

COMPARISON OF SWIMMING KINEMATICS BETWEEN TERRESTRIAL AND SEMIAQUATIC OPOSSUMS

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The kinematics of surface swimming of the Virginia opossum (*Didelphis virginiana*) and water opossum (*Chironectes minimus*) were studied to determine locomotor changes associated with the evolutionary transition from terrestrial to semiaquatic existence. Films of individual animals swimming across an aquarium were made and analyzed. *Didelphis* swam with a modified quadrupedal gait similar to a diagonal sequence run. Besides providing propulsive forces, this gait generated an upward force allowing the nasal apertures to remain above the water for breathing. In contrast, *Chironectes* paddled exclusively with the hind limbs in a manner similar to other semiaquatic mammals. The non-wettable fur of *Chironectes* seemed to provide sufficient buoyancy so that no additional forces were required to maintain the nares above the water surface. Transition to exclusive hind limb paddling in semiaquatic mammals appears to be associated with development of non-wettable fur for increased buoyancy and with increased swimming effectiveness resulting from lack of interference between forelimbs and hind limbs during the stroke cycle. Eliminating use of the forelimbs in paddling also permitted unrestricted movement of the hind limbs.

Key words: *Didelphis*, *Chironectes*, opossum, swimming, gait

The evolution in lineages of mammals from a terrestrial existence to one that is fully aquatic necessitated morphological and behavioral changes, particularly with regard to locomotion (Gingerich et al., 1990; Howell, 1930). It is expected that the swimming modes associated with semiaquatic and some fully aquatic mammals originated from quadrupedal paddling, itself based on a terrestrial gait, and progressed up to or through bipedal paddling (Fish, 1992; Rayner, 1985). Modification of the limbs for paddling is readily accomplished from terrestrial locomotion (Rayner, 1985).

Within the New World marsupial family Didelphidae two species, the Virginia opossum, *Didelphis virginiana*, and the yapok or water opossum, *Chironectes minimus*, are closely related (Kirsch, 1977; Stein, 1981). *Chironectes* is the only semiaquatic marsupial (Thompson, 1988). The swimming motions of *Didelphis* were described as a trot or pace in which all four legs were em-

ployed (Doutt, 1954; McManus, 1970). *Chironectes* was reported to exclusively use the hind legs for swimming by alternate paddling (Davis, 1966; Enders, 1935; Oliver, 1976). Stein (1981) examined the skeletons and limb myology of the two opossums and found differences, namely, *Chironectes* has muscles arranged for increased mechanical advantage, which were believed associated with its aquatic habits as compared to *Didelphis*. The purpose of this study was to investigate the morphological and behavioral changes associated with the transition from quadrupedal-terrestrial locomotion to bipedal-aquatic locomotion.

MATERIALS AND METHODS

Three adult male and one adult female *Didelphis virginiana* and three adult female *Chironectes minimus* were examined. One *Didelphis* was maintained at the Philadelphia Academy of Natural Sciences. The remaining three *Didelphis*

were field-captured individuals from Chester Co., Pennsylvania (39°57'N, 75°40'W), subsequently maintained at West Chester University. *Chironectes* were captured in Belize and housed at the Front Royal facility of the National Zoological Park, Smithsonian Institution. Body masses were 2.6–5.6 kg for *Didelphis* and 0.8–1.2 kg for *Chironectes*.

Swimming experiments were performed in either of two aquaria each having transparent walls for lateral viewing of the opossums. Dimensions of the aquaria were 180 by 44 by 46 cm and 157 by 34 by 33 cm. A 15-cm scale was affixed to the front wall of each aquarium to serve as a frame of reference. Aquaria were filled with water to levels that prevented opossums from touching the bottom while surface swimming. Water temperatures ranged from 18 to 23°C. Opossums were allowed to choose their swimming speeds.

Rectilinear surface swimming by opossums was filmed at 64 frames/s with a Bolex H-16 cine-camera equipped with a Kern Vario-Switar 100 POE zoom lens (1:1.9, $f = 16\text{--}100$ mm), using Kodak 4-X reversal film no. 7277 (ASA 320) or Kodak Tri-X reversal film no. 7278 (ASA 160). Lighting was augmented by two floodlamps.

