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HIPPOPOTAMUS UNDERWATER LOCOMOTION: REDUCED-GRAVITY MOVEMENTS FOR A MASSIVE MAMMAL

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Use of the aquatic environment by hippopotami (*Hippopotamus amphibius*) allows locomotive styles impossible to achieve on land by such heavy animals. Videos of the underwater locomotion of 2 hippopotami were analyzed frame by frame. Average horizontal velocity underwater was 0.47 m/s. Hippopotami used a gait underwater that was similar to a gallop with extended unsupported intervals. Ground contact time decreased with increasing horizontal velocity, vertical displacement during the unsupported intervals increased with an increase in ground contact time, and time between consecutive footfalls decreased with an increase in horizontal velocity. Hippopotami use an unstable gait underwater, which is facilitated by the increased buoyancy of water. Despite restrictions to movement on land due to its massive weight, locomotion of the hippopotamus underwater is analogous to movement in a microgravity environment.

Key words: hippopotamus, locomotion, microgravity, unsupported interval, walking

The hippopotamus (*Hippopotamus amphibious*) is a semi-aquatic mammal that is found throughout Africa south of the Sahara Desert in rivers and lakes surrounded by grasslands and reedbeds. Hippopotami prefer areas of slow and relatively shallow water with gently sloping banks (Vilojoen and Biggs 1998). Hippopotami graze on land for 5–6 h each night and remain in the water and submerged throughout most of the day (Klingel 1995; Nowak 1999). This amphibious mammal has been reported to be an excellent diver and swimmer (Feldhamer et al. 1999; Howell 1930). However, hippopotami are poorly streamlined with little modification of the feet for swimming (Eltringham 1999; Fish 1993; Howell 1930).

The hippopotamus is rarely found out of contact with the bottoms of rivers and lakes, and walks underwater rather than swims (Eltringham 1999; Feldhamer et al. 1999; Fisher et al. 2007; Klingel 1991; Nowak 1999). Maintenance of foot contact with the bottom is accomplished by control of the specific gravity of the body and high bone density (Nowak 1999; Wall 1983).

Adult hippopotami weigh approximately 1,000–4,500 kg and reach a height of about 1.5 m at the shoulder (Nowak 1999). Their massive size and relatively robust and short legs can potentially restrict terrestrial locomotion (Biewener 1989; Hildebrand 1980). Although they are capable of running, analysis of hippopotami locomoting on land has shown that a walking gait is used with 3 feet always in contact with the ground (Hildebrand 1976, 1980, 1989). Therefore, the alternating 3 limbs form a highly stable triangle of support in which the projected center of mass of the animal is enclosed. In the water, however, increased buoyancy allows the hippopotamus greater latitude in gait selection (Edwards 1989). Hippopotami have been observed to undergo much longer swing phases in water than on land (Niemitz 2001). In addition, quadrupedal support is infrequent, with bipedal support predominating underwater. There are periods in which the hippopotami are ''in flight'' with no feet in contact with the ground (Niemitz 2001). In deep water, they locomote by ''a series of porpoise-like leaps off the bottom'' or in ''a series of high, prancing steps'' (Eltringham 1999).

The purpose of this study was to examine the kinematics of underwater locomotion of the hippopotamus by video analysis. The aquatic environment, although increasing resistance to movement, buoys the animal up. This increased buoyancy effectively acts to make water a microgravity environment. Such conditions should allow the use of gaits that would be unstable in the terrestrial environment.

Materials and Methods

Two adult female hippopotami were observed at the Adventure Aquarium in Camden, New Jersey. Each hippopotamus weighed approximately 1,360 kg. They were maintained in an indoor exhibit 523 m^2 in size, which contained both an area of dry land and a pool. The pool held a volume of 246 m^3 and had a maximum depth of 2.4 m.

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The hippopotami were observed through a viewing window, which constituted 1 side of the pool. The viewing window had an area of 46.5 m^2 (11.3 × 4.0 m). The locomotion of each hippopotamus was recorded with a Sony DCR-TRV 240 NTSC digital video camera recorder (Sony Electronic Corp., San Diego, California) at 60 Hz set on a tripod. The video recordings were imported into a Macintosh iBook (OS 9.2) using iMovie (Apple Inc., Cupertino, California) and analyzed frame by frame at 30 frames/s with VideoPoint (version 2.5; Lenox Softworks, Lenox, Massachusetts).

