

## LOCOMOTION IN AQUATIC, TERRESTRIAL, AND ARBOREAL HABITAT OF THICK-TAILED OPOSSUM, *LUTREOLINA CRASSICAUDATA* (DESMAREST, 1804)

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The reasons *Lutreolina crassicaudata* is always captured in close proximity to water are not clear. We investigated locomotory behavior and performance in swimming, running, climbing, and jumping of *L. crassicaudata*. One adult male was videotaped in the laboratory while swimming, walking on the ground and on a horizontal tube 1.2 m from the ground, climbing a tree trunk angled 45°, and jumping gaps between supports. The locomotor cycles in these different activities were described by speed, stride length, stroke or stride frequency, time of power and recovery phases or stance and swing phases, and by displacement of points on the animal. *L. crassicaudata* employed a quadruped paddling gait in swimming. Swimming speed was similar to that of terrestrial didelphids, but stroke frequency and buoyancy ability were more similar to those of the water opossum. Different gaits were used for locomotion in each habitat type and we conclude that *L. crassicaudata* cannot be considered a specialized species for aquatic locomotion.

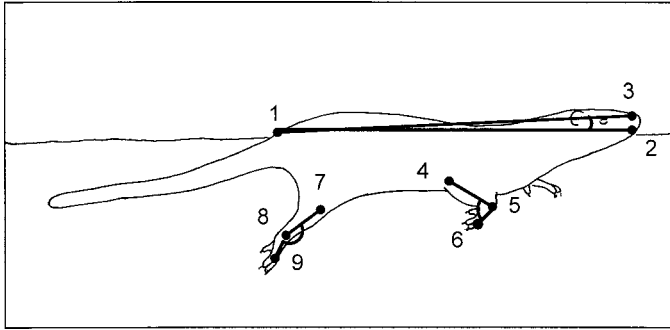
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The thick-tailed opossum, *Lutreolina crassicaudata* (Desmarest, 1804), has a wide distribution, occurring in Brazil, northern Argentina, Paraguay, Uruguay, and part of Bolivia, and in a disjunct area in northern South America encompassing Colombia, Venezuela, and Guyana (Eisenberg and Redford 1999; Emmons and Feer 1990; Graipel et al. 1996; Marshall 1978; Monteiro-Filho and Dias 1990). However, information on the overall biology of *L. crassicaudata* is scarce. In the state of Rio de Janeiro, Brazil, this species is registered on the list of locally endangered species (Bergallo et al. 2000), and is rarely seen in local mammal catalogues. *L. crassicaudata* is the most carnivorous species in the family Didelphidae, preferentially eating animal items but also consuming fruit (Astúa de Moraes et al.

2003; Cáceres et al. 2002; Marshall 1978; Monteiro-Filho and Dias 1990). It occurs in close proximity to water bodies and associated flooded areas (Monteiro-Filho and Dias 1990), but the reason for this habitat preference is still puzzling (Davis 1966). *L. crassicaudata* is frequently considered to be semiaquatic (Marshall 1978; Stein 1989), but some consider it to be terrestrial (Lee and Cockburn 1987). According to Marshall (1978), it is capable of swimming and diving with ease. More information on its locomotory behavior could illuminate reasons for its association with semiaquatic habits or preference for wet habitats.

Didelphids are good swimmers (Hunsaker and Shupe 1977). The most extensive study on didelphid swimming (Fish 1993) compared the Virginia opossum, *Didelphis virginiana*, and the water opossum, *Chironectes minimus*. Other observations on swimming included didelphids such as *D. virginiana* (Doutt 1954), *D. marsupialis* (Wilber and Weidenbacher 1961), *C. minimus*, and *L. crassicaudata* (Davis 1966). Swimming behavior of terrestrial and arboreal didelphids also was observed by one of us in laboratory (R. T. Santori) for *Metachirus*

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**FIG. 1.**—Points of reference on body of *Lutreolina crassicaudata*, with points chosen to analyze displacement of the nose, body inclination, and variation in the angles formed by the manus and radius-ulna and the metatarsus and tibia-fibula during the locomotor cycle. (Numbered points described in the text.)

