

## POSTURAL CLIMBING BEHAVIOUR OF DIDELPHID MARSUPIALS: PARALLELS WITH PRIMATES

Vanina Zini Antunes <sup>1</sup>, Ana Cláudia Delciellos <sup>1</sup> & Marcus Vinícius Vieira <sup>1\*</sup>

<sup>1</sup>Universidade Federal do Rio de Janeiro (UFRJ), Instituto de Biologia, Departamento de Ecologia, Laboratório de Vertebrados. Ilha do Fundão, CP 68020, Rio de Janeiro, RJ, Brasil. CEP: 21941-902

E-mails: vanina.antunes@gmail.com, anadelciellos@yahoo.com.br, mvvieira@biologia.ufrj.br

### ABSTRACT

Differences in body size and in the use of arboreal strata limit the climbing behaviour and performance of didelphids. Similarly to primates, the arboreal canopy dweller, *Caluromys philander* exhibits a diagonal-sequence gait. In contrast, terrestrial didelphids use a symmetrical lateral sequence in horizontal locomotion. Postural behaviour along thin supports may allow understanding the mechanisms behind the higher performance of arboreal didelphids climbing. Here in, we describe and compare gait sequence and postural behaviour of seven didelphids climbing a slender and flexible vertical support. Animals were stimulated to climb a vertical support of 1.25 cm diameter. Postural behaviour was qualitatively described for each species in the cycle of maximum velocity by a frame-by-frame analysis of gait cycles, evaluating (1) movements of the tail, (2) posture of hand and wrist when grasping, (3) distance of the body to the support, (4) lateral swinging of the body, (5) orientation of the head, (6) limb posture, and (7) stride cycle. Only arboreal species were capable of climbing with only two limbs grasping the support, keeping a straight body orientation at some distance from the support, and sustaining a more constant and regular climbing velocity. The tail played a role in didelphids with better climbing performance (*i.e.*, higher relative velocity), counteracting the lateral swinging of the body, helping with the animal balance. However, the prehensile ability of the tail was not used in climbing. The most stunning result is that all didelphids grasped the rope between digits 2-3, a schizaxonic grasp, involving a neutral hand orientation regarding the ulna. The didelphids protracted the humerus at forelimb touchdown, and the angle between the arm and the horizontal body axis was greater than 90°. The same postures were already observed in horizontal locomotion of *C. philander*, *Monodelphis domestica*, and primates. Locomotory and postural adaptations for an arboreal lifestyle in didelphids seem to be limited to small to medium body sizes, up to the size of species of *Caluromys*. The arboreal locomotion of didelphids is an important key to understand adaptation and evolution of mammals to an arboreal niche, and the comparison with small primates may help to identify adaptive convergence to arboreal locomotion.

**Keywords:** climbing ability; gait; locomotion; opossums; zygodactylous grasp.

### INTRODUCTION

Didelphids are frequently described as scansorial based on the morphology of their postcranial skeleton (Szalay 1994, Argot 2003), occupying a variety of spatial niches and vertical strata in Neotropical forests (Charles-Dominique *et al.* 1981, Fonseca & Kierulff 1989, Julien-Laferrrière 1991, Passamani 1995, Cunha & Vieira 2002, Grelle 2003, Vieira & Monteiro-Filho 2003, Delciellos & Vieira 2006). There is a direct relationship between body mass and the use of arboreal strata (Charles-Dominique *et al.* 1981), and differences in body size alone limit the climbing behaviour and performance of didelphids (Vieira 1997, Delciellos & Vieira 2006, 2007, 2009a, 2009b). However, *Caluromys*

*philander* uses preferentially the canopy in spite of being more than twice the body size of *Marmosops incanus*, also arboreal but restricted to the understory (Julien-Laferrrière 1991, Cunha & Vieira 2002, Loretto & Vieira 2008, Dalloz *et al.* 2012).

Anatomical differences between didelphids suggest different levels of climbing specialisation, not necessarily related to differences in body size (Grand 1983, Vieira 1997, Lemelin 1999, Argot 2001, 2002, 2003, Vieira & Delciellos 2012). These morphological specialisations could be related to the use of supports of different diameters and inclinations, which vary according to the forest strata used (Cunha & Vieira 2002, Loretto & Vieira 2008). Also, resource partitioning can originate differential use of the vertical strata by didelphids (Charles-Dominique *et al.* 1981).

Thus, vertical strata used by didelphids differ in subtle manners, even among species considered arboreal.

Differences on postural behaviour in the arboreal locomotion of didelphids related to the use of the forest strata and morphological specialisations are not well known, except for *C. philander*, a terminal branch feeder with effective hallucal grasping frequently used as a model in studies on primates origins and evolution (Youlatos 2008). The repertory of postural behaviours of *C. philander* is complex, and was already studied in the field (Daloz *et al.* 2012) and in laboratory (Cartmill *et al.* 2002, Schmitt & Lemelin 2002, Youlatos 2008, 2010, Delciellos & Vieira 2009b). Similarly to many primate species, *C. philander* exhibits a diagonal-sequence gait (Cartmill *et al.* 2002, Schmitt & Lemelin 2002, Youlatos 2008, Daloz *et al.* 2012). In contrast, terrestrial didelphid marsupials of the genera *Didelphis* and *Monodelphis* use a symmetrical lateral sequence in horizontal locomotion on the ground, on trunks and branches (McManus 1970, Pridmore 1992). A diagonal sequence on the ground was used by *Didelphis virginiana* only when individuals started to run (McManus 1970). Information on postural behaviour along thin arboreal supports may allow understanding the mechanisms behind the higher performance of arboreal didelphids climbing thin supports (Delciellos & Vieira 2009a). However, such information is still lacking for most didelphids.

Here in, we describe and compare the gait

sequence and postural behaviour of seven species of didelphid marsupials climbing a slender and flexible vertical support. The species studied comprise the arboreal, semi-terrestrial and terrestrial lifestyles of didelphid marsupials.

## MATERIAL AND METHODS

### *Species of study*

We studied seven didelphid species that differ in their use of the forest strata (Table 1). Among the arboreal species, *Caluromys philander* (Linnaeus, 1758) lives mostly in the canopy, rarely descending to the ground; *Gracilinanus microtarsus* (Wagner, 1842) and *Marmosa paraguayana* (Tate, 1931) are captured from the understory to the canopy, occasionally on the ground; *Marmosops incanus* (Lund, 1840) uses mostly the ground and the understory, rarely reaching the canopy (Cunha & Vieira 2002, Grelle 2003, Vieira & Monteiro-Filho 2003, Loretto & Vieira 2008). Two species are semi-terrestrial, *Didelphis aurita* Wied-Neuwied, 1826, and *Philander frenatus* Olfers, 1818, and one is exclusively terrestrial and cursorial, *Metachirus nudicaudatus* (Desmarest, 1817) (Miles *et al.* 1981, Cunha & Vieira 2002). Semi-terrestrial species also differ in their occasional use of the vertical strata, *D. aurita* reaching the canopy whereas *P. frenatus* only the understory (Cunha & Vieira 2002). These seven species encompass most of the body size range of didelphid marsupials (Table 1).

**Table 1.** Body measurements (mean  $\pm$  SD) of individuals studied of didelphids species. Species are listed according to the vertical strata use by didelphids, from more arboreal species (*C. philander*) to the cursorial one (*M. nudicaudatus*).

Species	Sample Size (female/male)	Body mass (g)	Head-body length (mm)	Tail length (mm)
<i>Caluromys philander</i>	5 (3/2)	212.31 $\pm$ 56.84	202.40 $\pm$ 12.75	283.40 $\pm$ 11.43
<i>Gracilinanus microtarsus</i>	8 (3/5)	36.03 $\pm$ 8.11	111.88 $\pm$ 11.33	160.00 $\pm$ 10.18
<i>Marmosa paraguayana</i>	15 (8/7)	131.06 $\pm$ 26.87	168.53 $\pm$ 11.17	250.47 $\pm$ 15.03
<i>Marmosops incanus</i>	6 (4/2)	51.59 $\pm$ 6.42	125.83 $\pm$ 10.55	193.25 $\pm$ 17.60
<i>Didelphis aurita</i>	6 (1/5)	1265.70 $\pm$ 300.74	360.17 $\pm$ 41.75	356.50 $\pm$ 25.13
<i>Philander frenatus</i>	10 (3/7)	403.16 $\pm$ 154.82	254.00 $\pm$ 29.80	294.50 $\pm$ 30.15
<i>Metachirus nudicaudatus</i>	6 (2/4)	347.51 $\pm$ 92.50	241.17 $\pm$ 16.42	319.67 $\pm$ 15.20

Animals were captured in two areas of Atlantic Forest, in Serra dos Órgãos National Park (22°28'S, 42°59'W), municipality of Guapimirim, and in a fragmented landscape in the municipalities of Guapimirim and Cachoeiras de Macacu (22°21'-22°39'S, 42°40'-43°01'W), state of Rio de Janeiro, Brazil (IBAMA/MMA, process no. 02001, 004671/98-51). Animals captured in fragments were part of the small mammal surveys of the Project of Conservation and Use of Brazilian Biological Diversity (PROBIO/MMA/GEF), carried by the Laboratório de Vertebrados/Universidade Federal do Rio de Janeiro. Captured individuals were housed individually in polypropylene cages, and water and food were offered *ad libitum*.

