ASSOCIATION OF PROPULSIVE SWIMMING MODE WITH BEHAVIOR IN RIVER OTTERS (*LUTRA CANADENSIS*)

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The propulsive swimming modes of river otters (*Lutra canadensis*) were examined relative to behavior. Six river otters were filmed in zoo enclosures that provided surface or submerged views. The repertoire of swimming modes observed for otters included quadrupedal paddling, forelimb paddling, alternate hind-limb paddling, simultaneous hind-limb paddling, and body and tail dorsoventral undulation. Paddling modes accounted for 88% of surface swimming observations and for 86% of observations involving submerged maneuvers. Dorsoventral undulation predominated during rectilinear submerged swimming. Transition from paddling to undulatory propulsion was accomplished by use of simultaneous hind-limb paddling in concert with dorsoventral body and tail flexion. These motions produced a posteriorly directed traveling wave in the tail with an average velocity 1.62 times the swimming velocity. The higher velocity in the tail could produce hydrodynamic thrust during all phases of the paddling cycle.

Key words: swimming, *Lutra canadensis*, otter, paddling, kinematics, hydrodynamics

The evolution of fully aquatic mammals from quadrupedal, terrestrial mammals is considered a prime example of morphological change by convergence with aquatic vertebrates (Howell, 1930). In addition to changes in body morphology (e.g., streamlined body shape, presence of flippers and flukes, reduced hair covering), changes in propulsive swimming mode also were an important evolutionary element in this transition. A key component in this shift was a change from paddling or drag-based propulsion to undulatory propulsion (Fish, 1992; Thewissen et al., 1994). Paddling is used for swimming by terrestrial and semi-aquatic mammals, such as minks (*Mustela vison*—Williams, 1983) and muskrats (*Ondatra zibethicus*—Fish, 1984), and is associated with slow swimming at the water surface and precise maneuverability (Webb and Blake, 1985). Undulatory swimming is found in aquatic mammals, including cetaceans, pinnipeds, and sirenians (Fish and Hui, 1991; Fish et al., 1988; Hartman, 1979; Lang and Daybell, 1963), and is associated with rapid, submerged swimming

(Fish, 1992; Williams, 1989). Furthermore, differences between paddling and undulation are associated with swimming performance in mammals (i.e., speed, acceleration, efficiency). The thrust force is larger and is developed more efficiently from undulatory propulsion than from paddling (Weihs and Webb, 1983).

A major difficulty in understanding the evolutionary transition from a paddling mode to an undulatory mode is that different parts of the body are employed in each. This suggests a simultaneous requirement for rapid evolutionary changes in body design, neuromotor patterns, and musculoskeletal function. Paddling uses paired appendages, whereas undulation is accomplished by motion of the axial skeleton (Howell, 1930; Weihs and Webb, 1983). Williams (1989) noted that the transition to a high-performance undulatory mode was coincident with a fully aquatic lifestyle and shift from surface to subsurface swimming.

The North American river otter (*Lutra canadensis*) represents an excellent species in which to examine the transition in swim-

ming mode. These semiaquatic mammals demonstrate a wide range of propulsive modes, including paddling and undulation (Chanin, 1985; Estes, 1989; Liers, 1951; Tarasoff et al., 1972). River otters possess webbed feet and an elongate, robust, dorsoventrally flattened tail. In addition, otters are capable of rapid swimming (Baker, 1983; Liers, 1951), diving underwater (Chanin, 1985), and performing tight turning maneuvers (F. E. Fish, pers. observ.). Although gross movements of swimming otters have been described (Tarasoff et al., 1972), there has been no detailed analysis of swimming kinematics and their relationship with swimming mode and behavior. The purpose of this study was to examine swimming by otters and to determine correspondence between behavioral conditions and propulsive mode. In addition, kinematic examination of the undulatory mode was made to ascertain its contribution to swimming.

MATERIALS AND METHODS

Swimming motions and behaviors of three pairs of adult river otters were observed in artificial ponds at the Philadelphia Zoo (Philadelphia, PA), Brandywine Zoo (Wilmington, DE), and National Zoo (Washington, DC). The pond at the Philadelphia Zoo was oval shaped with long and short axes of 17.1 and 12.2 m, respectively, with a water depth of ca. 1.0 m. About two-thirds of the exhibit area was water. The structure of the pond provided overhead viewing. The pond at Brandywine Zoo was irregularly shaped and covered an area of 35.5 m². The bottom of the pond gradually sloped to a maximum depth of 1.4 m. The irregularly shaped pond at the National Zoo covered an area of 11.1 m² with a depth from 1.2 to 1.8 m. Ponds at the Brandywine Zoo and the National Zoo provided underwater viewing through glass windows with dimensions of 1.5 by 0.8 m and 6.1 by 0.8 m, respectively.