*nudicaudatus*, *Philander frenatus*, *Didelphis albiventris*, and *Didelphis aurita*. Members of the genus *Marmosa* and *Monodelphis domestica* also are able to swim (Hunsaker and Shupe 1977; Kimble 1997). Because of its elongated body, primarily carnivorous food habits, and short legs, *L. crassicaudata* is considered a weasel-like species, sometimes is called the mink-opossum, and resembles a mustelid (Davis 1966; Lee and Cockburn 1987; Nowak 1991; Stein 1989).

In this study, we investigated locomotory behavior and performance in swimming, running, climbing, and jumping of *L. crassicaudata*. We also compared *L. crassicaudata* with semiaquatic and terrestrial didelphids, and with mustelid species in order to understand the locomotory habits of this marsupial.

## MATERIALS AND METHODS

Several locomotory sequences of 1 adult male (head-body length 308 mm, tail length 290 mm, mass 860 g) of *L. crassicaudata* were studied. The opossum was captured in Américo Brasiliense, São Paulo State, Brazil, by using a Tomahawk live trap (Tomahawk Live Trap Co., Tomahawk, Wisconsin) and was maintained in a 10 × 10-m outdoor enclosure on a diet of fruit, meat, and dog food. A swimming pond was available in the enclosure, along with shrubs, a wooden framework where the opossum could climb to exercise, and nesting boxes where it could find shelter. To avoid animal suffering, our procedures followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

**Swimming.**—The animal was videotaped in lateral view at 30 frames/s when swimming in a 1.5 × 0.2 × 0.3-m aquarium in lateral view. Mean water temperature was 25°C. A 50-cm scale was placed along the back wall of the aquarium as a reference frame for the distances traveled. Video sequences taken were digitized by using a videocassette recorder connected to a computer with APAS software (Ariel Performance Analysis System, Trabuco Canyon, California) at the Laboratório de Zoologia de Vertebrados-Tetrapoda, Universidade do Estado do Rio de Janeiro, and analyzed frame by frame to describe swimming behavior, gait, and swimming performance.

The locomotory cycle of hind limbs and forelimbs during swimming were divided into power and recovery phases. The beginning of power phase was indicated by the farthest anterior extension of a foot before it was swept ventrally and posteriorly, and the end of the power phase

was indicated by the farthest extension of the foot before it was moved anteriorly. The locomotor cycle was described by its speed, frequency, time of power and time of recovery phases, and stride length. We marked reference points on the image of the opossum body to take the following measurements as function of time (Fig. 1): body inclination in relation to water surface (Fig. 1, points 1, 2, and 3), vertical displacement of the nose above water surface (Fig. 1, point 3), angle formed by manus and radius-ulna (Fig. 1, points 4, 5, and 6), and angle formed by metatarsus and tibia-fibula (Fig. 1, points 7, 8, and 9). Angles formed by limb segments were measured only in the power phase. Only sequences where locomotion was rectilinear without interference from lateral walls or floor of the aquarium were considered appropriate for analyses.

**Terrestrial locomotion, jumping, and climbing.**—As in the swimming analysis, to study terrestrial locomotion, the opossum was videotaped in lateral view at 30 frames/s, walking on the ground of the outdoor enclosure during its normal activities. Climbing ability was analyzed by the arboreal walking of the opossum on a 3-m-long polyvinyl chloride tube of 58-mm diameter placed horizontally 1.2 m above the ground, and climbing a tree trunk of similar diameter angled at 45° from the horizontal. The tube was covered with adhesive tape to produce a rough surface. Speed, stride length, frequency, and time of stance and swing phases were measured on the sequences of terrestrial locomotion, arboreal walking, and climbing. Jumping behavior was simply described frame by frame when the opossum jumped gaps of 0.3 and 0.6 m between supports. Results are given as mean ± SD.