Only segments of video in which the hippopotami were moving parallel to the viewing window were used for analysis. The hippopotamus's eye that was facing the camera was used as a marker to record the position of the hippopotami in each frame. Data on position and time were used for calculations of horizontal displacement (HD) and vertical displacement (VD), average and maximum velocities (Vs), and maximum acceleration. Footfall data were recorded by counting the number of frames in which an individual foot was in contact with the ground. The number of frames of contact was multiplied by 1/30 s to determine the amount of time each foot was in contact with the ground. Multiple contacts in the same video sequence were averaged for the forefeet and hind feet.

Data were analyzed statistically using Microsoft Excel 2003 (Microsoft Corporation, Redmond, Washington) and Statistical Program for Social Sciences (version 15.0; SPSS Inc., Chicago, Illinois). Variation about means was expressed as ±1 *SD*. All least-squares regressions and correlation coefficients (r) were calculated using KaleidaGraph software (version 3.0.2; Synergy Software, Reading, Pennsylvania). Statistical significance was set at a level of $P < 0.05$.

Results

The hippopotami were observed between 0800 and 1000 h immediately after their feeding period. The hippopotami entered the water and proceeded to move in a counterclockwise direction around the pool, while contacting the bottom. The animals remained at the bottom unless pushing off from the bottom to breathe. The animals were never observed to swim in the water. A total of 102 sequences were recorded of the 2 hippopotami. Of these sequences, 31 were selected for analysis. The selected sequences showed the hippopotami moving parallel to the viewing window, without direct contact, and the feet and eye of the focal animal were visible. A total of 52 forefoot contacts with the ground was recorded, with 36 consecutive forefoot contacts. Twenty-three hind-foot contacts with the ground were recorded.

The gait of the hippopotamus resembled an extended gallop (Hildebrand 1980, 1989) with only 1 foot contacting the ground at any time and prolonged unsupported intervals or suspensions (i.e., no feet contacting the ground). The entire foot was observed to contact the ground with each step. A large time duration was observed for periods of ground contact by forefeet and hind feet (2.17 ± 0.70 s). However, time duration between successive ground contacts of forefeet or hind feet was longer (2.73 ± 0.79 s). In many sequences, movements of animals along the bottom were affected solely by extension and retraction of the forefeet. The forefoot contact would alternate or a forefoot on 1 side could be used multiple times, while the forefoot on the opposite side was held against the body. During these periods, the hind feet were extended posteriorly. The head and body were pitched down 5–10° leading into steps by the forefeet, and pitched up 5° after steps by forefeet or hind feet.

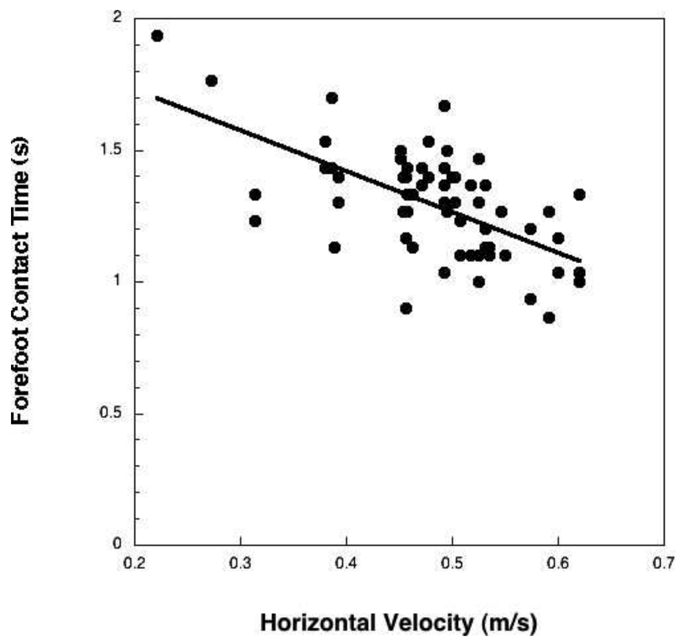

Fig. 1.—Plot of contact time of the forefeet (FFCT) of the hippopotamus (*Hippopotamus amphibius*) as a function of horizontal velocity (V) during locomotion underwater.