Propulsive swimming modes and behaviors of the otters were recorded on videotape or cine films. Otters at the Brandywine and Philadelphia zoos were videotaped (30 frames/s) with a Panasonic Camcorder (Model PV-200). Videotapes were played back in the laboratory frame-by-

frame with a video recorder (Panasonic AG-6300). Cine films (16 mm, Kodak Tri-X Reversal film 7278, ASA 320) of otters at the National Zoo were taken with a Bolex H-16 camera equipped with a Kern Vario-Switar 100 POE zoom lens (1:1.9, f = 16–100 mm) at 64 frames/s. Analysis of cine films was performed using a stop-action projector (Lafayette Instrument Co., Model 100). In addition, sequential images of otters swimming using an undulatory mode were projected onto a digitizer tablet (GTCO Digi-Pad 5) interfaced to an IBM PC microcomputer. Digitized points from these images were used to determine average swimming velocity (anterior velocity) and characteristics of the tail wave including amplitude and average velocity (posterior velocity). Posterior velocity was measured as the distance the crest of the tail wave moved between sequential film images, divided by the time (0.0156 s). Data were plotted using a three-point moving average.

For statistical treatment of behavioral data, swimming by otters was categorized according to propulsive mode (paddling and undulation), to water depth (surface and submerged), and to displacement pattern (rectilinear and maneuvering). To test the independence among these variables, a three-dimensional contingency table was constructed and analyzed with the chi-square statistic (Zar, 1984). Behavioral observations were not independent, and individual animals at each zoo could not be marked and, hence, distinguished during behavioral observations. Nonetheless, nothing suggests that the number of observations per individual was biased in a systematic fashion; as a result, chi-square analysis minimally represents a heuristic tool for the detection of associations between levels of propulsive mode, depth, and displacement pattern. Because of differences in the facilities of the three zoos, data collected at the Philadelphia Zoo (overhead viewing) were analyzed separately from data collected at the Brandywine and National zoos (underwater viewing). Observations of submerged and surface swimming were made at the Philadelphia Zoo, whereas observations on swimming otters at the Brandywine and National zoos were restricted to submerged swimming.

RESULTS

Swimming modes.—Analysis of 208 swimming sequences from cine films and

videotapes showed that otters used a variety of swimming modes, including alternate limb-paddling and undulation. Paddling modes included forelimb paddling, hind-limb paddling, and all-limb (quadrupedal) paddling. In all-limb paddling, the four legs moved in an alternating manner similar to a terrestrial mammalian gait such as a walk or trot, or forelimbs and hind limbs moved simultaneously in a gait reminiscent of a gallop (Hildebrand, 1980; Howell, 1930). The body was held straight in modes using alternating movements of the limbs during rectilinear swimming. Body flexion occurred when the animals were maneuvering and when otters used simultaneous thrusts of the hindlimbs or all limbs.

All paddling modes used by the otters displayed both power and recovery phases of the stroke cycle (Fish, 1984). During the power phase, the limb was extended and swept posteriorly through a wide arc between 90 and 140°. The forelimbs initiated the power phase from a starting position almost parallel to the long axis of the body, whereas the hind limbs initiated the stroke at a position approximately perpendicular to the long axis. The digits were dorsiflexed and abducted to fully spread the interdigital webbing. During the recovery phase, the limb was protracted, and the plantar area of the foot was reduced by ca. 50% by adduction and plantar flexion of the digits.