## RESULTS

**Swimming.**—Five valid video sequences were used for analysis of swimming behavior and performance. The opossum swam at  $0.43 \pm 0.02$  m/s with a frequency of  $2.8 \pm 0.21$  Hz. Positive buoyancy was maintained while swimming by using a quadruped paddling, with the dorsum, eyes, and nostrils above the water surface and the mouth below. Body position was roughly horizontal or inclined at a slight angle ( $\bar{X} = 1.7 \pm 0.6^\circ$ , range = 2.0–4.5°), with small vertical head displacements measured at the tip of the nose ( $\bar{X} = 1.1 \pm 0.6$  cm, range = 2.5–3.6 cm). The trunk and tail of the opossum displayed smooth undulating bilateral movements.

All 4 legs were used alternatively moving on a parasagittal plane when paddling (Fig. 2). Propulsion was accomplished mainly by hind limbs. In power phase, hind limbs were accelerated posteriorly and ventrally with digits abducted and extended. The angle formed by tibia-fibula and metatarsus increased gradually until the end of this phase (Figs. 2A–C). During recovery phase, this angle decreased as the hind limbs were swept anteriorly and ventrally with digits adducted and plantar flexed (Figs. 2D and 2E).

Forelimbs of *L. crassicaudata* displayed only rotational motion in a slower rhythm than the hind limbs. Power phase was achieved only by antebrachial extension and flexion of the manus (Fig. 2), with digits abducted and extended. During this phase the angle formed by radius-ulna and humerus segments increased. In the recovery phase, there was antebrachial flexion and extension of the manus, and decreasing of the corresponding angle with digits adducted and flexed (Fig. 2). Mean width of hind limb angle (minimum = 109.3°, maximum = 209.5°,  $\bar{X} = 60.1 \pm 27.5^\circ$ ) was greater than that of the forelimb (minimum = 83.8°, maximum = 112.9°,  $\bar{X} = 36.4 \pm 9.8^\circ$ ).

Forelimb motion differed from that of hind limbs. Movements of forelimbs do not seem to accelerate the opossum, but may help with balance. Mean power and recovery phases of the forelimb lasted  $0.11 \pm 0.02$  s and  $0.21 \pm 0.08$  s, respectively, corresponding to 37.4% and 62.6% of the forelimb cycle (cycle length =  $0.32 \pm 0.09$  s). Mean power and recovery phases of the hind limb lasted 0.17 s ( $SD < 0.000$ ) and 0.18 s ( $SD = 0.03$ ), respectively, corresponding to 47.48% and 52.52% of the hind-limb cycle (cycle length =  $0.35 \pm 0.03$  s). Based on the gait diagrams obtained from the video sequences, the paddling motion of *L. crassicaudata* resembles a homolateral gait, that is, soon after the beginning of the power phase of a forelimb, the next limb to enter the power phase is the hind limb from the same side of the body (Fig. 3A).

*Terrestrial locomotion, jumping, and climbing.*—Ten or 11 locomotory cycles were obtained for each locomotory mode, but only 1 cycle of each provided a good-quality image for detailed analysis. The gait of individual *L. crassicaudata* moving on the ground was a diagonal trot at low speed (Fig. 3B), changing to a gallop at high speed. Stance phase based on the right hind limb represented 69.23% (0.27 s) of the locomotory cycle, whereas for the left forelimb it represented 61.54% (0.24 s). Speed in terrestrial locomotion was 1.01 m/s. Total duration of the locomotory cycle was 0.39 s, with a 2.6-Hz frequency.

In arboreal walking on the horizontal tube, the opossum used a gait similar to terrestrial locomotion at low speed, a diagonal trot, with a speed of 0.17 m/s and 2.53-Hz frequency (Fig. 3C). Stance phases of hind limb and forelimb were 73.3% and 70.8%, respectively (0.36 s and 0.28 s), and gait size was 0.07 m. When climbing the angled trunk, the opossum used a gait resembling a bound (Figs. 3D and 4). The speed of the opossum was 0.35 m/s with a 2.75-Hz frequency. Stance phases of the hind limb and forelimb were 81.8% and 72.7%, respectively (0.30 s and 0.26 s), and gait size was 0.13 m. In this gait, the opossum 1st held onto the support tightly with the 4 limbs. After this, only forefeet were used to hold the body and hind limbs were moved anteriorly. At the encounter of hind limbs with forelimbs, and later, the hind limbs take the role of propelling opossum body anteriorly.

