotion, impulsion occurs using both fore and hindlimbs, being enhanced by the spine flexion (Hildebrand 1987, Fish 1993a, 1993b, 1996a, Seckel & Janis 2008). Thus, aquatic mammals that swim through trunk oscillations use the same neuromotor pathways of terrestrial species, swimming by bound and half-bound.

Semiaquatic rodents are not as derived as aquatic rodents in the aquatic locomotion, using drag-based swimming by bipedal paddling like *Oryzomys palustris*, *Ondatra zibethicus*, and *Hydromys chrysogaster* (Esher *et al.* 1978, Fish 1984, 1992, 1993b, Fish & Baudinette 1999), or using the quadrupedal swimming mode as the capybara (*Hydrochoerus hydrochaeris*) (Dagg and Windsor 1972, Williams 1983, Renous 1994). The swimming behaviors and performance of the semiaquatic *Nectomys rattus* and *Nectomys squamipes* were previously described by Santori *et al.* (2008) and Santori *et al.* (2014), respectively. These species presented three swimming behaviors: bipedal surface swimming, swimming bound, and quadruped symmetric submerged swimming (Santori *et al.* 2008, 2014). In the swimming bound the locomotor cycle starts with forelimbs acting simultaneously to generate power, followed by dorsoventral vertebral column undulation, with most of thrust coming from the hindlimbs (Santori *et al.* 2008). Postural changes during the swimming bound were not yet analyzed. In this study, we analyze and describe the postural behavior of *N. rattus* and *N. squamipes* during the swimming bound.

## MATERIAL AND METHODS

We used only adults, fifteen individuals of *N. squamipes* (ten females and five males), and fourteen individuals of *N. rattus* (three females and eleven males), maintained at the Laboratory of Biology and Parasitology of Wild Reservoir Mammals (Fundação Oswaldo Cruz, Brazil). Procedures of the rodent breeding colony are detailed in D'Andrea *et al.* (1986). 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 x 34 x 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). Individuals of *N. squamipes* were from the Municipality of Sumidouro, Rio de Janeiro state, and *N. rattus* from the Municipality of Teresina de Goiás, Goiás state, Brazil. Mean  $\pm$  SD head-body length (mm) of the individuals used was  $195.2 \pm 10.2$  for *N.*

*squamipes*, and  $203.4 \pm 11.0$  for *N. rattus*.