The undulatory mode used by swimming otters was characterized as dorsoventral flexion of the body and tail coupled with a simultaneous paddling motion of both hind limbs (Fig. 1). At the start of the power phase, hind limbs were swept simultaneously caudad. The posterior sweep of the limbs was extended by extension of the spine and pelvic rotation. This action produced a dorsal bending of the tail at the pelvis, which progressed posteriorly as a waveform toward the tail tip. In the recovery phase, the hind limbs and pelvis were rotated cranially, accompanied by dorsal flexion of the spine. This motion produced a ventral waveform in the tail that moved caudally.
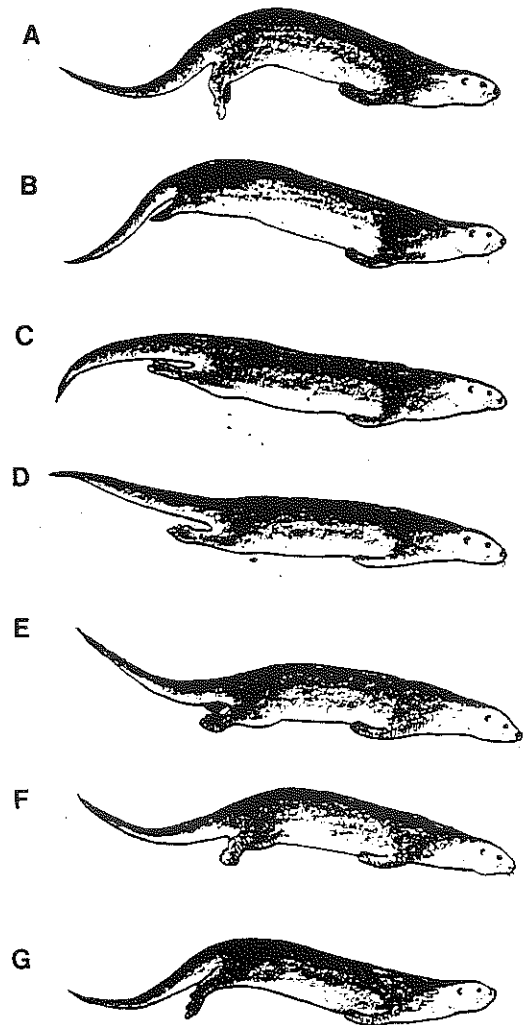

FIG. 1.—Sequence of swimming motions of a river otter through one stroke cycle using the undulatory mode. Time interval between successive drawings is 0.156 s. A, B, C) Power phase; D) glide phase; E, F, G) recovery phase.

The ventral waveform continued to progress toward the tail tip through the power phase. The otters would glide between successive power and recovery phases. During gliding, body and tail were held straight and limbs were held against the body.

Five sequences were digitized from otters at the National Zoo to detail the kinematics of the tail wave. Less than one wavelength was exhibited in the tail at any time. The
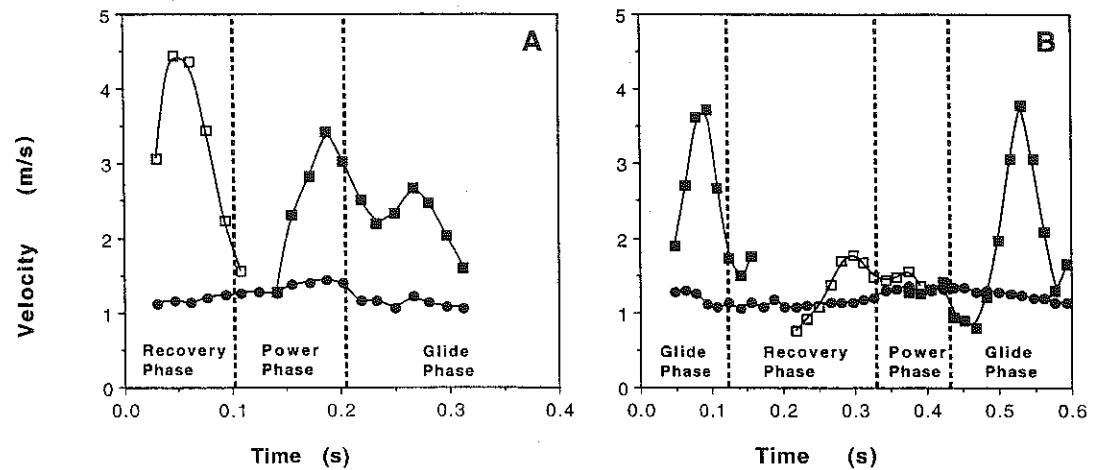
FIG. 2.—Two examples of plots of instantaneous velocities as a function of time for a single river otter swimming. Solid circles represent swimming velocity, and squares represent velocities of dorsal (solid) and ventral (open) tail waveforms. In both examples, tail-waveform velocities are greater than the forward velocity of the otter.

tail wave exhibited an asymmetry with regard to dorsoventral amplitude (Fig. 1). Ventral amplitude was maximally two times greater than dorsal amplitude when measured at the tip of the tail.