Film records were analyzed by sequentially tracing the pectoral and pelvic limbs as displayed with a stop-action projector (Lafayette Instrument Co., Model 00100). Data acquisition was restricted to film segments in which animals maintained steady rectilinear swimming while traversing the length of the aquarium and without interference from walls or floor of the aquarium.

For analysis, swimming-stroke cycle was divided into power and recovery phases. The beginning of the power phase was indicated by the farthest anterior extension of a foot before it was swept ventrally and posteriorly, whereas the end of the power phase was indicated by the farthest extension of that foot before it was moved anteriorly.

RESULTS

Upon introduction into the aquarium, the fur of *Didelphis* became saturated with water, providing little if any buoyancy. Because of this, only the dorsum of the head was above water while swimming; the body was canted at an average angle from the horizontal of $11.2^\circ \pm 1.7$ SE ($n = 21$; range

$= 0\text{--}34^\circ$). All four legs were used alternately in paddling (Fig. 1). For over one-half of the stroke cycle at least two legs were moving in the power phase. Swimming speeds (U) ranged from 0.19 to 0.46 m/s.

Chironectes swam at the water surface at speeds (U) of 0.19–0.72 m/s. The entire head and body dorsum remained above water. Average inclination of the body was $3.4^\circ \pm 0.7$ ($n = 25$; range = $0\text{--}13^\circ$) from horizontal. The attitude of the body seemed due to a high degree of buoyancy, mainly provided by air bubbles that were observed trapped in the fur. During rectilinear swimming, propulsion was provided exclusively by alternate paddling of the hind limbs (Fig. 1). The pectoral limbs were held anteriorly under the head, with the digits outstretched.

The power phase of the stroke cycle qualitatively was similar for both *Chironectes* and *Didelphis* (Figs. 2 and 3). The hind limb was accelerated posteriorly through an arc by plantarflexion of the pes, shank flexion, and femur extension. Femur extension was pronounced in *Didelphis* resulting in substantial translation of the pes, whereas the majority of hind limb motion in *Chironectes* was rotational. Digits of the pes were extended and fully abducted throughout the power phase.

Recovery phase of the stroke cycle in both species was characterized by flexion and adduction of the digits, shank extension, and femur flexion (Fig. 3). In addition, the pes of both opossums was dorsiflexed through the first one-half of the recovery phase and plantarflexed in the second one-half of the phase. For *Didelphis*, the pes remained approximately horizontal in its orientation through the second one-half of the recovery phase.

Forelimb motion by *Didelphis* showed translation and rotation (Fig. 2). During the power phase, paddling was affected by antebrachial extension, humeral extension, and a slight flexion of the manus. Paddling motion of the forelimb did not show a steady acceleration throughout the stroke. At the beginning of the power phase, the manus