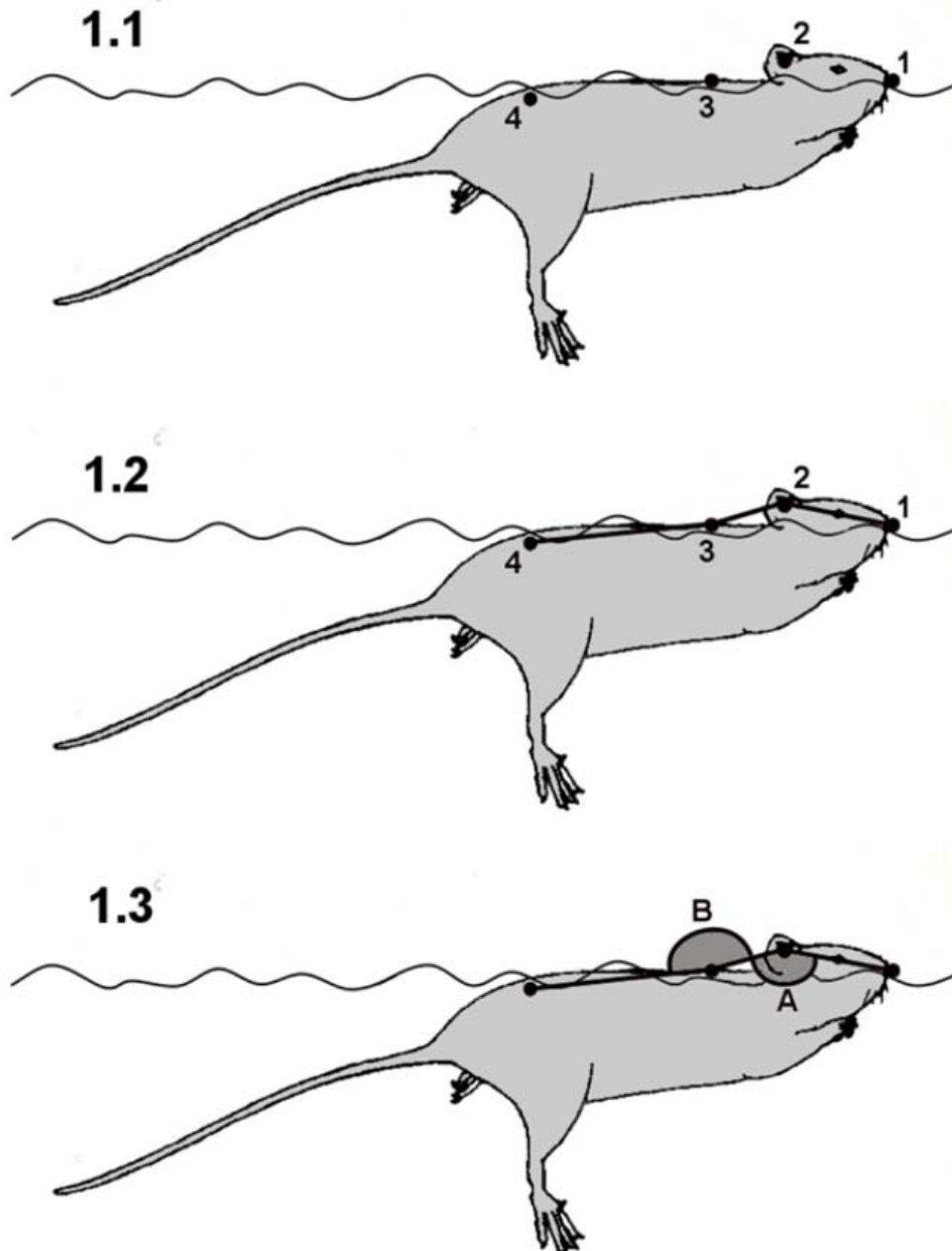
Methods of this study followed Santori *et al.* (2008, 2014). Rodents were filmed at 30 frames.s<sup>-1</sup> in lateral view, swimming in a 150 x 20 x 30 cm glass aquarium. The first 50 cm of the aquarium allowed rodents to accelerate. Rodent steady swimming was obtained by including in the camera field of vision only the region after the initial acceleration section of the aquarium. 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). Frame by frame image analysis was done at the Laboratório de Zoologia de Vertebrados – Tetrapoda (LAZOVERTE) (Universidade do Estado do Rio de Janeiro). Video sequences were analyzed with the software APAS (Ariel Performance Analysis System®, Ariel Dynamics, USA, California). 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 protracted (Fish 1993a, Santori *et al.* 2008, 2014).

We encouraged individuals to swim at their maximal speed by gently touching their back. 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, 2014).

To measure posture during swimming we marked four reference points and measure two angles on body of swimming rodents showed in the video sequences (Figure 1). Reference points were: (1) tip of the nose, (2) ear, (3) middle region of the spine near the shoulder girdle, and (4) spine near the pelvic girdle. Measured angles were (A) angle of head flexion and extension relative to the neck (variation in the angle formed by the lines determined by points 1, 2 and 3), and (B) angle of flexion and extension of the spine (variation of the angle formed by the lines determined by points 2, 3 and 4). As body parts move during

swimming, these points are also displaced producing changes in angles during a locomotor cycle. In APAS, these points were placed on a Cartesian coordinate

system calibrated by the reference grid digitalized with the image, allowing to calculate the position of these points during time intervals of locomotor cycle.