The traveling wave in the tail moved posteriorly at a velocity faster than the anterior velocity of the otter (Fig. 2). Mean posterior velocity over a propulsive cycle was 1.62 (range of 1.16 to 2.07) times anterior velocity. The tail wave accelerated from initiation near the pelvis to a maximum posterior velocity at approximately the tail center before decelerating at the tail tip. Mean maximum posterior velocity was 2.52 (range of 1.56 to 3.84) times anterior velocity. Dorsal tail waveform velocity was faster than anterior velocity during glide and power phases, whereas ventral waveform posterior velocity was greater than anterior velocity during the recovery phase (Fig. 2). During the power phase, actions of hind limbs and tail were associated with acceleration by otters to velocities 8.0–77.4% higher than at the start of this phase. The glide phase showed a decrease in anterior velocity by 11.5–25.0%. During the recovery phase, increases in anterior velocity of

6.2–36.8% were noted in cases where posterior velocity exceeded anterior velocity. However, a single case in which anterior and posterior velocities were approximately equal had a 36.8% decrease in anterior velocity over the time of the recovery phase.

Association of propulsive mode, depth, and displacement pattern.—For otters at the Philadelphia Zoo (Table 1), propulsive mode (paddling modes versus undulation), depth (surface versus submerged), and displacement pattern (rectilinear swimming versus maneuvering) were not mutually independent ($P < 0.001$). Paddling modes were used predominantly by otters swimming at the surface and when maneuvering. Lateral turns were accomplished by paddling with the limbs extended to the inside of the turn and lateral flexion of the body. Paddling motions by the limbs were used in >97% of all undulatory swimming bouts. Of these, 16.5% used all limbs in association with undulation.

Vertical maneuvers (i.e., surfacing and diving) were performed by dorsal or ventral bending of the body, which were followed typically by paddling motions of hind feet. Undulatory swimming was confined largely

TABLE 1.—*Percentage of observations of various propulsive modes for surface and submerged swimming of river otters at the Philadelphia Zoo and for submerged swimming at the Brandywine and National zoos.*

| Mode | Philadelphia | | | | Brandywine and National: submerged | |
| | Surface | | Submerged | | | |
	Rectilinear	Maneuvering	Rectilinear	Maneuvering	Rectilinear	Maneuvering
Forelimbs	4.2	40.7	0.0	27.3	0.0	33.3
Hind limbs	75.0	0.0	20.0	9.1	21.7	13.3
All limbs	10.4	44.4	2.9	50.0	4.3	40.0
Undulation	10.4	14.8	77.1	13.6	73.9	13.3
n	48	27	35	22	46	30

to rectilinear, submerged locomotion (77.1%). This mode was most apparent when otters were swimming at high speed (≤ 1.5 m/s). Except for rectilinear, submerged swimming, $<15\%$ of observations were recorded for undulatory swimming.

When the paddling mode was partitioned into forelimb, hind-limb, and all-limb paddling (Table 1), a significant χ^2 ($P < 0.001$) indicated an interdependence of propulsive mode, depth, and displacement pattern. A test of partial independence (Zar, 1984) showed specifically that propulsive mode was not independent of depth and displacement pattern ($P < 0.001$). Forelimbs were used predominantly for maneuvering both at the surface (85.1%) and when submerged (77.3%). Forelimbs were almost never employed in rectilinear swimming. Hind-limb paddling was used in 75% of the observations for rectilinear swimming at the surface and was never used for maneuvering on the surface.

Results from submerged swimming by otters at the Brandywine and National zoos (Table 1) were similar to those obtained from the Philadelphia Zoo. Of the four otters observed at the two zoos, none displayed any use of forelimbs solely for rectilinear, submerged swimming. A total of 73.3% of all observations during maneuvering used forelimb or quadrupedal paddling. Undulation was the predominant mode (73.9%) used for rectilinear swimming. A significant χ^2 ($P < 0.001$) indicated that propulsive mode and displacement pattern were not independent.

DISCUSSION

Observations of otters swimming suggest that these semiaquatic animals have a wide variety of swimming modes (Howell, 1930; Tarasoff et al., 1972). Otters exhibited various forms of paddle propulsion by using several combinations of their limbs at any one time. In addition, otters displayed a form of undulatory propulsion using their elongate, flexible bodies and tails in concert with simultaneous hind-limb paddling. Tarasoff et al. (1972) considered paddling to be the principal mode for sustained swimming, whereas undulation was used in bursts of rapid swimming.