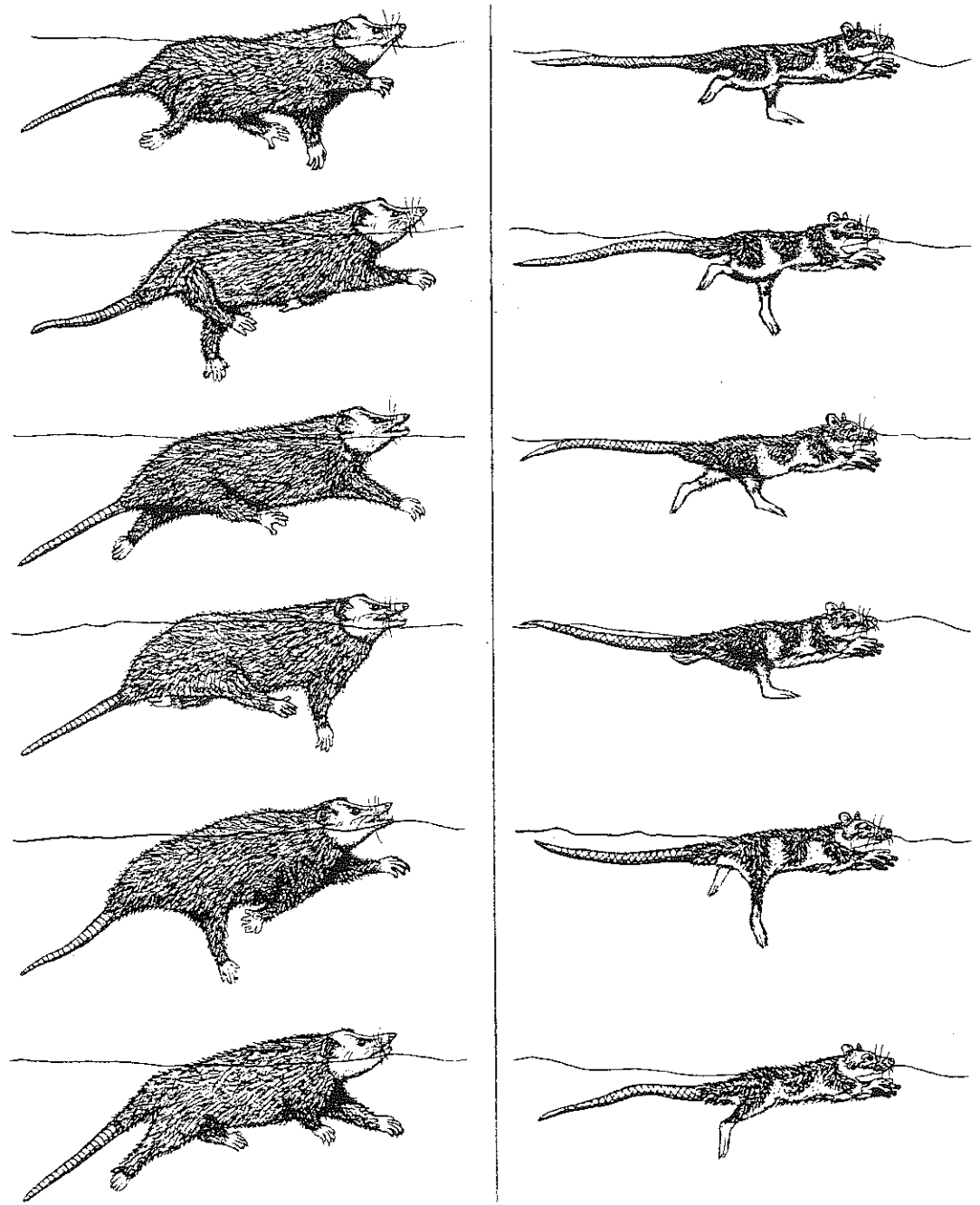


FIG. 1.—The sequence of limb movements observed in swimming of *Didelphis* (left) and *Chironectes* (right).

was held horizontal or at a slight angle ($<30^\circ$) as it was moved ventrally over a short distance. During the first one-half of the power phase, the manus traveled ca. 25% of the

total distance traversed over the entire phase. Little acceleration was perceptible at this time. Forelimb motion in the remainder of the power phase was similar to the

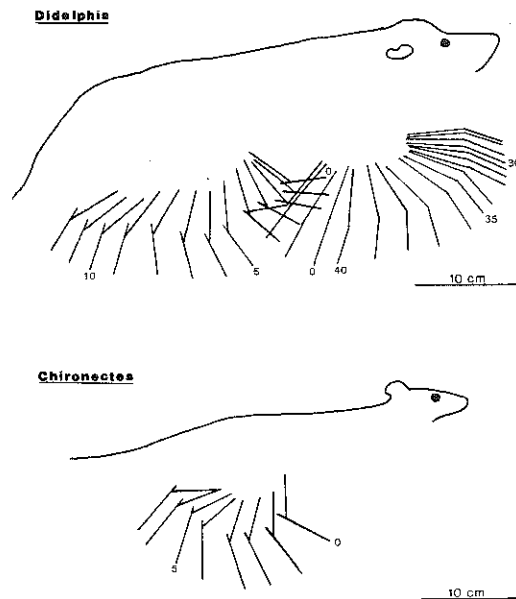


FIG. 2.—Sequential tracings from films of forelimbs and hind limbs through the power phase of the paddling cycle. The body positions of *Didelphis* ($U = 0.43$ m/s) and *Chironectes* ($U = 0.45$ m/s) are held constant as a fixed frame of reference. Numbers indicate film frames through the stroke cycle, where frame 0 indicates the start of the power phase for the hind limb.

paddling motion observed by the hind limb. Recovery phase of the forelimb was characterized by a pronounced flexion at the carpus, adduction of the digits, and extension of the ulna and humerus.