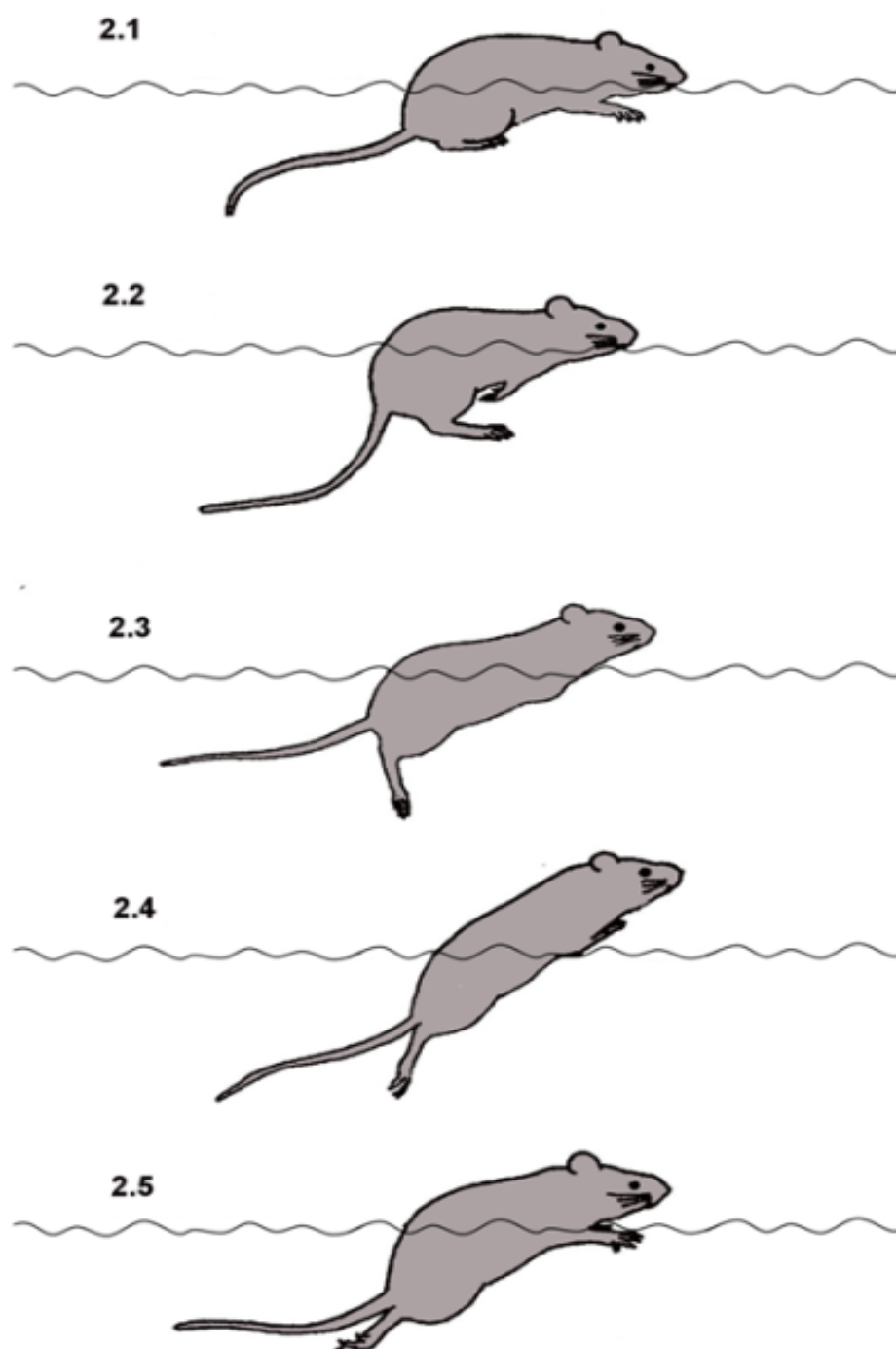


**Figure 1.** Landmarks and angles formed between them used to describe changes in posture during swimming. 1.1) Position of each landmark; 1.2) wireframe connecting landmarks; 1.3) angles analyzed during locomotor cycle.

## RESULTS

The swimming bound was performed by three individuals of *N. rattus* and one *N. squamipes* (Figure 2). During swimming by *Nectomys*, the transition between bipedal swimming to swimming bound passed

by the walking gait type. In this transition animals started using forelimbs, producing a short quadruped aquatic locomotion. The next step was the anticipation of forelimbs in simultaneous impulsion of forelimbs, followed by simultaneous impulsion of hindlimbs and oscillation of the spine (Figure 2).