Although otters are plastic in their choice of propulsive mode, that choice is determined by displacement pattern and water depth. Alternate hind-limb paddling was confined to rectilinear surface swimming, undulation was confined to rectilinear submerged swimming, and quadrupedal or forelimb paddling were used during maneuvering. Paddling typically is found in surface swimmers (Fish, 1984; Williams, 1983, 1989), which are terrestrial or semiaquatic mammals that do not exhibit pronounced aquatic adaptations, particularly with regard to diving (Fish, 1992; Fish and Stein, 1991; Howell, 1930). Conversely,

undulation is used by highly-derived aquatic mammals (i.e., cetaceans, pinnipeds, sirenians) that move considerable distances underwater (Fish, 1992; Fish et al., 1988).

The dichotomy in propulsive mode with regard to swimming depth by otters may relate to performance. Like the river otter, the sea otter (*Enhydra lutris*) can swim by paddling at the surface or by undulating underwater (Kenyon, 1969; Williams, 1989). Williams (1989) found that sustained paddling by sea otters was limited on the surface to speeds <0.8 m/s. Sea otters attained speeds ≤1.39 m/s with undulation underwater. Energy loss through production of waves at the water surface increases drag and limits swimming speed compared with submerged swimming (Fish, 1982; Hertel, 1966; Williams, 1989). Switching from surface paddling to submerged undulation at 0.8 m/s, sea otters decreased their drag 3.5-fold and their cost of transport by 41%.

Compared with paddling, undulation is associated with larger thrust forces for rapid swimming and with large body size, high-powered turns, and larger accelerations (Webb and Blake, 1985; Webb and de Buffrenil, 1990). These advantages were enhanced further with the evolution of a caudal hydrofoil (Webb, 1975). In addition, undulation is highly efficient as opposed to paddling (Fish, 1984, 1992; Fish et al., 1988; Webb and Blake, 1985). Paddling efficiency is low, because the net thrust force is reduced as energy is lost to drag in repositioning the limb during the recovery phase (Alexander, 1983; Fish, 1984). Undulatory movements have no recovery phase, so that thrust is generated throughout the stroke cycle.

Efficient dorsoventral undulatory swimming may be precluded from use at the surface. When body and tail bending occurs in the vertical plane, waves are created that will increase drag and reduce thrust. In one instance, an otter generated large waves from its upward tail motion even when at a depth of 0.14 m. In surface paddling by river otters, limbs are submerged sufficiently

so that movements generate thrust without increasing wave drag.

Paddling modes followed previous gross descriptions for river otters (Chanin, 1985; Estes, 1989; Howell, 1930; Savage, 1957; Tarasoff, 1972; Tarasoff et al., 1972). However, my description of the undulatory mode differs with descriptions characterizing the undulatory mode as carangiform (Tarasoff et al., 1972), the mode used by fish (Lighthill, 1969). Description of the undulatory mode by Tarasoff et al. (1972) stated that dorsoventral bending originated from the lumbar region of the otter and was transmitted through the pelvis to vertical sweeps by the tail without using the hind limbs. The limbs were reported to be held against the body or used for balance. My observations and kinematic data indicate that simultaneous paddling of the hind feet is integral to undulation. Power and recovery phases of the hind-limb stroke cycle are coupled tightly with generation of a traveling wave in the tail. Limb motions are reminiscent of an asymmetrical terrestrial gait, such as a bound or gallop (Hildebrand, 1980, 1989; Howell, 1930; Williams, 1983). In these gaits, pectoral and pelvic pairs of limbs move in unison or couplets, and the trunk is alternately flexed and extended. Such gaits are used in high-speed sprints.

The undulatory mode with all limbs was used by river otters during rapid accelerations (Moller and Reuther, 1985; present study). Collective use of all four limbs plus the tail for propulsion should greatly enhance acceleration performance. Once a high velocity was obtained, otters held the forelimbs against the body and continued to undulate with simultaneous strokes of the hind limbs. This shift from propulsion requiring all four limbs to propulsion using hind limbs only could result in decreased drag on the body and increased energetic efficiency (Weihs and Webb, 1983).