Frequency of the stroke cycle as a function of U is illustrated in Fig. 4. At $U < 0.28$ m/s, *Didelphis* displayed a constant frequency of ca. 1.1 Hz. Above 0.28 m/s the frequency increased linearly for both species of opossums. This trend was similar to the increasing frequencies of the propulsive appendages reported for beavers, *Castor fiber*, minks, *Mustela lutreola*, muskrats, *Ondatra zibethicus*, and nutria, *Myocastor coypus* (Mordvinov, 1976). However, frequency of opossum strokes was different from the constant frequencies reported for muskrats, *O. zibethicus* (Fish, 1984), minks, *Mustela vison* (Williams, 1983), and humans (Nadel, 1977).

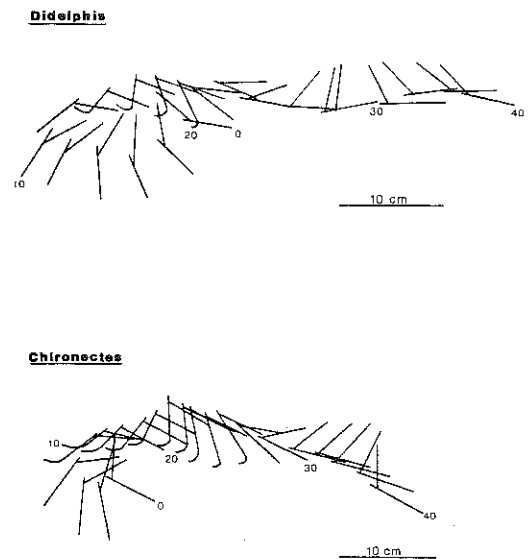


FIG. 3.—Sequential tracings from films of hind limbs of *Didelphis* ($U = 0.43$ m/s) and *Chironectes* ($U = 0.45$ m/s) through a complete stroke cycle. Body position is not held constant.

Durations of recovery and power phases were asymmetrical for swimming opossums. In *Didelphis*, recovery phase was 1.6 and 2.3X longer than power phases for forelimb and hind limb, respectively; whereas for the hind limb of *Chironectes*, recovery phase was 1.8X longer than power phase. These differences were all significant ($P < 0.0005$; paired t -test). Power and recovery phases of stroke cycles were negatively and linearly correlated with frequency in both species (Table 1; Ryan et al., 1976). Comparisons of the slopes (t -test; Zar, 1984) found no significant differences between cycles of forelimb and hind limb paddling for *Didelphis* with respect to power or recovery phases. In addition, slopes for power phases of the hind limbs for *Didelphis* and *Chironectes* were not significantly different from one another, but a significant difference ($P < 0.001$; t -test; Zar, 1984) was found between slopes of the recovery phases for these two opossums. Comparison of the elevations (t -test; Zar, 1984) of the power phase of the hind limb between the two species resulted in no significant difference. How-

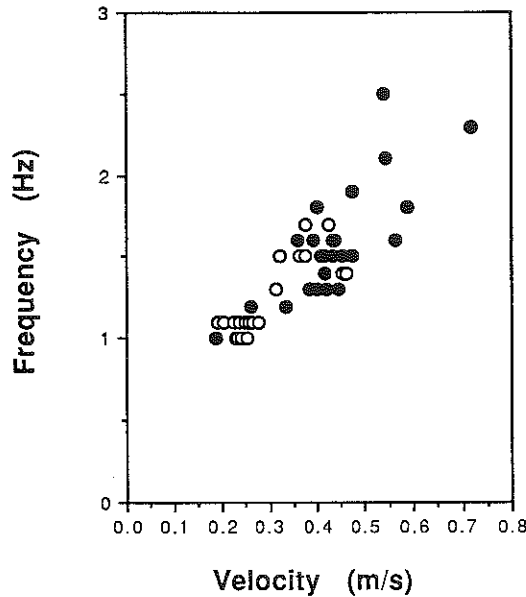


FIG. 4.—Stroke frequency as a function of swimming velocity, U . Closed symbols represent *Chironectes*; open symbols represent *Didelphis*.

ever, significantly different ($P < 0.001$; t -test) elevations were found in comparisons between forelimbs and hind limbs in *Didelphis* for both phases of the stroke cycle.