We observed jumping behavior when the opossum walked on the horizontal tube, reached the end of the tube, and jumped to a nearby tube or trunk. To prepare to jump, the opossum positioned hind limbs near forelimbs, then flexed and extended hind limbs, generating power to jump (Fig. 5). Before jumping, the spinal column was completely flexed, extending when

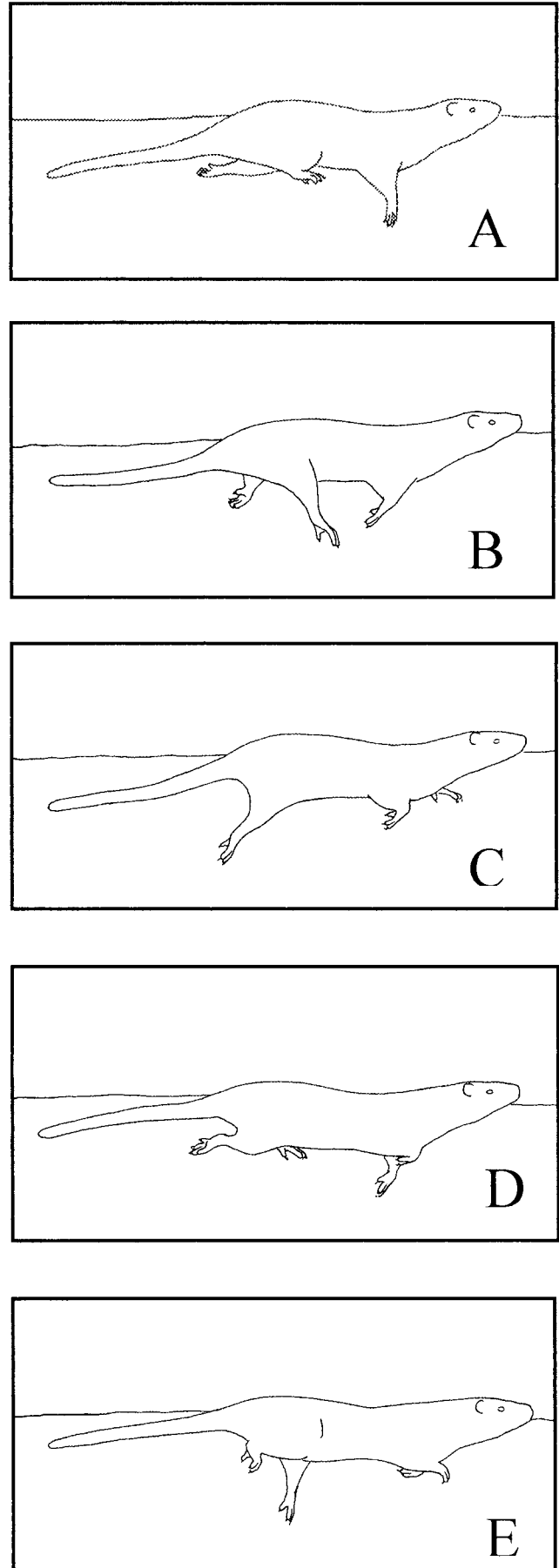
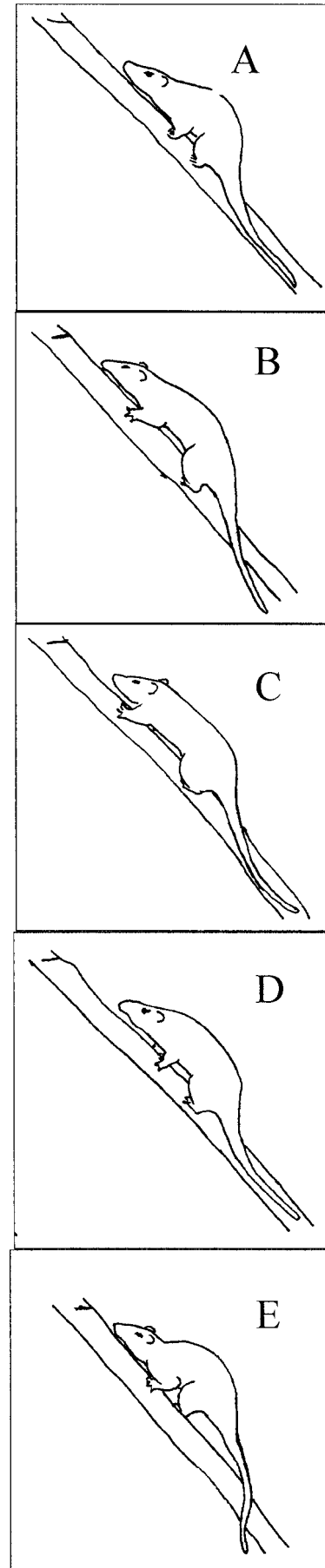
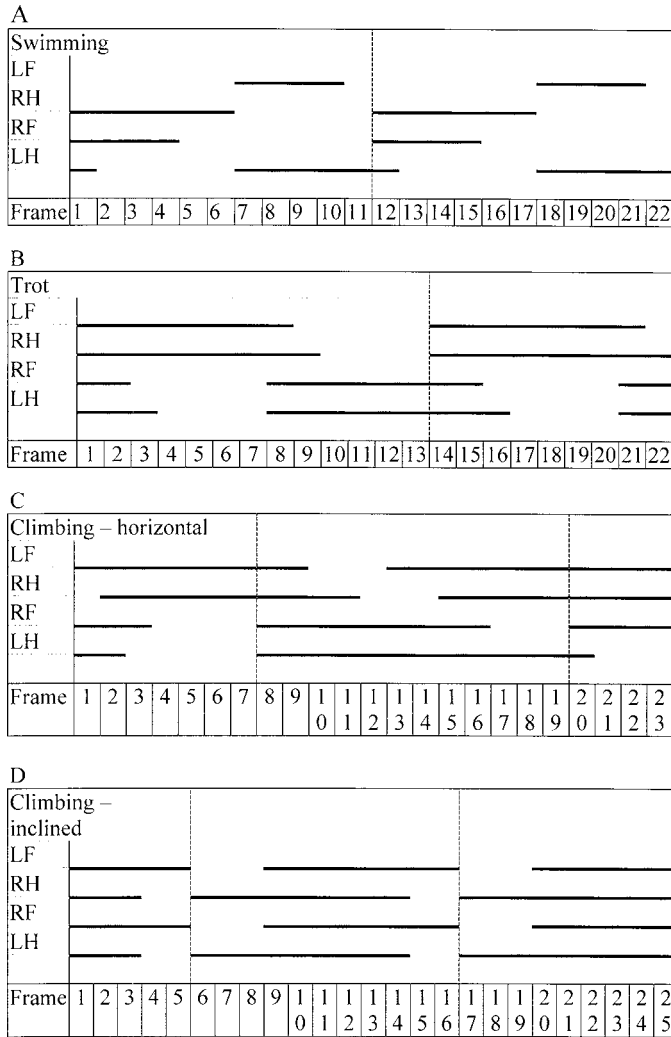