Vertical oscillations were noted through the gait cycle. The eye of the animal moved in a sinusoidal manner. Maximum VD occurred at the midpoint of an unsupported interval. The mean VD due to oscillations through the stride cycle was 0.20 ± 0.06 m ($n = 22$). The maximum VD was 0.39 m, and the minimum VD was 0.10 m. The vertical velocity of the initial phase of the unsupported interval was 0.27 ± 0.14 m/s (range: 0.10–0.73 m/s).

The mean horizontal V of the hippopotami underwater was 0.47 ± 0.09 m/s ($n = 31$), with a range of 0.22–0.62 m/s. *V* exhibited an inverse relationship with forefoot contact time (FFCT; Fig. 1). This relationship was described by the regression equation:

$$\text{FFCT} = 2.11 - 1.69\text{V}, \quad (1)$$

with $r = 0.77$ ($P < 0.001$). A direct relationship was found between FFCT and the VD of the hippopotami (Fig. 2), according to the equation:

$$\text{FFCT} = 1.13 + 1.02\text{VD}, \quad (2)$$

with $r = 0.35$ ($P < 0.02$). No correlation was found between hind-foot contact time and V. The time interval between forefoot contacts (ICFF) with the ground decreased with increasing V (Fig. 3) as:

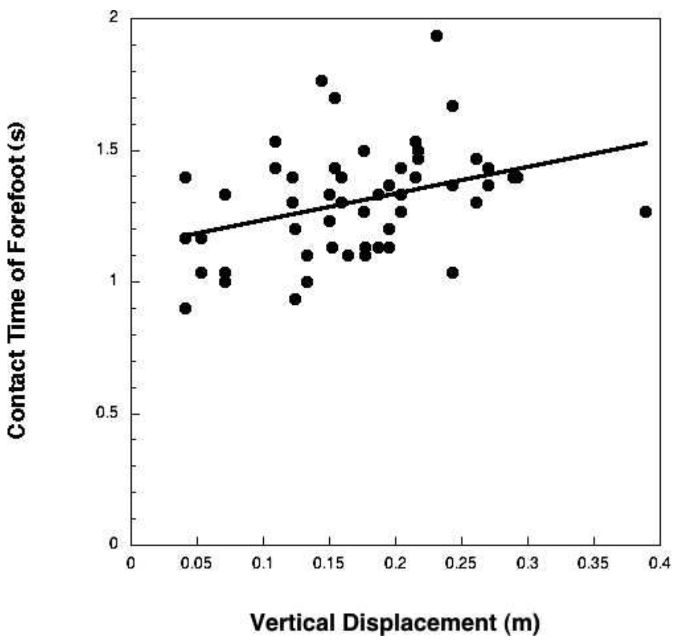

FIG. 2.—Relationship of forefoot contact time (FFCT) and vertical displacement (VD) of unsupported intervals during underwater locomotion by the hippopotamus (*Hippopotamus amphibius*).

$$\mathrm{ICFF} = 4.58 - 4.58\mathrm{V}, \tag{3}$$

with $r = 0.49$ ($P < 0.001$).

The HD during the unsupported interval was 1.45 ± 0.37 m ($n = 21$), with a range of 0.98–2.39 m. The mean V of the unsupported interval was 0.46 ± 0.11 m/s ($n = 31$). The maximum V was 0.70 m/s, which was almost 50% greater than the mean V of the animal.