The length of the arc circumscribed by the distal ends of the propulsive appendages is shown as a function of U in Fig. 5. For *Didelphis*, both forelimb and hind limb arcs were relatively constant over the range of U . Average arcs were the same for forelimbs and hind limbs at 0.35 ± 0.01 m. Arcs of hind limbs measured for *Chironectes* increased linearly with increasing U . This trend

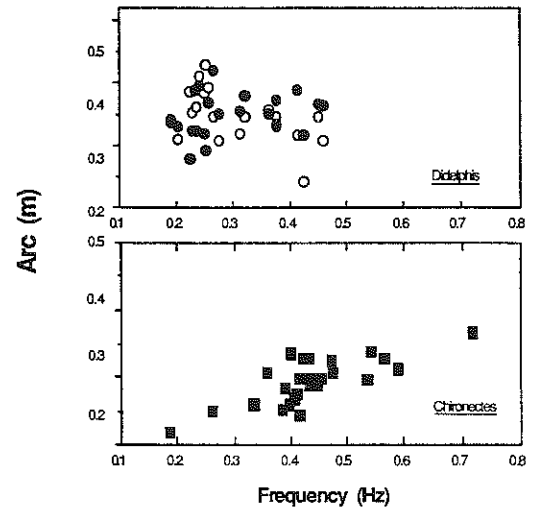


FIG. 5.—Arc traversed by feet of swimming opossums as a function of swimming velocity, U . Open symbols represent forefeet; closed symbols represent hind feet.

was similar to the relationship of arc and U reported for muskrats (Fish, 1984).

Further differences in bipedal and quadrupedal paddling were observed when the pattern of limb movements was displayed as a gait diagram (Fig. 6). As opposed to terrestrial locomotion in which the gait diagram indicates support by each foot against a time scale (Hildebrand, 1989), diagrams in Fig. 6 indicate the length of time that the feet are in the power phase of the stroke cycle. For *Didelphis*, the percent of stride for which forefoot followed hind foot on the same side of the body ranged from 63 to 83%, while the percent of the cycle that each

TABLE 1.—Regression equations and correlation coefficients, r , for time of power, t_p , and recovery, t_r , phases as a function of frequency of stroke cycle, f .

Animal	Foot	n	Equation	r
<i>Didelphis</i>	Fore	21	$t_p = 0.520 - 0.158f$	-0.670*
	Fore	21	$t_r = 1.089 - 0.461f$	-0.948*
	Hind	21	$t_p = 0.402 - 0.116f$	-0.691*
	Hind	21	$t_r = 1.165 - 0.463f$	-0.914*
<i>Chironectes</i>	Hind	25	$t_p = 0.410 - 0.110f$	-0.742*
	Hind	25	$t_r = 0.831 - 0.255f$	-0.935*

* Significant at $P < 0.001$.