Is the undulatory mode of otters simply a consequence of a terrestrial gait by which thrust is generated solely through paddling

and without participation from the tail? For a traveling wave to generate thrust, the wave velocity must be faster than the forward velocity of the animal (Webb, 1975). Indeed, from the results presented above, the traveling wave in the otter's tail moves with a posterior velocity that is 62% faster than anterior velocity. This pattern suggests that the tail may generate thrust in this species. Blight (1977) proposed the hybrid-oscillator model as a general mechanism for thrust generation by swimming animals. In this model, flexion due to muscular contraction at a "stiffness-dominated" anterior end is translated as a propulsive wave posteriorly through a flexible, "resistance-dominated" posterior. The lumbo-sacral region of *Lutra* has large epaxial and hypaxial muscle masses in conjunction with elongate neural spines and transverse processes (Howell, 1930; Tarasoff, 1972). Active movement of the relatively stiff lumbo-sacral region by muscular contraction could produce a propulsive traveling wave through the flexible tail in accordance with Blight's model.

The contribution of the tail to swimming can be important when coupled with simultaneous hind-foot paddling in otters. Because both hind feet were accelerated posteriorly, they affected a large water mass and developed a large thrust force. This action accelerated the whole body through the power phase (Fig. 2). However, both feet must be repositioned during the recovery phase for the next stroke. Consequently, no thrust would be developed by the feet, and drag would increase (Fish, 1984), causing a deceleration. Thrust generated by the tail, particularly during recovery and glide phases, can maintain a constant swimming velocity, cause acceleration, or minimize deceleration. Continuous high-performance locomotion is required by river otters in pursuit of elusive, fast-swimming prey, such as fish and frogs (Baker, 1983; Brzezinski et al., 1993; Erlinge, 1969; Lager and Ostenson, 1942; Liers, 1951).

Because tail propulsion minimizes oscil-lations in velocity (i.e., acceleration-deceleration) through the stroke cycle, the energy requirement for high-speed swimming may be reduced in otters. Unsteady swimming by an animal requires the instantaneous thrust force to be balanced by the force to overcome its drag, inertia, and acceleration reaction (the reaction in the fluid to changes in velocity—Daniel, 1984, 1985). Changes in velocity over time will increase forces associated with inertia and with the acceleration reaction. This results in increased energy consumption and lowered mechanical efficiency (Blake, 1979; Fish, 1984, 1985). For unsteady swimming, the cost of locomotion can be about one order of magnitude greater than the cost for steady undulatory swimming (Daniel, 1985).

Increased performance using caudal undulation is achieved by expanding the tail distally. This has culminated in the rapid evolution of several vertebrate lineages that use high-efficiency caudal hydrofoils (i.e., flukes), facilitating steady swimming performance (Webb and de Buffrenil, 1990). Although robust and compressed, the tails of otters taper to a point (Baker, 1983; Chanin, 1985; Tarasoff et al., 1972); thus, the mass of water affected to generate thrust progressively decreases toward the tip (Lighthill, 1970; Webb, 1975). In addition, the unsteady nature of posterior velocity, particularly with regard to a deceleration from mid-tail to tip, will further reduce thrust production by the tail. Caudal segments of the tapering tail can contribute little thrust compared with anterior segments and may add to drag and kinetic energy loss into the wake.

An intermediate morphology between river otters and mammals with caudal hydrofoils is displayed by the giant river otter, *Pteronura brasiliensis. Pteronura* possesses webbed hind feet and a broad, flattened tail (Chanin, 1985; Howell, 1930; Sanderson, 1956). Films by Cousteau and Cousteau (1984) show that *Pteronura* is capable of rapid, submerged swimming by undulation of the tail with simultaneous strokes by the

hind limbs. At present, it remains to be determined if tail waves of *Pteronura* have posterior velocity greater than anterior velocity for thrust production. However, the change in tail morphology of *Pteronura* should allow for increased thrust and suggests with *Lutra* a possible route in the evolution of aquatic mammals from drag-based paddling to lift-based undulation (Howell, 1930; Sanderson, 1956).

Propulsive modes and associated swimming behaviors demonstrated by the river otter may reflect transitional swimming patterns employed by ancestors to highly derived aquatic mammals. The evolution of these aquatic mammals from their terrestrial ancestors would have required increased swimming performance with minimal compromise to terrestrial movement. Key to the evolutionary transition from terrestrial to fully aquatic habits was the change from paddling to undulatory swimming (Fish, 1982). This mode change improves swimming performance by enhanced thrust generation and drag reduction. Cetaceans, pinnipeds, or sirenians independently evolved propulsive modes based on undulatory swimming. Although otters are not directly related to these highly derived aquatic mammals (Barnes et al., 1985), the change from paddling to undulatory swimming as displayed by the river otter could have been undertaken by the ancestors of aquatic mammals with only slight modification to the neuromotor pattern used for terrestrial locomotion.

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