#### *Experimental apparatus*

Climbing performance tests were developed in previous studies with didelphid marsupials (Vieira 1995, Delciellos & Vieira 2006, 2009a, Vieira & Delciellos 2012). The tests consisted of climbing a vertical nylon rope of 1.25 cm diameter, simulating vertical supports such as vines and lianas (Delciellos & Vieira 2009a). This diameter corresponds to the range observed for *M. incanus*, *D. aurita* and *P. frenatus* climbing vertical supports in the field (Cunha & Vieira 2002, Loretto & Vieira 2008). Only individuals with four functional molars were considered adults and tested (Macedo *et al.* 2006). Nursing females or females with pouch young and sick animals were not tested.

One end of the rope was passed through a pulley and left hanging free at one meter above the floor (Delciellos & Vieira 2009a). The remaining rope on the other side of the pulley was held by an observer. An animal was placed on the hanging end of the rope, head up, and encouraged to climb by proximity of an observer, touching the tail of the animal or producing sounds with a key ring if necessary (Delciellos & Vieira 2009a). Animals were kept climbing but within the visual field of a camcorder (National Television System Committee [NTSC] standard, 30 complete frames/s, shutter speed  $\frac{1}{4}$  0.01 s) by releasing rope from the other side of the pulley. The same individual repeated the performance test three times and in each trial it had at least 10 stride cycles recorded for the smaller

species. Individuals reached their maximum velocity in the beginning of the trial, around the third stride cycle. Animals that did not respond to these stimuli or did not climb were excluded. Animals were tested during the afternoon in normal daylight conditions because no difference was observed between diurnal and nocturnal tests (Vieira 1995, Delciellos & Vieira 2006, 2007, 2009a, 2009b). The floor was covered with 5-cm thick foam to prevent any injury to the animal in case of a fall (Delciellos & Vieira 2009a). The study was conducted following the guidelines of the American Society of Mammalogists (Gannon *et al.* 2007).

#### *Postural behaviour*

Postural behaviour was qualitatively described for each species in the cycle of maximum velocity by a frame-by-frame analysis of gait cycles, evaluating (1) movements of the tail, (2) posture of hand and wrist when grasping, (3) distance of the body to the support, (4) lateral swinging of the body, (5) orientation of the head, (6) limb posture, and (7) stride cycle. Lateral swinging was observed from a ventral view. The cycle of each limb was divided into power and recovery phases (Cartmill *et al.* 2002, Santori *et al.* 2005). At the power phase the limb contributes to the upward displacement of the animal, the hindlimb exerting a thrusting force, and the forelimb of the opposite side of the body exerting a traction force. The beginning of the power phase of a hindlimb marks the beginning and end of a stride cycle. At the recovery phase the limbs are in the air, returning to the previous position to start another cycle. When the power phase of a hindlimb started, the forelimb of the same side began its recovery phase. A gait diagram was used to analyse the sequence of limb movements and the duration of the contact of the each foot on the substrate (Hildebrand 1965).

## RESULTS

Arboreal species were faster than non-arboreal species, with the smaller *Gracilinanus microtarsus* reaching the highest velocity, followed by *Marmosa paraguayana*, *Marmosops incanus*, and *Caluromys philander* (Table 2). In non-arboreal species, *P.*

*frenatus* was the fastest, followed by *Metachirus nudicaudatus* and *D. aurita* (Table 2). The detailed analyses of measures of climbing performance can be found in Delciellos & Vieira (2009a).

**Table 2.** Measurements of performance of seven species of didelphids climbing a vertical support of 1.25 cm diameter. Relative stride length was the stride length of each individual divided by its head–body length, and relative velocity was the absolute stride frequency multiplied by relative stride length. Therefore, relative velocity is in units of body lengths covered by unit of time (bl/s), and relative stride length in units of body length (bl).

Species	Relative velocity (bl/s)	Frequency (strides/s)	Relative stride length (bl)
<i>Caluromys philander</i>	2.10 ± 0.61	2.73 ± 0.55	0.76 ± 0.12
<i>Gracilinanus microtarsus</i>	6.15 ± 2.18	6.72 ± 1.20	0.90 ± 0.21
<i>Marmosa paraguayana</i>	2.45 ± 0.87	2.92 ± 0.75	0.83 ± 0.13
<i>Marmosops incanus</i>	2.13 ± 1.19	3.05 ± 0.44	0.67 ± 0.29
<i>Didelphis aurita</i>	0.33 ± 0.12	1.06 ± 0.08	0.31 ± 0.09
<i>Philander frenatus</i>	1.35 ± 0.82	1.96 ± 0.73	0.64 ± 0.16
<i>Metachirus nudicaudatus</i>	0.48 ± 0.50	1.30 ± 0.76	0.31 ± 0.14

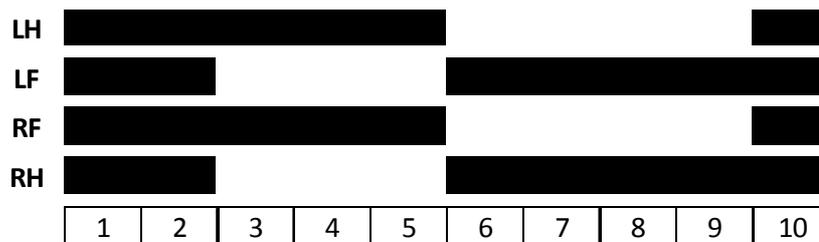
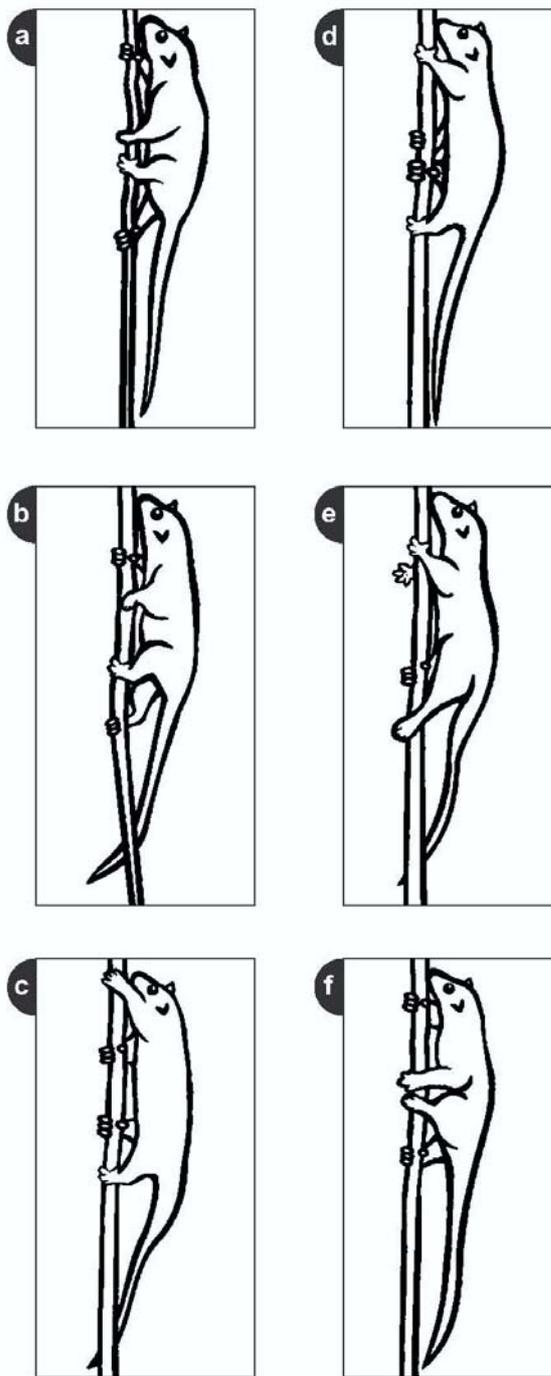
Arboreal species spent most of the stride cycle with only two limbs on the rope (Figures 1-4). However, between the recovery phases of opposite pairs of limbs, almost all species employed a quadrupedal support, at least at one frame, making a pause between the cycles (Figures 1, and 3-7), except *G. microtarsus* (Figure 2). More terrestrial species (*D. aurita*, *P. frenatus*, and *M. nudicaudatus*) stayed most of the stride cycle with three limbs on the support (Figures 5-7). Some individuals of *P. frenatus* at maximum velocity were able to spend most of the stride cycle with two limbs on the rope (Figure 6), similarly to arboreal species.