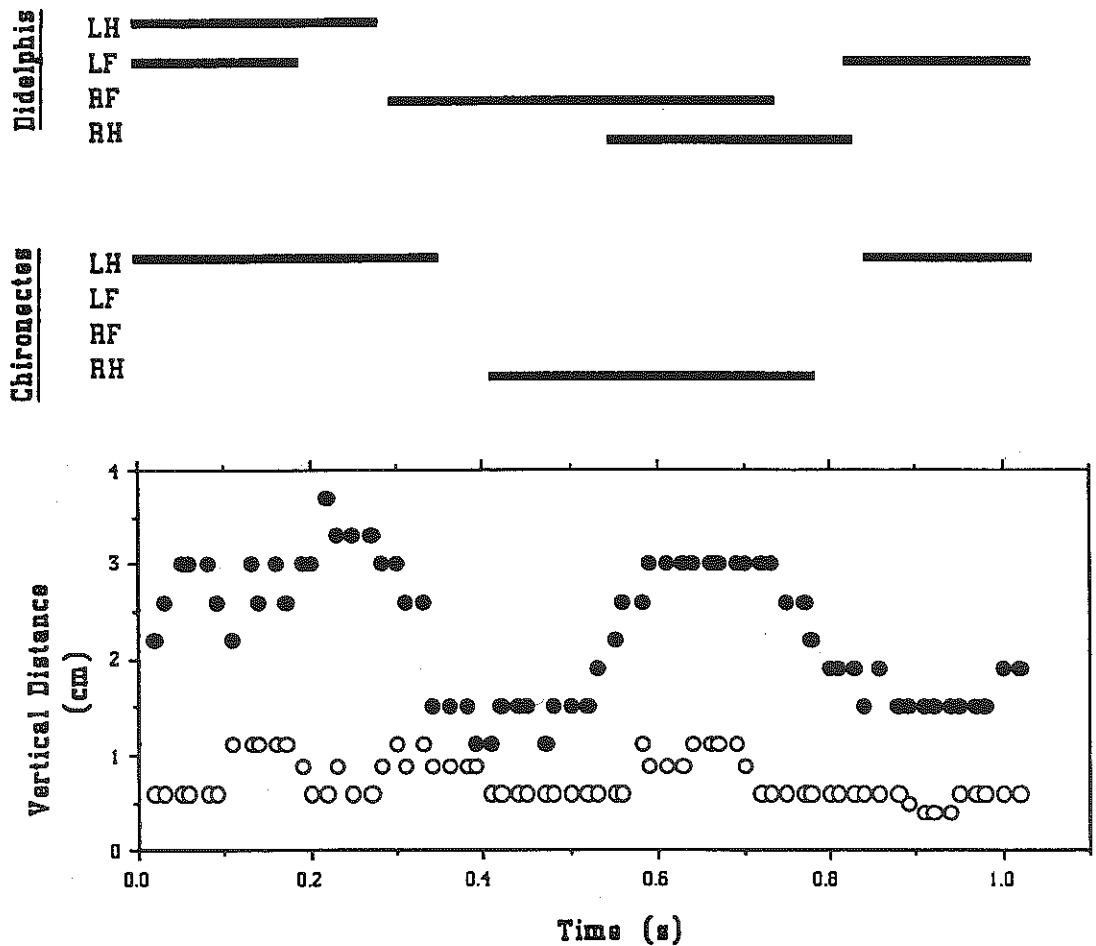


FIG. 6.—Gait diagrams and vertical displacement of nose above water surface as a function of time. In the gait diagrams, horizontal bars indicate time of power phase for left hind foot (LH), left forefoot (LF), right forefoot (RF), and right hind foot (RH). Elevation of the nose above the water cycled with respect to swimming gait in *Didelphis* (closed symbol; $U = 0.24$ m/s). No substantial vertical displacements were observed through the gait cycle of *Chironectes* (open symbol; $U = 0.26$ m/s).

foot was in the power phase ranged from 25 to 39%. Such a pattern is similar to a diagonal sequence, moderate to fast run (Hildebrand, 1976, 1980, 1989). For the bipedal paddling gait of *Chironectes*, the percent of the cycle that each hind foot was in the power phase ranged from 27 to 44%, indicating a slow to fast run.

Large vertical oscillations of the nose of *Didelphis* were observed with respect to the gait pattern employed by this opossum (Fig. 6). The nose was forced upward during the beginning one-third to one-half of the power

phase of the forelimbs. This corresponds to the point in the stroke cycle when the forelimb shows high acceleration. Large forces generated by the paddling motion would be expected to be oriented ventrally and posteriorly. A downward displacement of the nose was observed at the termination of the forelimb power phase. In comparison, *Chironectes* showed a nearly constant displacement of its nose above the water (Fig. 6). The nose of *Chironectes* averaged only 32% of the vertical displacement of that observed for *Didelphis*. The average displace-

ment of *Didelphis* was 2.4X greater than for *Chironectes* when corrected for size differences between opossums by dividing the displacement by the length of each animal.

DISCUSSION

The Virginia opossum, *D. virginiana*, was characterized as a strong but slow swimmer (Doutt, 1954; McManus, 1970) that is capable of extended periods in the water (Wilber and Weidenbacher, 1961). *Didelphis* is able to swim underwater (Moore, 1955), but predominantly swims at the surface with its nose and dorsal portion of its head above the water (Doutt, 1954; McManus, 1970). Previous investigators of swimming by *Didelphis* have noted that the opossum uses terrestrial gaits in the water (Doutt, 1954; McManus, 1970). These swimming gaits were described as either a walk or a pace. During a pace, the forelimbs and hind limbs on the same side of the body move in unison.