FIG. 2.—Swimming locomotor behavior of *Lutreolina crassicaudata*: A) right forelimb power phase begins; B) right hind-limb power phase begins as right forelimb power phase is still in progress; C) right forelimb recovery phase begins; D) right forelimb recovery phase is in progress and recovery phase of the right hind limb begins; and E) recovery phase of the right hind limb is in progress and right forelimb power phase is about to begin. The limb used as reference was the right hind limb.



**FIG. 3.**—Gait diagrams of *Lutreolina crassicaudata* as a function of time. Each frame or videotaped sequence represents 0.033 s. Black horizontal lines indicate the time of power phase for left forefoot (LF), right hind foot (RH), right forefoot (RF), and left hind foot (LH). The space between the lines indicates the recovery phase of the same limb. Vertical dashed lines indicate transition between cycles. A) Swimming locomotion, homolateral pattern; B) terrestrial locomotion, trot; C) arboreal walking on an horizontal tube, diagonal trot; and D) climbing an inclined tube, bound gait.

powering for the jump. Soon after, in an unsupported phase before landing, total body and limbs were extended.

**DISCUSSION**

In this study, *L. crassicaudata* employed a homolateral paddling gait to generate thrust for swimming. Quadrupedal, or

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**FIG. 4.**—Climbing behavior of *Lutreolina crassicaudata* on a 45° inclined tube: A) with trunk flexed, the opossum holds the support tightly with the 4 limbs; B) with extension of the trunk, forelimbs are moved anteriorly; C) the opossum prepares itself to move hind limbs anteriorly; D) forelimbs hold the support, while hind limbs move forward; and E) the opossum flexes the trunk, preparing for a new impulsion to move forelimbs again.

drag-based paddling, as employed by this species, has been considered a low-performance and more primitive form of propulsion than the bipedal, undulatory, and lift-based mode of more aquatically specialized mammals (Fish 1994, 1996). Typical semiaquatic mammals have abandoned forelimb motion and use bipedal, pelvic paddling to swim (Fish 1993). However, swimming using alternated movements of the 4 limbs is also observed in some species of semiaquatic mammals (Fish 1994; Lodé 1999; Renous 1994; Santori 2004; Williams 1983), and terrestrial species (Dagg and Windsor 1972; Fish 1993; Hickman and Machiné 1986; Lodé 1999). An example is *Lutra canadensis*, which uses a variety of paddling modes, including forelimb paddling, hind-limb paddling, and all-limb paddling (Fish 1994). In addition, some terrestrial mammals are able to swim by using hind feet alternately (Dagg and Windsor 1972; Santori 2004). Thus, quadrupedal or bipedal paddling per se, out of a comparative context, does not seem sufficient to classify *L. crassicaudata* as a terrestrial or semiaquatic mammal.

In a comparative context, however, the homolateral gait of the opossum we studied differed from the bipedal paddling exhibited by the semiaquatic didelphid marsupial, the water opossum, *C. minimus* (Fish 1993), and from the quadrupedal diagonal swimming of the semiaquatic mustelids *Mustela vison* and *Mustela lutreola* (Lodé 1999; Williams 1983). The swimming gait used by *L. crassicaudata* also differed from the swimming gait employed by the terrestrial didelphid *D. virginiana* (Doutt 1954; Fish 1993; Williams 1983). The terrestrial opossum *D. virginiana* swims by using a quadrupedal paddling stroke identified as a slow to fast diagonal sequence run (Fish 1993). The homolateral gait also was observed in swimming *D. virginiana*, similar to *L. crassicaudata*, but the 1st swimming mode was the most frequently used gait by *D. virginiana* (Doutt 1954). Kimble (1997) concluded that alternate, contralateral leg movements are employed by *D. virginiana* in slow swimming and the homolateral gait in fast swimming. The terrestrial mustelid *Mustela putorius* uses the 4 limbs alternately to swim (Lodé 1999). In fact, terrestrial and semiaquatic mammals frequently use terrestrial gaits when swimming (Doutt 1954; Fish 1993, 1994; Williams 1983). However, individual *L. crassicaudata* used only the homolateral swimming gait, which suggests a locomotory specialization for swimming.

Stroke frequency also suggests specialization for swimming by *L. crassicaudata*. The swimming speed of the animal studied here (0.43 m/s) was lower than that of *C. minimus* (0.72 m/s), and comparable to that of *D. virginiana* (0.46 m/s—Fish 1993). However, stroke frequency of *L. crassicaudata* (2.8 Hz) was similar to that of *C. minimus* (2.5 Hz), and almost twice that of *D. virginiana* (1.4 Hz—Fish 1993). Differences in speed between *L. crassicaudata* and *C. minimus* can be explained by a more powerful stroke by *C. minimus*.