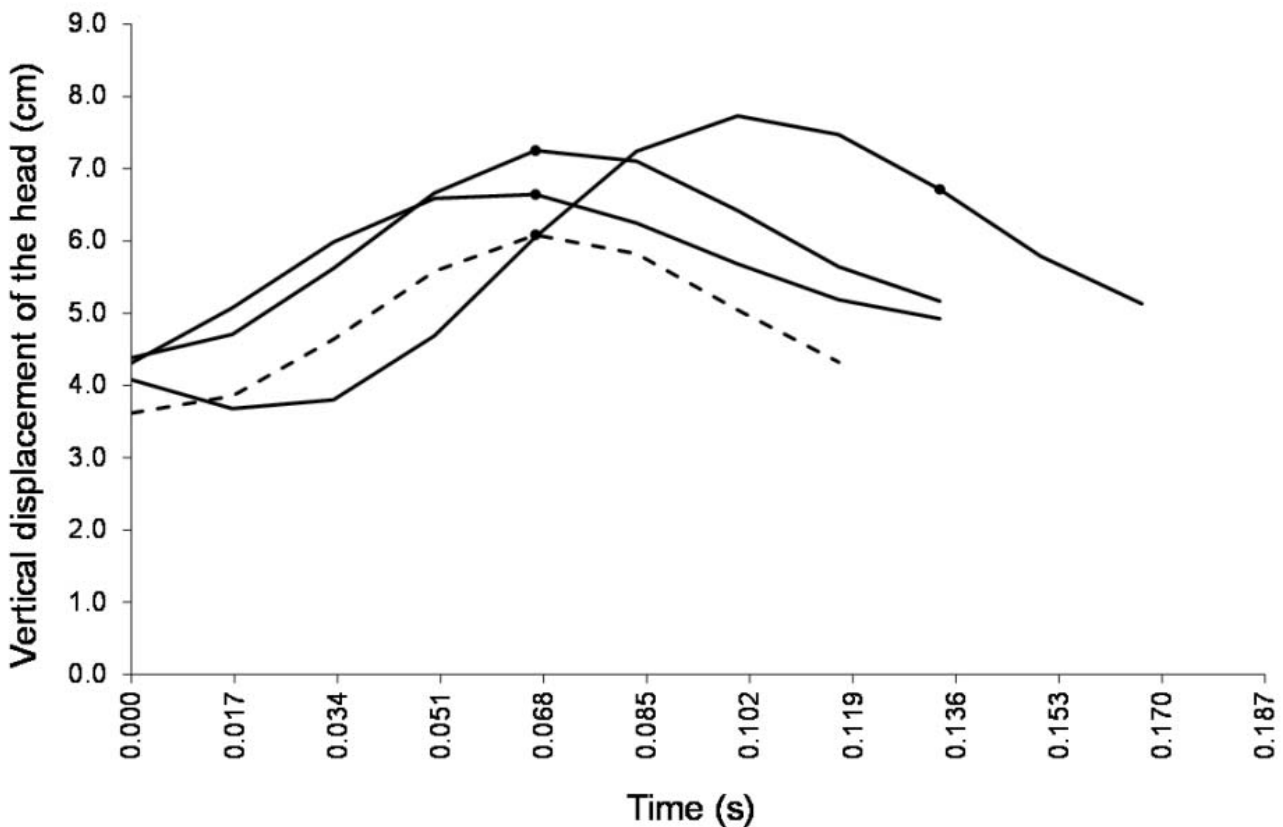
**Figure 2.** Locomotor posture of *Nectomys* on swimming bound. 2.1) Forelimb power phase begins; 2.2) forelimb power phase ends and hindlimbs power phase begins; 2.3) hindlimbs power phase in progress; 2.4) hindlimbs power phase ends 2.5) displacement concluded.

The two species presented the same general behavioral pattern in swimming bound, with subtle differences in posture between the only individual of *N. squamipes* and the group of three individuals of *N. rattus*. These differences in posture are shown by the values of the variables analyzed (Figures 3, 4 and 5). The

tendency of variation of these variables along the locomotor cycle was the same in the two species, but the values of the variables of *N. squamipes* were frequently lower than *N. rattus*. However, these comparisons do not have statistical power, since there is just one individual of *N. squamipes* and three *N. rattus*.