Based on the method of gait analysis modified from Hildebrand (1976, 1980, 1989), the quadrupedal paddling stroke of *Didelphis* observed in this study was identified as a slow to fast, diagonal sequence run. This gait is used by primates, the kinkajou (*Potos flavus*), and forest-dwelling artiodactyls such as the muntjak (*Muntiacus muntjak*) and duiker (*Cephalopus* sp.—Hildebrand 1976, 1989). The slow, diagonal sequence walk and run are used on land by *Didelphis*, although the run is at the extreme of the opossum's range of gaits (Hildebrand, 1976; Jenkins and Weijs, 1979; White, 1990). *Didelphis* commonly trots or moves with a lateral sequence walk (Hildebrand, 1976; White, 1990). Use of a diagonal sequence run for swimming *Didelphis* appears to be an exaggeration of a rapid land-based gait.

In general, the particular quadrupedal gait used by a swimming mammal would affect locomotor performance. A walk, although highly stable on land (Hildebrand, 1976), would be extremely slow if used for aquatic propulsion. Walking enhances stability on

land through a prolonged foot-contact interval coupled with a short time for repositioning the foot. This phase sequence usually includes phases having three feet in contact with the ground, producing a support triangle that encloses the center of gravity of the animal (Hildebrand, 1980). However, buoyancy accounts for much of an animal's stability in water (Fish and Stein, 1991), and thus the power phase may be shorter than the recovery phase during swimming without sacrificing stability. Propulsive efficiency is enhanced through a short power phase and long recovery phase by generating large propulsive forces and minimizing drag forces, respectively (Fish, 1984). Running gaits would provide the speed necessary for effective paddling.

As observed for *Didelphis*, the use of the diagonal sequence run while swimming, however, presented a problem in the effective use of a quadrupedal gait for locomotion in water. This gait placed colateral feet in close proximity to one another during the stroke cycle. This occurred at the end of the forefoot power phase and at the beginning of the hind foot power phase (Fig. 2). Occasionally, direct contact between these forefeet and hind feet was noted and resulted in physical interference of the respective foot strokes. In these instances, interference would disrupt pattern of gait, causing loss of momentum to the animal and reducing swimming efficiency.

In comparison to the terrestrial *Didelphis*, the semiaquatic *Chironectes* displays numerous external morphological characteristics associated with a semiaquatic existence. These include streamlined body shape, large webbed hind feet, non-wettable fur, robust vibrissae, eyes displaced dorso-laterally, reduced closable external ears, waterproof marsupium in females, and pouch in males to retract the scrotum and testes when swimming (Augustiny, 1942; Davis, 1966; Enders, 1937; Oliver, 1976; Rosenthal, 1975; Sokolov, 1962; Stein, 1981).

Pelvic paddling, as observed in *Chironectes*, is a typical swimming mode used by

semiaquatic mammals (Fish, 1984, 1992; Howell, 1930; Tarasoff et al., 1972). Development of such a mode was likely a modification from a terrestrial gait in which movements of the forelimbs were abandoned in water. Indeed, paddling movements of the hind limbs for both species of opossums examined were qualitatively similar.

The switch from a terrestrial gait to bipedal paddling in swimming mammals could not have occurred without effective control of stability. Internal and external modifications for stability, particularly buoyancy control, have been of prime importance in the evolution of an aquatic lifestyle (Domning and De Buffrenil, 1991; Fish and Stein, 1991; Stein, 1989). Large, fully aquatic mammals maintain buoyancy through increased body fat and enlarged lungs (Howell, 1930; Kooyman, 1973; Slijper, 1976). For semiaquatic mammals, non-wettable fur provides buoyancy via an entrapped layer of air that subsequently reduces body density (Dagg and Windsor, 1972; Esher et al., 1978; Fish and Stein, 1991; Johansen, 1962; Ling, 1970). Without a layer of air, mammals have difficulty floating. This generally results in a more vertical orientation of the body compared to semiaquatic mammals with non-wettable fur (Slijper, 1976). Such an orientation would increase drag during swimming by presenting a greater frontal surface area to the water flow and reducing streamlining (Vogel, 1981). Slijper (1976) noted that the vertical orientation of terrestrial mammals floating in water was due to a torque developed from the anterior position of the center of buoyancy with respect to the center of gravity. Such a body orientation was noted in this study and by McManus (1970) for *Didelphis*. When fur of semiaquatic mammals was rubbed with detergent as a wetting agent, these mammals were unable to maintain a horizontal body orientation and struggled to keep their noses above water (Dagg and Windsor, 1972).