The motion of hind limbs was more important than that of forelimbs in swimming propulsion of *L. crassicaudata*. In the power phase, mean angle width and duration of hind-limb motion was greater than those of forelimbs. Thus, in this phase, hind limbs generated more thrust through a greater arc and longer duration of motion, whereas in recovery phase forelimbs

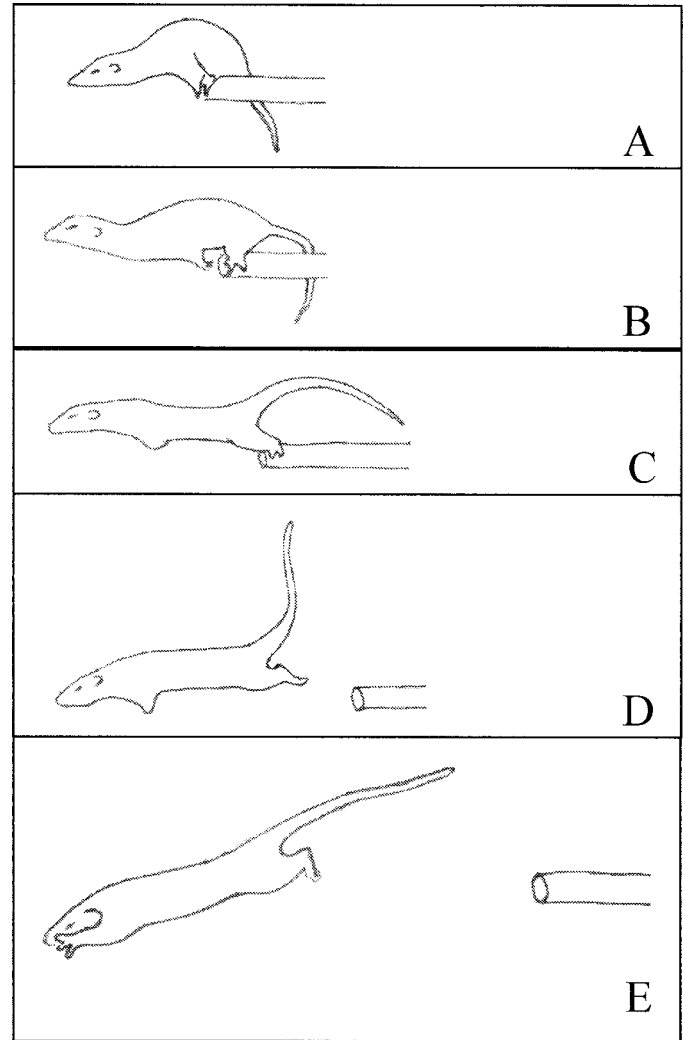


FIG. 5.—Jumping behavior of *Lutreolina crassicaudata* crossing 0.3- to 0.6-m gaps between supports: A) the opossum prepares itself to jump, flexing trunk and positioning forelimbs and hind limbs in close proximity; B) the opossum generates power with hind limbs; C) power generation to jump continues with extension of the trunk; D) aerial phase of the jump; and E) body and limbs totally extended before landing.

spent more time in motion than hind limbs. The short rotational movements of the small-sized forelimbs could contribute more to maintaining stability of the body than to generating thrust. Conversely, in the mustelids *M. putorius* (terrestrial), *M. lutreola* (semiaquatic), and *M. vison* (semiaquatic), forelimb motion was more important to generating thrust in swimming (Lodé 1999; Williams 1983).

The quadrupedal gait used by *L. crassicaudata* does not seem to reduce swimming performance, as observed by Fish (1993) for *D. virginiana*, where occasional foot contact of collateral limbs resulted in loss of momentum. Physical interference between collateral limbs is avoided in *L. crassicaudata* by its homolateral swimming gait and elongated body. The solution has similarities in mustelids, where avoidance of physical interference between collateral limbs was accomplished by shortening of the legs and lengthening of the body (Fish 1993). In the swimming of *D. virginiana* using a diagonal quadrupedal

gait, the water flow from the forelimb is accelerated posteriorly toward the advancing hind limb, causing hydrodynamic interference (Fish 1993). In a homolateral gait pattern, collateral limbs accelerate water posteriorly simultaneously, which would reduce this interference.