At the beginning of the power phase in terrestrial species the hindfoot was grasping the rope, but the hind limb was flexed (Figures 5-7a). In arboreal species, the hind foot also grasped the rope, but the hind limb was already protracted upwards (*i.e.*, limb greater than 90° relative to horizontal body axis), reaching a higher point on the rope near the forelimb of the same side (Figures 1-4a). In *D. aurita* and *P. frenatus*, the hindfoot did not reach the position of the forefoot at the end of the cycle, touching and grasping the support one or two centimetres below the forefoot (Figures 5h and 6f, respectively).

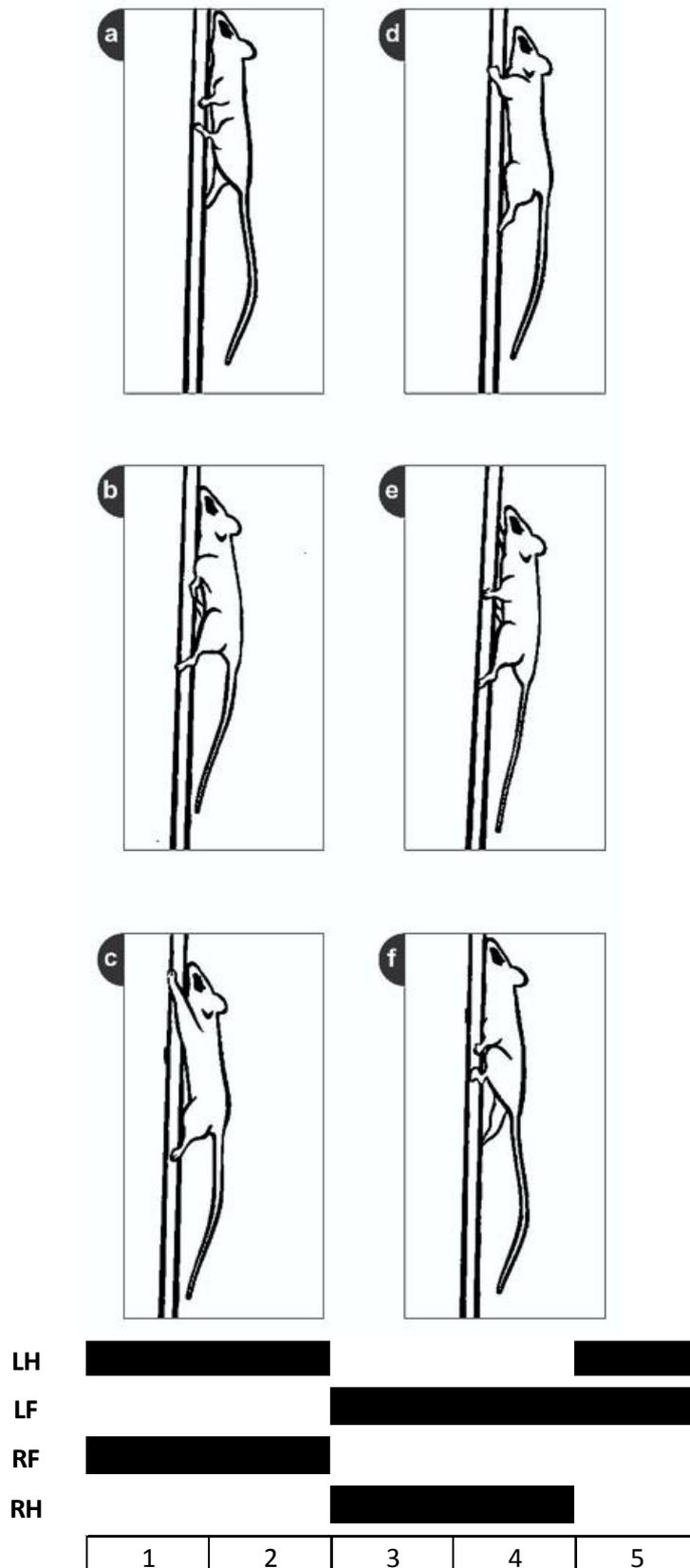
The traction action of a forelimb was synchronized with the thrusting action of the opposite hind limb as expected. At the beginning of the traction phase, the forelimb doing the traction was extended

because it had just reached the support (Figures 1d, 2-5c, and 6-7b). The flexors of the elbow joint pushed the body up, and brought the centre of gravity close to the support, flexing the forelimb. At the end of the traction phase the forelimb reached its maximum flexion, when the elbow was retracted (Figures 1f, 2e, 3f, 4e, 5h, and 6-7e). Individuals of *M. nudicaudatus* and *P. frenatus* were exceptions because they kept a retracted arm position in most of the cycle (Figures 6-7).

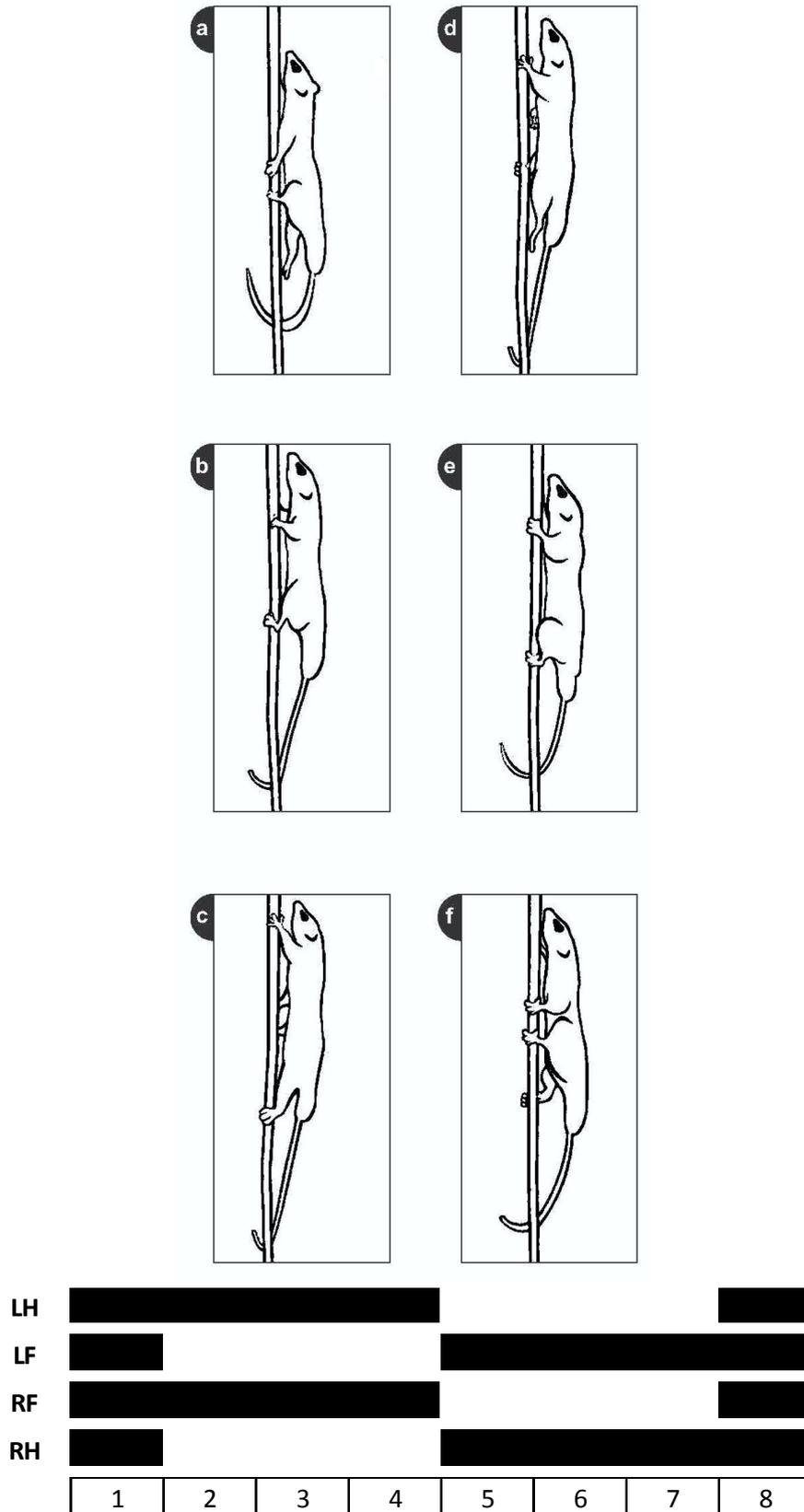
During the recovery phase of the forelimb the wrist was loose, with hand and fingers relaxed, dropping downwards (Figures 1-4b, 5e, and 6a). *Metachirus nudicaudatus* did not show this forelimb posture, and usually caught the air twice with the hands before successfully grasping the rope in a clumsy manner. As the forelimb protracted, it made an obtuse angle with the body, except in *M. nudicaudatus*, whose angle was acute. The arm protraction at the forelimb touchdown was higher in arboreal species. During the forelimb extension, the fingers and the thumb were stretched and abducted before grasping the rope (Figures 1e, 5f and 6d). At the end of the movement, when the hand touched the rope, it was near the snout (Figures 1-5c and 6b). Again, *M. nudicaudatus* was an exception because its hand did not extend so far, and gripped the rope at a point under the ear of the animal (Figure 7b).