Chironectes maintained a nearly horizon-

tal body orientation and showed only slight vertical oscillations during swimming. Its buoyancy probably was supplied from non-wettable fur. The possibility of *Chironectes* possessing enlarged lungs for use as a floatation organ, as reported for the sea otter, *Enhydra lutris* (Kooyman, 1973), has not been investigated. The inability of *Didelphis* to maintain proper buoyancy was due to the rapid uptake of water by the fur. This resulted in a large angular displacement of the body from the horizontal. Forelimbs were used to compensate for the reduced buoyancy. By paddling downward in the first one-half of the power phase, the action of the forelimbs lifted the nose above the water surface to insure continued breathing.

While a shift from use of a terrestrial gait to paddling motions that are more effective for swimming is aided by the acquisition of a non-wettable pelage, the question remains as to why semiaquatic mammals generally, and *Chironectes* specifically, use bipedal paddling. It might be expected that swimming performance is enhanced by the use of four propulsors as opposed to two. However, studies by Fish (1982) and Williams (1983) indicate that aerobic efficiency is higher for a bipedal paddler than a quadrupedal paddler.

Although forelimbs and hind limbs of *Didelphis* appeared to generate sufficient forces for buoyancy control and thrust production, distinct functional disadvantages were observed as a result of using quadrupedal swimming. Substantial pitching action (i.e., vertical displacement) was produced by alternating paddling action of the forelimbs. The energetic cost of pitch is expected to be high, because the opossum must work against gravity to raise its nose above the water surface. In addition, propulsive efficiency should be reduced, because the forelimbs, although active for lift generation, would provide little thrust due to the small size of the unwebbed feet. In human swimmers, the leg kick serves mainly to generate lift and hold the body horizontal and to minimize energy loss from drag; however,

the large muscle mass of the legs requires such a large energy consumption that overall efficiency is reduced (DiPrampero et al., 1974).

Use of four limbs for swimming by some mammals can reduce overall propulsive efficiency due to physical interference between forelimbs and hind limbs. Avoidance of such interference requires either a relative shortening of the legs or lengthening the body. Mustelids exhibit both of these morphological characteristics (Estes, 1989). Minks (*M. vison*), as an example, swim with a quadrupedal gait similar to their terrestrial gait, i.e., two diagonal legs move in synchrony (Williams, 1983). However, the more aquatic river otter (*Lutra canadensis*), although capable of paddling quadrupedally, swims predominantly with two feet (Chanin, 1985; Tarasoff et al., 1972). In *Lutra*, paddling is confined mainly to hind feet, whereas forefeet are used for turning (Tarasoff et al., 1972). For semiaquatic rodents such as muskrats, which do not exhibit an elongate body, paddling is confined to enlarged pelvic appendages. The forelimbs are reduced and have little function in steady swimming (Fish, 1982; Starrett and Fisler, 1970).

Although the forelimbs of *Chironectes* show no decrease in size, they are not used for swimming. These limbs are extended anteriorly with expanded digital pads functioning as tactile sensors when foraging (Davis, 1966; Stein, 1981).

Hydrodynamic interference also could result from disturbance of the water flow due to interaction between the limbs. Because the forelimb accelerates water posteriorly toward the advancing hind limb, the drag on the downstream limb would increase, particularly during the recovery phase. This occurs, because drag is directly proportional to velocity (Vogel, 1981). The relative velocity during recovery (i.e., anterior velocity of the limb plus velocity of the body) experienced by the hind limb is higher than if the limb is working in undisturbed water. It also is possible that hydrodynamic inter-

ference from the forelimb would limit thrust production by the hind limb, thereby reducing overall efficiency.

In the transition from terrestrial quadruped to semiaquatic paddler, several morphological and behavioral changes were necessary for effective aquatic locomotion by mammals (Fish, 1992; Howell, 1930). Ancestors of aquatic mammals may have swum with a modified quadrupedal gait (Rayner, 1985). With such a gait, the forelimbs could have been used to generate lift and keep the nares above water for respiration. The addition of a non-wettable fur could have uncoupled buoyancy control from swimming movements and thus allowed semiaquatic mammals to adopt a bipedal paddling mode.

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