The overall posture during swimming of the specimen of *L. crassicaudata*—maintaining the trunk almost horizontal in relation to water surface and slight vertical head position—was more similar to that of *C. minimus* than to that of *D. virginiana*. This ability could be attributed to the nonwetable fur of *L. crassicaudata* (Marshall 1978), which would provide buoyancy and efficient swimming control. Bipedal paddling of *C. minimus* was associated with nonwetable fur (Fish 1993). Having the posture almost horizontal when swimming reduces drag, and buoyancy control is of prime importance in the evolution of an aquatic lifestyle (Fish 1993). These abilities are fundamental in the transition from a terrestrial gait to bipedal paddling in swimming mammals (Fish 1993).

Therefore, the individual studied suggests that *L. crassicaudata* has specializations for aquatic locomotion, some similar to the semiaquatic opossum *C. minimus*. However, in spite of these similarities, such as stroke frequency and buoyancy control, *L. crassicaudata* cannot be considered equally specialized for a semiaquatic life. The pelage of *L. crassicaudata* is not as water repellent as that of *C. minimus*, and hind feet are not webbed and enlarged. Davis (1966) observed that the individual *L. crassicaudata* he studied used the water tank provided in captivity only to drink from and not to swim in. *L. crassicaudata* is also capable of diving underwater (Marshall 1978), but this ability is shared with the semiaquatic as well as the terrestrial common opossums (Fish 1993).

The individual studied used different gaits for swimming, walking, and climbing. Thus, divergent gaits were used in response to the physical demands from different supports and environments. In terrestrial locomotion the vertebral column did not undulate, which could help in the suspension phase of the gallop. Consequently, the efficiency in ground locomotion is reduced (Hildebrand 1995). The relatively high gait frequency during ground locomotion suggests a high energetic demand due to a more elevated muscular contraction rate. Indeed, the anatomical characteristics of *L. crassicaudata* are not those of a fast runner: the elongated body length in relation to short limbs reduces speed as a result of the small undulation of the column or as consequence of the short time of suspension, where the animal rarely takes the 4 limbs off the ground simultaneously (Hildebrand 1995; Rocha-Barbosa 1997; Rocha-Barbosa et al. 1996a, 1996b).

*Lutreolina crassicaudata* has been described as a good climber, although its tail is not prehensile like the tail of arboreal didelphids (Hunsaker and Shupe 1977; Marshall 1978). When climbing the angled trunk, the opossum modified the gait from a diagonal trot (symmetrical gait) used on land to a bound (asymmetrical gait—Hildebrand 1966, 1977; Renous 1994). In this situation, the stance phase was longer and the frequency higher than in the horizontal, but an increase in speed was noticeable. This occurred because the opossum increased gait size. Power for this movement is generated mainly

by hind limbs. The same bound was observed in the semi-terrestrial didelphids *D. albiventris*, *D. aurita*, and *P. frenatus* when climbing almost vertical supports of similar diameter (M. V. Vieira, pers. comm.). Therefore, climbing ability of *L. crassicaudata* is more likely an ancestral ability, shared with other members of the group.

*Lutreolina crassicaudata* possesses a specialized swimming gait not shared by other semiaquatic or terrestrial didelphid species. Stride frequencies are high and similar to those of *C. minimus*, and their buoyancy and postures during swimming also are similar, but actual swimming speed is similar to that of other terrestrial didelphids. Thus, *L. crassicaudata* is a strong swimmer, but not as truly semiaquatic and efficient as *C. minimus*. The terrestrial locomotion is similar to that of other didelphids, but the efficiency is reduced because of the elongated body and short limbs, with no undulation of the vertebral column. Also, the good climbing ability of *L. crassicaudata* is an ancestral feature, shared with other species of group.

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