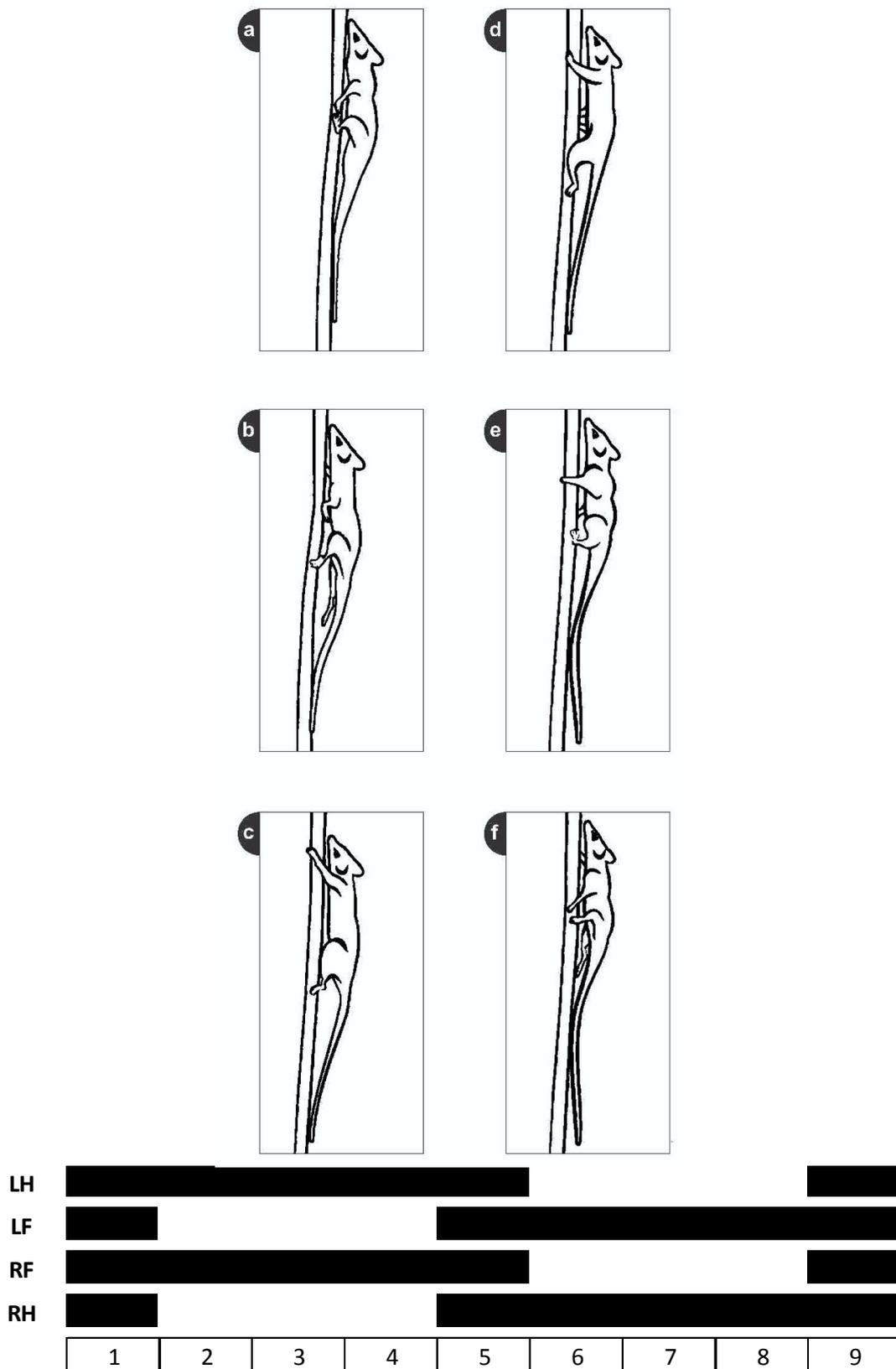
**Figure 1.** Sequence of limb movements and the duration of the contact of the each foot on a gait cycle of *Caluromys philander*. a) Touchdown of the left hindlimb (LH) and beginning of the power phase; b) Upward displacement of the left forelimb (LF) and of the right hindlimb (RH); c) Touchdown of the LF and RH; d) All limb grasping the support; e) Upward displacement of the right forelimb (RF) and LH and f) Touchdown of the LH and upward displacement of the LF and ending of the gait cycle.



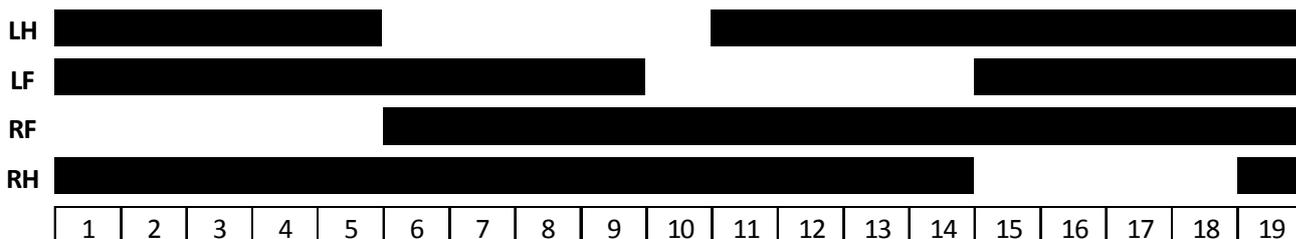
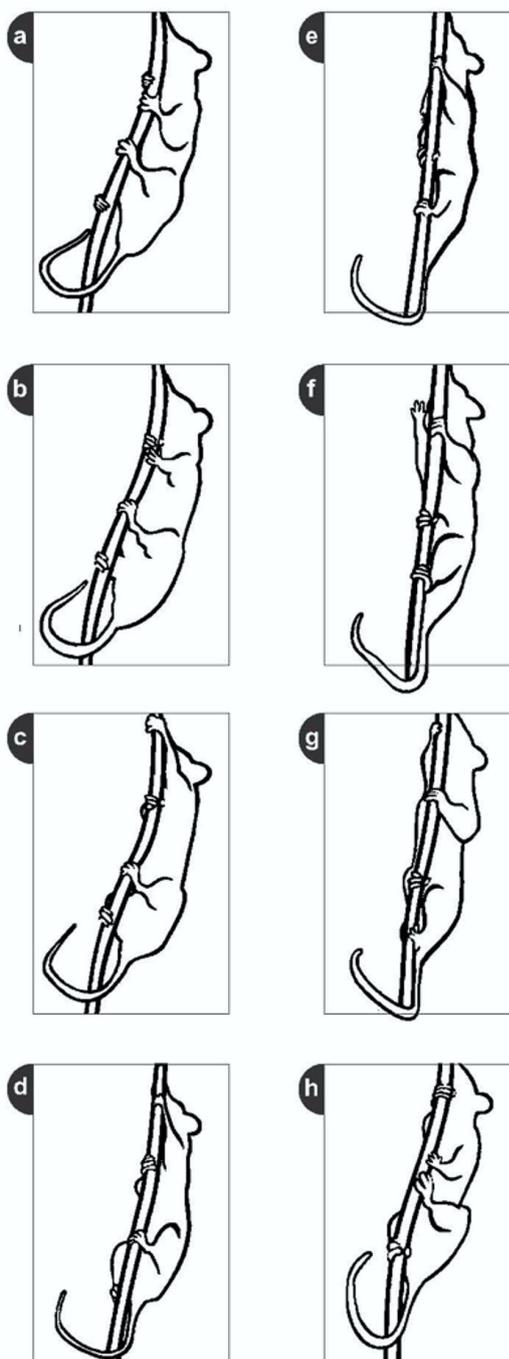
**Figure 2.** Sequence of limb movements and the duration of the contact of the each foot on a gait cycle of *Gracilinanus microtarsus*. a) Touchdown of the left hindlimb (LH) and beginning of the power phase; b) Upward displacement of the left forelimb (LF) and of the right hindlimb (RH); c) Touchdown of the LF and RH; d) All limb grasping the support; e) Upward displacement of the right forelimb (RF) and LH and f) Touchdown of the LH and upward displacement of the LF and ending of the gait cycle.