Both species presented vertical displacement of the head during impulsion, reaching its maximum displacement above water surface at the end of this phase (Figure 3). The end of the impulsion corresponded to the time of maximum elevation of the body above the water surface (Figure 3). Along the

recovery phase the head move back to a lower position on the vertical axis (Figure 3). The power phase of the forelimbs was faster and its effect on the elevation of the body was lower than the effect of the hindlimbs, which were primarily responsible for the animal propulsion.

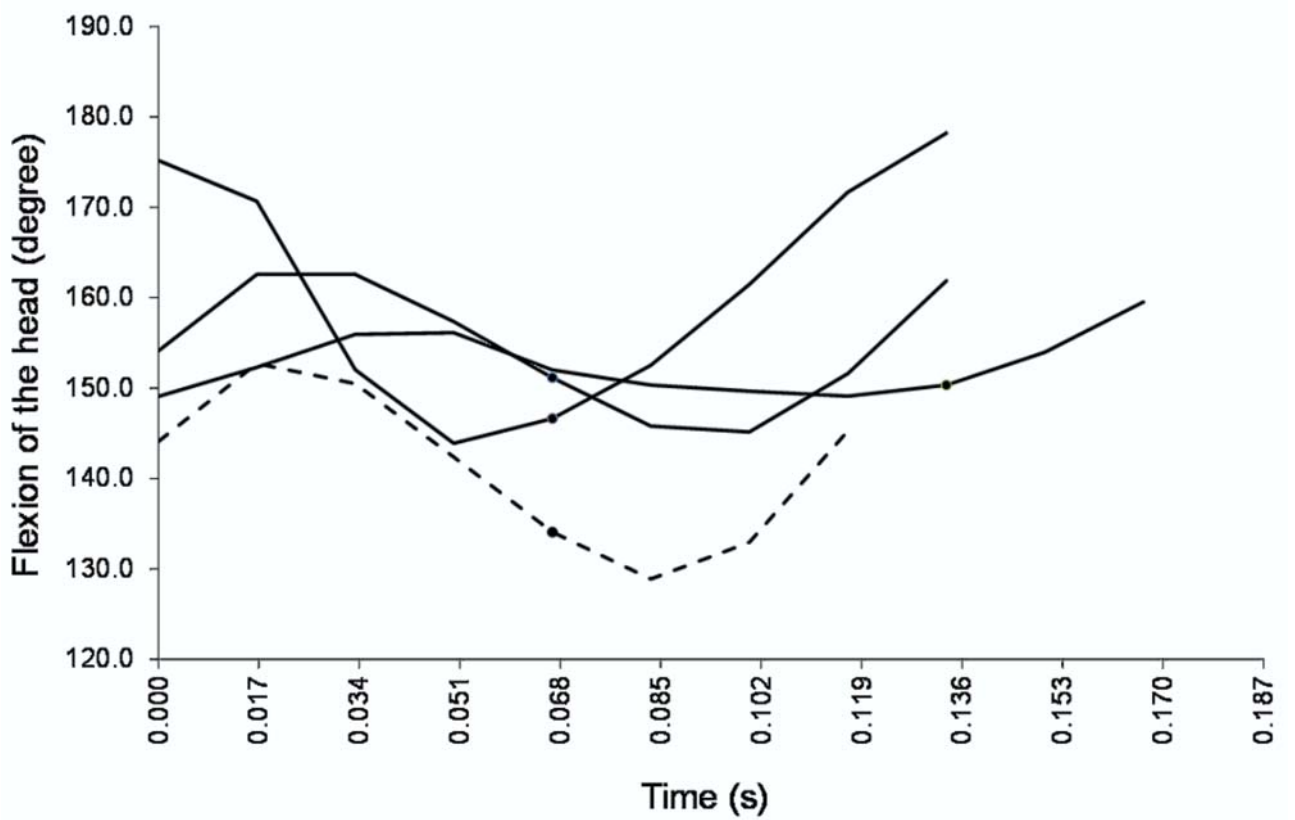


**Figure 3.** Vertical displacement of the head of *Nectomys* during swimming bound. *Nectomys rattus* = 3 (continuous line); *Nectomys squamipes* = 1 (dashed line). End of power phase marked with circles.