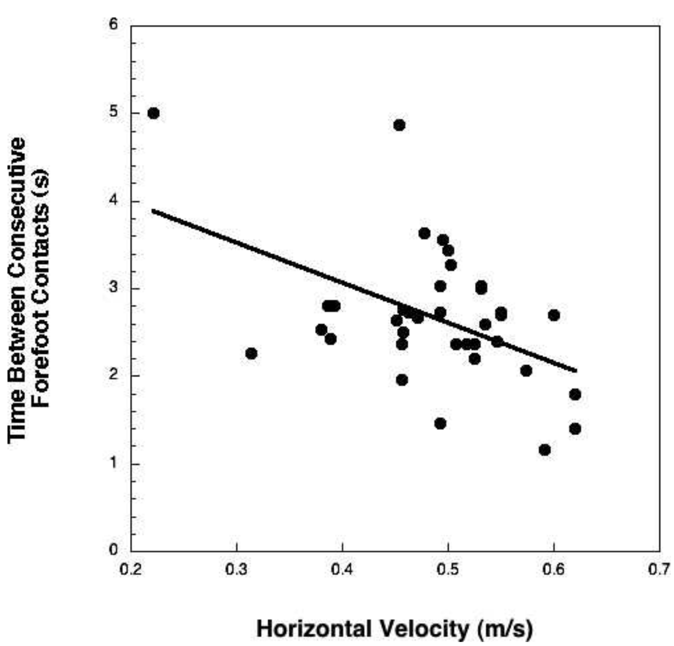

FIG. 3.—Plot of time between consecutive forefoot contacts (ICFF) with the ground and horizontal velocity (V) during underwater locomotion by the hippopotamus (*Hippopotamus amphibius*).

The mean vertical acceleration of the unsupported interval was 0.78 ± 0.37 m/s^2, with a range of 0.19–1.99 m/s^2. The maximum vertical acceleration was taken from a hippopotamus that was pushing off the ground in an attempt to reach the surface of the water. The mean vertical acceleration was 92% lower than the acceleration due to gravity (9.8 m/s^2).

DISCUSSION

The amphibious hippopotamus spends the majority of its time in the water during the day. *H. amphibius* can remain submerged for up to 30 min, and mate and give birth in water (Eltringham 1999; Feldhamer et al. 1999; Nowak 1999; Prothero and Schoch 2002). These animals have a number of anatomical adaptations associated with the aquatic environment. Hippopotami have partially webbed feet, nearly naked skins that are glandular, valvular nostrils and ears, and dorsally protruding nostrils and eyes, although the eyes of the pygmy hippopotamus (*Hexaprotodon liberiensis*) are located more laterally than in *H. amphibius* (Eltringham 1999; Howell 1930; Nowak 1999). The musculature in the forelimb shows increased size and muscle fusions that are associated with increased power to support the massive body and overcome resistance of the water when locomoting (Fisher et al. 2007).

Hippopotami, including both *H. amphibius* and *H. liberiensis*, use a lateral sequence walk on land (Hildebrand 1989; Niemitz 2001). This is a highly stable gait in which hippopotami have 3 limbs in contact with the ground at any time. This arrangement of limbs causes the projected center of mass to fall in the center of a triangle formed by the supporting legs at low speeds (Biewener 2003; Gray 1944; Hildebrand 1980). Niemitz (2001) reported that hippopotami have 3 or 4 feet on the ground simultaneously for three-fourths of a stride cycle on land, but they employ bipedal support for the other one-fourth of the cycle (Niemitz 2001; C. Niemitz, Freie Universität Berlin, pers. comm.). *H. amphibius* runs using a trotting gait, which can have a brief suspension (Hildebrand 1980). Diagonally opposite legs swing in unison in a trot (Hildebrand 1980, 1989). The trot is used by mammals with short to medium legs, where some relative stability is achieved from the projected center of mass falling on a line between the supporting diagonal legs (Hildebrand 1976, 1989).

The underwater gait observed in bottom walking by hippopotami differed substantially from that used for terrestrial locomotion. However, hippopotami may use a trot underwater, as indicated in a photograph published by Klingel (1991). For animals observed in this study, movement underwater used a gallop with extended unsupported intervals. This type of aquatic pedestrian locomotion has been referred to as ''punting.'' Underwater punting involves the limbs pushing off the substrate for alternating phases of thrust generation and gliding through the water (Koester and Spirito 2003; Martinez et al. 1998). As in a terrestrial gallop, intervals between forefoot and hind-foot couplets in the hippotamus were short (Hildebrand 1980, 1989).