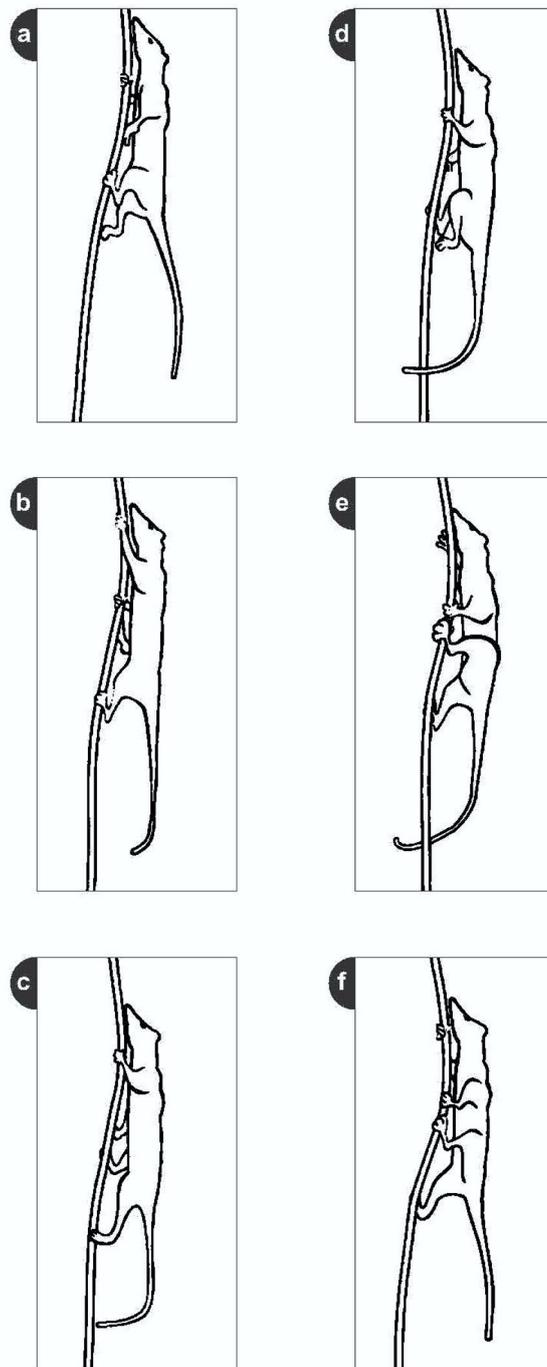
**Figure 3.** Sequence of limb movements and the duration of the contact of the each foot on a gait cycle of *Marmosa paraguayana* a) Touchdown of the left hindlimb (LH) and beginning of the power phase; b) Upward displacement of the left forelimb (LF) and of the right hindlimb (RH); c) Touchdown of the LF and RH; d) All limb grasping the support; e) Upward displacement of the right forelimb (RF) and LH and f) Touchdown of the LH and upward displacement of the LF and ending of the gait cycle.



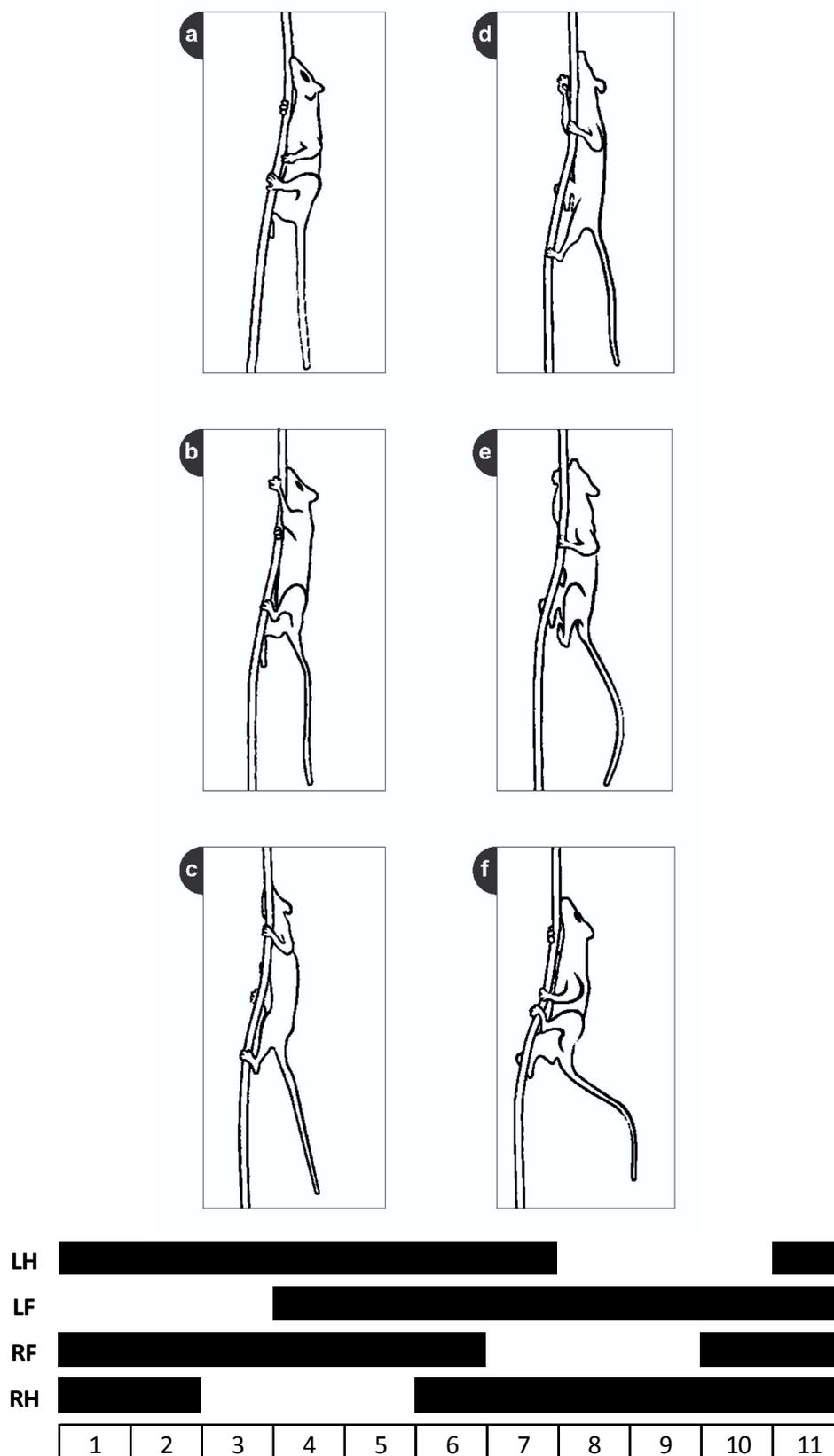
**Figure 4.** Sequence of limb movements and the duration of the contact of the each foot on a gait cycle of *Marmosops incanus*. a) Touchdown of the left hindlimb (LH) and beginning of the power phase; b) Upward displacement of the left forelimb (LF) and of the right hindlimb (RH); c) Touchdown of the LF and RH; d) All limb grasping the support; e) Upward displacement of the right forelimb (RF) and LH and f) Touchdown of the LH and upward displacement of the LF and ending of the gait cycle.