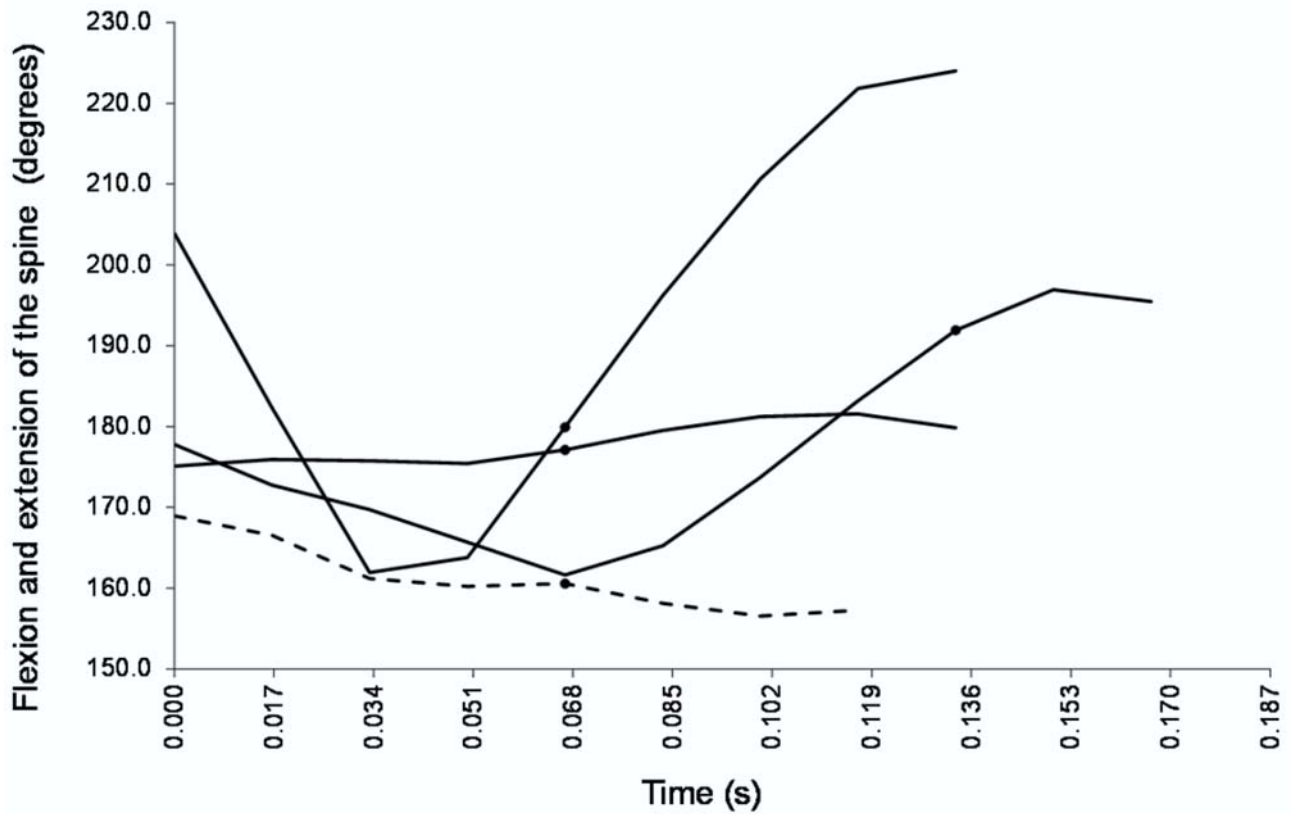
During impulsion occurred the flexion of the head relative to the neck, demonstrated by reducing angle A, which reached its minimum value at the end of this phase (Figure 4). In the recovery phase there was a progressive increase in angle A, with the extension of the neck (Figure 4).

During the first power phase, corresponding to the impulse generated by forelimbs, *N. rattus* showed a decrease in angle B by the flexion of the spine (Figure

5). During the second power phase, corresponding to the impulse generated by hindlimbs, angle B increased by the extension of the spine (Figure 5). The strong impulse of the hindlimbs raised the body of the animal above the water surface and this impulse was improved by the great extension of the spine extending during the recovery phase (Figure 5). Flexion and extension of spine in the individual of *N. squamipes* was lower than in *N. rattus* (Figure 5).