As originally predicted, the hippopotamus in water used an unstable gait, which was characterized by a gallop, decreased contact time of the feet with increasing speed, predominant use of the forefeet, and prolonged unsupported intervals (Hildebrand 1980, 1989). Gallops are typically highly unstable gaits (Edwards 1989; Hildebrand 1980, 1989). Terrestrial gallops are used at relatively high speeds for dynamic equilibrium to compensate for the increased instability (Hildebrand 1980). However, in water, with its increased buoyancy to maintain stability, gallops can be performed at extremely slow speeds (Edwards 1989).

Niemitz (2001) noted a dominance of the forefeet in the underwater locomotion of the hippopotamus. The predominant use of the forefeet is believed to be associated with the weight distribution of the body. The head of *H. amphibius* is massive (Eltringham 1999). It was estimated that approximately 60% of the weight of the hippopotamus was supported by the forefeet (Niemitz 2001). This is high compared to another graviportal mammal, the elephant, which has only 55% of its weight supported by the forelimbs (Rollinson and Martin 1981). The tendency for the head of the submerged hippopotamus to pitch downward at the end of an unsupported interval would be a direct consequence of a heavy anterior end.

The underwater gait of the hippopotamus was distinguished by vertical displacement during the unsupported intervals. The vertical displacement varied directly with an increase in ground contact time. An increase in ground contact time translates to an increase in the amount of time allowed for generation of vertical force and associated vertical displacement (Farley et al. 1991). The effect of galloping in water with increased buoyancy results in less contact time with the substrate (Ashley-Ross and Bechtel 2004; Edwards 1989; Martinez et al. 1998). This effect has been likened to locomoting in a microgravity environment (Niemitz 2001). Under conditions of reduced gravity, humans switch from a walk to a run at slower speeds (Kram et al. 1997). A velocity increase is associated with smaller duty factors (i.e., ground contact time as a percentage of total cycle [Alexander 1984; Donelan and Kram 1997, 2000]), whereas a decrease in body weight results in decreased time of ground contact (Farley et al. 1993). In addition, longer stride lengths occur with reduced gravity (Donelan and Kram 2000). Humans prefer to run with an extended unsupported interval or ''lope'' in reduced gravity (He et al. 1991; Newman et al. 1994).

Effective bottom walking requires a body that is denser than water when submerged. Increasing body density by increased deposition of compact bone in the appendicular skeleton has been cited as a means that semiaquatic mammals can use to increase their specific density to overcome buoyancy (Fish and Stein 1991; Wall 1983). Osteosclerosis is an increase in bone density by the replacement of cancellous bone with compact bone or by increasing cortical bone thickness at the expense of the medullary cavity (Domning and de Buffrénil 1991; Thewissen et al. 2007; Wall 1983). Osteosclerosis is a common adaptation in semiaquatic and aquatic mammals for buoyancy control (Domning and de Buffrénil 1991; Fish and Stein 1991; Gray et al. 2007; Wall 1983). Additional bone density is achieved by tightly packing cancellous bone into the medullary cavity, as occurs in *H. amphibius* (Wall 1983).

The increased ballast of the denser limb bones in the hippopotamus aids in stabilization when submerged. Extension of the heavy limbs under the body positions the center of mass below the center of buoyancy. The greater the vertical difference between these centers, the greater the stability with respect to movement around the roll axis of the body (Fish 2002). This orientation allows bottom walking underwater without incurring unstable motions.

Aquatic locomotion in mammals by bottom walking is not confined to the hippopotamus. The nine-banded armadillo (*Dasypus novemcinctus*) walks on the bottom of shallow bodies of water for short distances (Taber 1945). The hydrophilic African mousedeer or water chevrotain (*Hyemoschus aquaticus*) takes to water when threatened and hides on the bottom under floating objects (e.g., logs or mats of vegetation). The water chevrotain is considered to be a good swimmer and can walk along the bottom (Dubost 1978; Prothero and Foss 2007; Prothero and Schoch 2002). Thewissen et al. (2007) suggested that bottom walking may have been employed by the ancestors of cetaceans. A sister taxon of cetaceans, *Indohyus* (Raoellidae), had an aquatic lifestyle. This fossil artiodactyl is considered to have waded in water with heavy bones for ballast, analogous to hippopotami (Thewissen et al. 2007). The heavy skeleton of the quadrupedal sirenian *Pezosiren portelli* may have similarly allowed bottom walking to graze on aquatic plants (Domning 2001a, 2001b).

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