**Figure 5.** Sequence of limb movements and the duration of the contact of the each foot on a gait cycle of *Didelphis aurita*. a) Touchdown of the left hindlimb (LH) and beginning of the power phase; b) Upward displacement of the left forelimb (LF); c) All the limbs are grasping the support; d) Upward displacement of the right hindlimb (RH); e) End of RH grasping; f) Upward displacement of the right forelimb (RF); g) Upward displacement of the LH and h) Touchdown of the RH ending the gait cycle.



**Figure 6.** Sequence of limb movements and the duration of the contact of the each foot on a gait cycle of *Philander frenatus*. a) Touchdown of the left hindlimb (LH) and beginning of the power phase; b) Upward displacement of the left forelimb (LF) and of the right hindlimb (RH); c) Touchdown of the LF and RH; d) All limb grasping the support; e) Upward displacement of the right forelimb (RF) and LH and f) Touchdown of the LH and upward displacement of the LF and ending of the gait cycle.

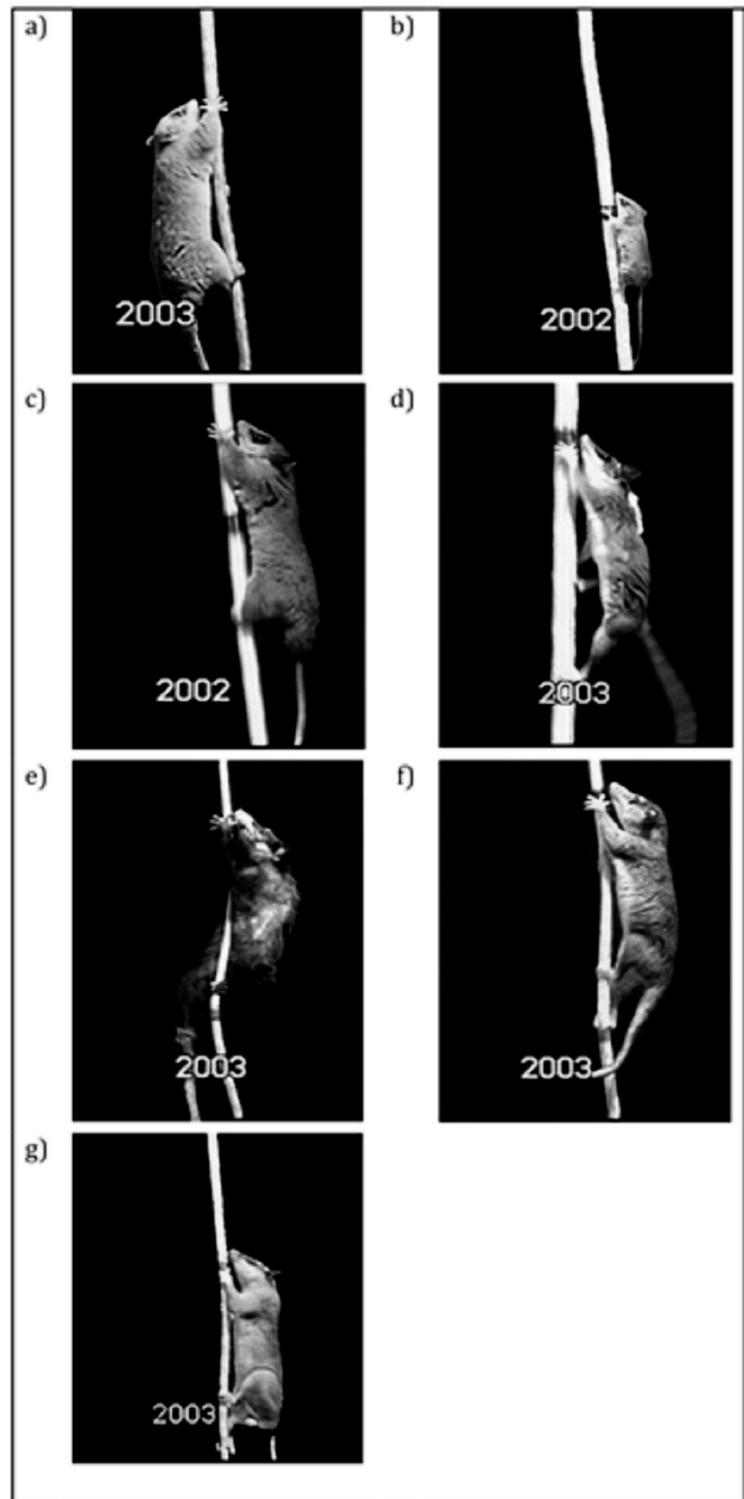


**Figure 7.** Sequence of limb movements and the duration of the contact of the each foot on a gait cycle of *Metachirus nudicaudatus*. a) Touchdown of the left hindlimb (LH) and beginning of the power phase; b) Upward displacement of the left forelimb (LF) and of the right hindlimb (RH); c) Touchdown of the LF and RH; d) All limb grasping the support; e) Upward displacement of the right forelimb (RF) and LH and f) Touchdown of the LH and upward displacement of the LF and ending of the gait cycle.

All species showed lateral oscillation of the body, which occurred at the end of the recovery phase of the hindlimb, as the animal bent its trunk to the opposite side of the hindlimb that was touching the rope. Arboreal species grasped the support more firmly and quickly than semi-terrestrial and terrestrial species. Arboreal species (Figures 1-4) and *P. frenatus* (Figure 6) kept their body always far from the rope, without touching it during the whole cycle. Conversely, *D. aurita* touched the rope with its chest and snout (Figure 5), and the whole body of *M. nudicaudatus* was always close or touching the rope with its elbows close to the body (Figure 7).

The head of all species pointed upward during the whole stride cycle with subtle oscillation to the opposite side of the forelimb that was stretched at the recovery phase (Figures 1-7). The tail was placed far from the rope, firmly stretched downward, but swinging laterally in most species (Figures 1-4 and 6). This lateral swinging of the tail was always in opposite direction to the lateral swinging of the body, reducing the net swinging effect on the vertical support. The exceptions were *D. aurita*, whose tail was motionless (Figure 5), and *M. nudicaudatus*, which made uncoordinated movements, occasionally curling its tail on the rope to help propulsion (Figure 7).

All species gripped the ropes with the hands between the second and third digits (Figure 8). When climbing slowly *M. nudicaudatus* uses telaxonic grasp, with the rope between 1(thumb) and 2(index) digits. The digits of larger didelphids were able to wrap around the rope, irrespective of their arboreal, semi-terrestrial and terrestrial lifestyle. As expected, the digits of smaller didelphids were unable to wrap the rope, but claws seem to play a more important role in the climbing of small didelphids.



**Figure 8.** Schizaxonic grasp observed in the seven didelphids species climbing a vertical support of 1.25 cm diameter. a) *Caluromys philander*; b) *Gracilinanus microtarsus*; c) *Marmosa paraguayana*; d) *Marmosops incanus*; e) *Didelphis aurita*; f) *Philander frenatus*; g) *Metachirus nudicaudatus*.

## DISCUSSION

Climbing ability is fundamental to the arboreal lifestyle of didelphids, allowing the exploration of different niches in the highly structured environment of the understory and canopy (Vieira & Monteiro-Filho 2003, Delciellos & Vieira 2006). On climbing a slender vertical support, didelphids studied differed in gait pattern and postural behaviour, but their sequence of limbs was mostly symmetrical. The symmetric sequence is considered to provide more stability, manoeuvrability, agility, and energy conservation on terrestrial locomotion (Hildebrand 1989), which seems to apply to arboreal walking on horizontal supports (Delciellos & Vieira 2007), and climbing as well.

Diagonal sequence of footfalls is characteristic of primate gaits, in contrast to lateral sequence of many ground dwelling mammals, supposed to improve stability moving on tree branches (Martin 1990). For didelphid marsupials, the use of diagonal sequence gaits moving on the ground or on horizontal supports simulating tree branches was previously described only for *Caluromys philander* (Schmitt & Lemelin 2002, Lemelin *et al.* 2003). At the frequency of 30 frames/s, the video speed did not allow enough resolution to determine the exact sequence of footfalls for arboreal species, as fore and hind limbs of opposite sides were always synchronized, simultaneously grasping the support or moving up in the air to grasp another point on the rope. However, only arboreal species were capable of climbing with only two limbs grasping the support, keeping a straight body orientation at some distance from the support, and sustaining a more constant and regular climbing velocity.