**Figure 4.** Flexion and extension of the head in relation to the neck in *Nectomys* during swimming bound. *Nectomys rattus* = 3 (continuous line); *Nectomys squamipes* = 1 (dashed line). End of power phase marked with circles.



**Figure 5.** Flexion and extension of the spine in *Nectomys* during swimming bound. *Nectomys rattus* = 3 (continuous line); *Nectomys squamipes* = 1 (dashed line). End of power phase marked with circles.

## DISCUSSION

As a general tendency, with a lesser degree in *N. squamipes*, both species showed a large capacity to flexion the spine in the swimming bound, caused by the position of fore and hindlimbs under the animal's trunk between the two power phases. The force generated by the limbs, along with the flexion of the spine, was responsible for the high velocities and body oscillation attained (Santori *et al.* 2008, 2014). Accordingly, in the model for evolution of aquatic locomotion proposed by Fish (1996b), body oscillation in asymmetrical terrestrial gaits (*e.g.*, gallop, jump) is one of the main traits in the transition to the more derived swimming gaits, used either by semiaquatic species such as otters (Fish 1994), or by aquatic species such as sea lions (Fish 1996b). As an asymmetric gait, each pair of limbs, fore or hindlimbs, provide support simultaneously to generate power (Rocha-Barbosa *et al.* 2005). Terrestrial mammals that use asymmetric gaits, such as the half-bound, have great spine flexibility associated with changes in the articular surface of the vertebrae (Walker Jr. and Liem 1994). In this context the swimming bound appears to be derived from the half-bound practiced by small terrestrial mammals (Renous 1994, Fish 1996a, 1996b). The main difference between swimming bound and terrestrial half-bound is in the timing of the forelimbs: in the half-bound the forelimbs do not generate power simultaneously, occurring the anticipation of the right forelimb as in terrestrial locomotion (Hildebrand 1987, Seckel & Janis 2008).

The spine flexibility demonstrated in the swimming bound by *Nectomys* is supported by the enlarged and laterally compressed height of the neural process of the atlas, the first cervical vertebra, compared to other Sigmodontinae rodents (Carrizo *et al.* 2014). This seems to be a common trait to all semiaquatic genera of rodents such as *Holochilus*, *Pseudoryzomys*, *Zygodontomys*, and *Scapteromys* (Carrizo *et al.* 2014). Therefore, these genera and semiaquatic rodents in general are likely to use the swimming bound as well. Other traits of the appendicular skeleton also differentiate semiaquatic rodents from arboreal, fossorial, and terrestrial rodents, mainly related to hindlimb bones and feet: a long

olecranon process, particularly large humeral epicondyles, and increased femoral epicondyle size (Samuels & Van Valkenburgh 2008), and external features of the feet (Rivas & Linares 2006, Rivas *et al.* 2010). The importance of hindlimbs and feet for an efficient bipedal swimming by semiaquatic rodents must be clearly involved, but hindlimbs are also important for the strong thrust necessary in the swimming bound. This thrust raises the body out of the water, and occurs during the second power phase, which is generated by the hindlimbs.

Forelimbs are almost not used in bipedal paddling, free to manipulate objects and help capture prey in the water as much as in land (Santori *et al.* 2008). Forelimbs participate in the swimming bound, but the main thrust is provided by the hindlimbs. Accordingly, forelimb morphology does not distinguish semiaquatic from other habits in rodents (Coutinho *et al.* 2013). Even their muscular anatomy in general is similar to other rodents, but tendon insertion may have specializations in semiaquatic rodents (Carrizo *et al.* 2014).

The swimming bound is part of the behavioral repertoire involved in aquatic locomotion by *Nectomys*, an adaptation of the half-bound used in terrestrial locomotion to swimming. Although used less frequently than bipedal paddling, it allows a burst of speed and likely escape predation (Santori *et al.* 2014), hence involving specific behavioral adaptations described here for the first time. These specific behaviors are related to morphological adaptations of spine that allows extension beyond the abilities of terrestrial rodents. The thrust of the body above the water surface also requires power generated by the hindlimbs, further explaining specific morphological adaptations of hindlimbs and feet of semiaquatic rodents.

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