The tail played a role in didelphids with better climbing performance (*i.e.*, higher relative velocity), counteracting the lateral swinging of the body produced by the limb movements, helping with the animal balance. However, the prehensile ability of the tail was not used in climbing, with no grasping role during ascension. The tail is important for safety while foraging or feeding on slender branches, and to cross discontinuities in the canopy, hence to explore the fine-branch niche (Lemelin 1999, Delciellos & Vieira 2009b). Accordingly, *C. philander* uses its tail for grasping during locomotor manoeuvres such as bridging

and leaping (Youlatos 2008) and hindlimb suspension (Lemelin & Schmitt 2007), but keep the tail curly and close to the branch in slow arboreal locomotion (Daloz *et al.* 2012, Rupert *et al.* 2014). Also, *C. philander*, as other didelphids species, is capable of jumping to effectively cross discontinuities between supports without use the tail to grasp the support as a fifth member (Delciellos & Vieira 2009b).

The most stunning result of our study is that all didelphids grasped the rope between digits 2-3, a schizaxonic grasp, involving a neutral hand orientation regarding the ulna (Reghem *et al.* 2012). This postural behaviour had been previously observed only for *C. philander* (Youlatos 2010). It must be a common posture to all didelphids when climbing thin and slender supports, from smaller to larger species, arboreal, semiterrestrial and terrestrial didelphids, which also confirms the ancestral nature of this character as previously suggested by Cartmill (1974). The same hand posture was the most frequent observed in the grey mouse lemur (*Microcebus murinus*) climbing vertical supports and walking along horizontal supports (Reghem *et al.* 2012). Only when climbing larger supports (3 cm diameter), *M. murinus* used an ulnar deviated hand with grasp between digits 1-2 (Reghem *et al.* 2012). Ulnar deviation of the hand was related to the use of arboreal supports and not to morphology or primate infraorder affinity (Lemelin & Schmitt 1998). It is possible that the unspecialized neutral hand posture of didelphids may be the more common posture as in *M. murinus*, but other hand postures may be used depending on the relative diameter of the support as in *M. murinus*. Further studies will be taken on didelphids climbing vertical tick perches to verify if they change hand behaviour to ulnar deviation, using telaxonic grasp (1-2 digits) in these substrates.

The didelphid species studied protracted the arm (humerus) at forelimb touchdown, and the angle between the arm and the horizontal body axis was greater than 90°. The same postures were already observed in horizontal locomotion of two other didelphids, *C. philander* and *Monodelphis domestica*, and of primates (Lemelin & Schmitt 2007). Conversely, most nonprimate mammals have a retracted arm position at touchdown, *i.e.*, the arm lies behind a vertical line going through the glenohumeral

joint (*i.e.*, angle between the arm and the horizontal body axis is less than 90°) (Larson 1998, Larson *et al.* 2000, 2001). The only truly cursorial didelphid species (*i.e.*, morphologically specialized for more efficient locomotion on the ground) is *M. nudicaudatus*, which showed the same arm posture of nonprimate mammals. This suggests that the ability to protract the arm at forelimb touchdown in arboreal climbing is a general adaptation to arboreal locomotion, common to most didelphid marsupials and primates.

In spite of its scansorial adaptations (Szalay 1994, Argot 2003) and habits (Vieira 1997, Cunha & Vieira 2002), *D. aurita* climbed slowly and in a methodical manner, similarly to *D. virginiana* moving through the understory (McManus 1970). This behaviour is probably related to its large body mass, because climbing is energetically more expensive for larger animals of a geometrically similar body build (Cartmill 1974). Therefore, the locomotory and postural adaptations for an arboreal lifestyle in didelphid marsupials seem to be limited to small to medium body sizes, up to the size of species of *Caluromys* (ca. 250g). The gradual increase in body size through the evolutionary history of the group (Amador & Giannini 2016) may have imposed limits to efficient climbing in arboreal locomotion.

The arboreal locomotion of didelphid marsupials is an important key to understand adaptation and evolution of mammals to an arboreal niche, and the comparison with small primates may help to identify adaptive convergence to arboreal locomotion (Lemelin & Schmitt 2007). The present study provides the first comprehensive comparison of climbing postural behaviour among arboreal and terrestrial didelphid species. Previous comparisons between didelphids and primates were limited to one arboreal (*C. philander*) and one terrestrial species (*M. domestica*). Arboreal didelphid marsupials are the only nonprimate mammals exhibiting diagonal couplets climbing slender supports, allowed by a protracted arm, but a neutral hand posture. These are examples of convergent locomotory adaptations to an arboreal locomotion.

## ACKNOWLEDGMENTS

We thank to all students and staff of the Laboratório de Vertebrados ó Universidade Federal do Rio de Janeiro for the

invaluable assistance in the fieldwork and in the performance tests, especially Nélio P. Barros. Climbing animals were kindly portrayed by Ricardo Brito. Boris Ríos-Uzeda for the assistance with Figure 8. Trapping and handling conformed to guidelines sanctioned by the American Society of Mammalogists. This study was approved by the IBAMA/MMA (Proc. no. 02001, 004671/98-51), and supported by grants from Conselho Nacional de Pesquisa e Desenvolvimento-CNPq and Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro-FAPERJ to Marcus V. Vieira. Ana C. Delciellos was supported by scholarships from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior-CAPEs, CAPEs/FAPERJ (PAPD- E-26/202.144/2015), and CNPq (Programa de Pesquisa em Biodiversidade-PPBio).

## REFERENCES

- Amador, L. I., & Giannini, N. P. 2016. Phylogeny and evolution of body mass in didelphid marsupials (Marsupialia: Didelphimorphia: Didelphidae). *Organisms Diversity & Evolution*, 16:17. DOI: 10.1007/s13127-015-0259-x
- Argot, C. 2001. Functional-adaptive anatomy of the forelimb in the Didelphidae, and the paleobiology of the Paleocene marsupials *Mayulestesferox* and *Pucadelphys andinus*. *Journal of Morphology*, 247(1), 51679. DOI: 10.1002/1097-4687(200101)247:1<51::AID-JMOR1003>3.0.CO;2-#
- Argot, C. 2002. Functional-adaptive analysis of the hindlimb anatomy of extant marsupials and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. *Journal of Morphology*, 253(1), 766108. DOI: 10.1002/jmor.1114
- Argot, C. 2003. Functional-adaptive anatomy of the axial skeleton of some extant marsupials and the Paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. *Journal of Morphology*, 255(3), 2796300. DOI: 10.1002/jmor.10062
- Cartmill, M. 1974. Pads and claws in arboreal locomotion. In: F. A. Jenkins Jr. (Ed.), *Primate locomotion*. pp. 45683. New York: Academic Press.
- Cartmill, M., Lemelin, P., & Schmitt, D. 2002. Support polygons and symmetrical gaits in mammals. *Zoological Journal of the Linnean Society*, 136(3), 4016420. DOI: 10.1046/j.1096-3642.2002.00038.x
- Charles-Dominique, P., Atramentowicz, M., Charles-Dominique, M., Gérard, H., Hladik, A., Hladik, C. M., & Prévost, M. F. 1981. Les mammifères frugivores arboricoles nocturnes d'une forêt guyanaise: inter-relations plantes-animaux. *Revue d'Écologie (La Terre et la Vie)*, 35(3), 3416435.
- Cunha, A. A., & Vieira, M. V. 2002. Support diameter, incline, and vertical movements of four didelphid marsupials in the Atlantic Forest of Brazil. *Journal of Zoology*, 258(04), 4196426. DOI: 10.1017/S0952836902001565
- Daloz, M. F., Loretto, D., Papi, B., Cobra, P., & Vieira, M. V. 2012. Positional behaviour and tail use by the bare-tailed woolly opossum *Caluromys philander* (Didelphimorphia, Didelphidae). *Mammalian Biology*, 77(5), 3076313. DOI: 10.1016/j.mambio.2012.03.001
- Delciellos, A. C., & Vieira, M. V. 2006. Arboreal walking performance in seven didelphid marsupials as an aspect of

- their fundamental niche. *Austral Ecology*, 31(4), 4496457. DOI: 10.1111/j.1442-9993.2006.01604.x
- Delciellos, A. C., & Vieira, M. V. 2007. Stride lengths and frequencies of arboreal walking in seven species of didelphid marsupials. *Acta Theriologica*, 52(1), 1016111. DOI: 10.1007/BF03194205
- Delciellos, A. C., & Vieira, M. V. 2009a. Allometric, phylogenetic, and adaptive components of climbing performance in seven species of didelphid marsupials. *Journal of Mammalogy*, 90(1), 1046113. DOI: 10.1644/07-MAMM-A-115.1
- Delciellos, A. C., & Vieira, M. V. 2009b. Jumping ability in the arboreal locomotion of didelphid marsupials. *Mastozoología Neotropical*, 16(2), 2996307.
- Fonseca, G. A. B., & Kierulff, M. C. M. 1989. Biology and natural history of Brazilian Atlantic forest small mammals. *Bulletin of Florida State Museum Biological Sciences*, 34(3), 996152.
- Gannon, W. L., Sikes, R. S., & The Animal Care and Use Committee of The American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, 88(3), 8096823. DOI: 10.1644/06-MAMM-F-185R1.1 809-823
- Grand, T. I. 1983. Body weight: its relationship to tissue composition, segmental distribution of mass, and motor function III. The Didelphidae of French Guyana. *Australian Journal of Zoology*, 31(3), 2996312. DOI: 10.1071/ZO9830299
- Grelle, C. E. V. 2003. Forest structure and vertical stratification of small mammals in a secondary Atlantic Forest, southeastern Brazil. *Studies on Neotropical Fauna and Environment*, 38(2), 81685. DOI: 10.1076/snfe.38.2.81.15926
- Hildebrand, M. 1965. Symmetrical gaits of horses. *Science*, 150(3697), 7016708. DOI: 10.1126/science.150.3697.701
- Hildebrand, M. 1989. The quadrupedal gaits of vertebrates. *BioScience*, 39(11), 7666775. DOI: 10.2307/1311182
- Julien-Laferrrière, D. 1991. Organisation du peuplement de marsupiaux en Guyane Française. *Revue d'écologie (La Terre et la Vie)*, 46(2), 1256144.
- Larson, S. G. 1998. Unique aspects of quadrupedal locomotion in nonhuman primates. In: E. Strasser, J. G. Fleagle, A. L. Rosenberger, & H. M. McHenry (Eds.), *Primate Locomotion - Recent Advances*. pp. 1576173. New York: Springer.
- Larson, S. G., Schmitt, D., Lemelin, P., & Hamrick, M. 2000. Uniqueness of primate forelimb posture during quadrupedal locomotion. *American Journal of Physical Anthropology*, 112(1), 876101. DOI: 10.1002/(SICI)1096-8644(200005)112:1<87::AID-AJPA9>3.0.CO;2-B
- Larson, S. G., Schmitt, D., Lemelin, P., & Hamrick, M. 2001. Limb excursion during quadrupedal walking: how do primates compare to other mammals? *Journal of Zoology*, 255(3), 3536365. DOI: 10.1017/S0952836901001455
- Lemelin, P., & Schmitt, D. 1998. The relation between hand morphology and quadrupedalism in primates. *American Journal of Physical Anthropology*, 105(2), 1856197. DOI: 10.1002/(SICI)1096-8644(199802)105:2<185::AID-AJPA6>3.0.CO;2-U
- Lemelin, P. 1999. Morphological correlates of substrate use in didelphid marsupials: implications for primates origins. *Journal of Zoology*, 247(2), 1656175. DOI: 10.1111/j.1469-7998.1999.tb00980.x
- Lemelin, P., Schmitt, D., & Cartmill, M. 2003. Footfall patterns and interlimb co ordination in opossums (Family Didelphidae): evidence for the evolution of diagonal sequence walking gaits in primates. *Journal of Zoology*, 260(4), 4236429. DOI: 10.1017/S0952836903003856
- Lemelin, P., & Schmitt, D. 2007. Origins of grasping and locomotor adaptations in primates: comparative and experimental approaches using an opossum model. In: M. J. Ravosa & M. Dagosto (Eds.), *Primate origins: Adaptations and evolution*. pp. 3296380. New York: Springer.
- Loretto, D., & Vieira, M. V. 2008. Use of space by the marsupial *Marmosops incanus* (Didelphimorphia, Didelphidae) in the Atlantic Forest, Brazil. *Mammalian Biology*, 73(4), 2556261. DOI: 10.1016/j.mambio.2007.11.015
- Macedo, J., Loretto, D., Vieira, M. V., & Cerqueira, R. 2006. Classes de desenvolvimento em marsupiais: um método para animais vivos. *Mastozoología Neotropical*, 13(1), 1336136.
- Martin, R. D. (Ed.). 1990. *Primate Origins and Evolution: A Phylogenetic Reconstruction*. London: Chapman and Hall: p. 804.
- McManus, J. J. 1970. Behavior of captive opossums, *Didelphis marsupialis virginiana*. *The American Midland Naturalist*, 84(1), 1446169. DOI: 10.2307/2423733
- Miles, M. A., Souza, A. A., & Póvoa, M. M. 1981. Mammal tracking and nest location in Brazilian forest with an improved spool-and-line device. *Journal of Zoology*, 195(3), 3316347. DOI: 10.1111/j.1469-7998.1981.tb03469.x
- Passamani, M. 1995. Vertical stratification of small mammals in Atlantic hill forest. *Mammalia*, 59(2), 2766279.
- Pridmore, P. A. 1992. Trunk movements during locomotion in the marsupial *Monodelphis domestica* (Didelphidae). *Journal of Morphology*, 211(2), 1376146. DOI: 10.1002/jmor.1052110203
- Reghem, E., Byron, C., Bels, V., & Pouydebat, E. 2012. Hand posture in the grey mouse lemur during arboreal locomotion on narrow branches. *Journal of Zoology*, 288(1), 76681. DOI: 10.1111/j.1469-7998.2012.00926.x
- Rupert, J. E., Schmidt, E. C., Moreira Soto, A., Herrera, B. R., Vandeberg, J. L., & Butcher, M. T. 2014. Myosin isoform expression in the prehensile tails of didelphid marsupials: functional differences between arboreal and terrestrial opossums. *The Anatomical Record*, 297(8), 136461376. DOI: 10.1002/ar.22948
- Santori, R. T., Rocha-Barbosa, Vieira, M. V., Magnan-Neto, J. A., & Loguercio, M. F. C. 2005. Locomotion in aquatic, terrestrial and arboreal habitat of thick-tailed opossum, *Lutreolina crassicaudata* (Desmarest, 1804). *Journal of Mammalogy*, 86(5), 9026908. DOI: 10.1644/1545-1542(2005)86[902:LIATAA]2.0.CO;2
- Schmitt, D., & Lemelin, P. 2002. Origins of primate locomotion: gait mechanics of the woolly opossum. *American Journal of Physical Anthropology*, 118(3), 2316238. DOI: 10.1002/ajpa.10048
- Szalay, F. S. (Ed.). 1994. *Evolutionary history of the marsupial and an analysis of osteological characters*. Cambridge: Cambridge University Press: p. 481.

- Vieira, E. M., & Monteiro-Filho, E. L. A. 2003. Vertical stratification of small mammals in the Atlantic rain forest of south-eastern Brazil. *Journal of Tropical Ecology*, 19(05), 5016507. DOI: 10.1017/S0266467403003559
- Vieira, M. V. 1995. Ecomorphology of two neotropical marsupials: body size, form, climbing and walking the tight rope. Department of Systematics and Ecology, University of Kansas. p. 102.
- Vieira, M. V. 1997. Body size and form in two Neotropical marsupials, *Didelphis aurita* and *Philander frenata* (Marsupialia, Didelphidae). *Mammalia*, 61(2), 2456254. DOI: 10.1515/mamm.1997.61.2.245
- Vieira, M. V., & Delciellos, A. C. 2012. Locomoção, morfologia e uso do habitat em marsupiais neotropicais: uma abordagem ecomorfológica. In: N. C. Cáceres (Ed.), *Os Marsupiais do Brasil: biologia, ecologia e conservação*. pp. 3656384. Campo Grande: Editora UFMS.
- Youlatos, D. 2008. Hallucal grasping behavior in *Caluromys* (Didelphimorphia: Didelphidae): implications for primate pedal grasping. *Journal of Human Evolution*, 55(6), 10966 1101. DOI: 10.1016/j.jhevol.2008.03.009
- Youlatos, D. 2010. Use of zygodactylous grasp by *Caluromys philander* (Didelphimorphia: Didelphidae). *Mammalian Biology*, 75(6), 4756481. DOI: 10.1016/j.mambio.2009.10.004

Submitted: 06 July 2016  
Accepted: 09 August 2016