Footfall patterns and stride parameters of Common hippopotamus (*Hippopotamus amphibius*) on land

John R Hutchinson [Corresp., 1] , **Emily V Pringle** [1]

[1] Comparative Biomedical Sciences, Structure and Motion Laboratory, The Royal Veterinary College, North Mymms, Hertfordshire, United Kingdom

Corresponding Author: John R Hutchinson
Email address: jrhutch@rvc.ac.uk

Common hippopotamuses (hippos) are among the largest extant land mammals. They thus offer potential further insight into how giant body size on land influences locomotor patterns and abilities. Furthermore, as they have semi-aquatic habits and unusual morphology, they prompt important questions about how locomotion evolved in Hippopotamidae. However, basic information about how hippos move is limited and sometimes contradictory. We aimed to test if hippos trot at all speeds and if they ever use an aerial (suspended) phase, and to quantify how their locomotor patterns (footfalls and stride parameters) change with speed. We surveyed videos available online and collected new video data from two zoo elephants in order to calculate the data needed to achieve our aims; gathering a sample of 169 strides from 32 hippos. No hippos studied used other than trotting footfall patterns, but at the fastest relative speeds hippos used brief aerial phases, apparently a new discovery. Hippos exhibit relatively greater athletic capacity than elephants in several ways, but perhaps not greater than rhinoceroses. Our data help form a baseline for assessing if other hippos use normal locomotion; relevant to clinical veterinary assessments of lameness; and for reconstructing the evolutionary biomechanics of hippo lineages.

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4 John R. Hutchinson and Emily V. Pringle

5 Structure and Motion Laboratory, Department of Comparative Basic Sciences, The Royal
6 Veterinary College, North Mymms, Hertfordshire, United Kingdom

8 Corresponding author: John R. Hutchinson

9 Structure and Motion Laboratory, Department of Comparative Basic Sciences, The Royal
10 Veterinary College, Hawkshead Lane, North Mymms, Hertfordshire, AL9 7TA, United
11 Kingdom

12 Email address: jhutchinson@rvc.ac.uk

14 **Abstract**

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29 lineages.

Introduction

Common hippopotamus (*Hippopotamus amphibius* Linnaeus 1758) are the fifth heaviest extant land mammals (vs. three species of elephants, and white rhinoceros) albeit close in size to black rhinoceros (references); at ~1500 kg adult body mass (Owen-Smith, 1988; Silva and Downing, 1995), with the largest recorded individuals surpassing 3800 kg (cited in Garland, 1983). At such large sizes, they offer important comparative information on how body size influences locomotor abilities on land. In general, mammals >100 kg are able to move more slowly than medium-sized mammals, and at extreme sizes >1000 kg, maximal speed and even gait capacities decrease (Garland, 1983; Dick and Clemente, 2017; Hutchinson, 2021). For example, elephants are well known to not move faster than about 7 ms^{-1} (25 kph), retaining a lateral sequence symmetrical footfall pattern (i.e., foot contact sequence: left hind, left fore, right hind, right fore; Muybridge, 1887; Slijper, 1946; Cartmill et al., 2002; Struble and Gibb, 2022) never with an aerial (suspended) phase (e.g., Gambaryan, 1974; Hutchinson et al., 2003, 2006). The largest extant rhinoceroses might not move much faster than elephants, although reliable data are very scarce for them -- yet they can use an asymmetrical transverse galloping gait with an aerial phase (Slijper, 1946; Dagg, 1973; Gambaryan, 1974; Hildebrand, 1977; Alexander and Pond, 1992; Paul and Christiansen, 2000). Giraffes, which are substantially smaller (<1300 kg), use a lateral sequence walk and rotary gallop; not trotting (e.g., Hildebrand, 1965, 1980, Dagg, 1973, 1979; Gambaryan, 1974; Hildebrand, 1977; Basu, 2019a,b).

Similarly, there are few empirical data for terrestrial locomotion in the Common hippopotamus or their relatives the pygmy hippopotamus (*Choeropsis liberiensis* or *Hexaprotodon liberiensis*). Maximal speeds have not been reliably measured but have been claimed (without empirical documentation) at up to ~8 ms^{-1} (~30 kph; Dagg, 1973; Bakker, 1975; Garland, 1983; Kingdon, 1989; Nowak, 1999). Hildebrand (1989) provided some footfall pattern data for the pygmy hippopotamus, indicating a lateral sequence walk, but noted that Common hippopotamus (onwards here, simply "hippos") will use a walking trot (Hildebrand, 1962, 1965, 1967, 1976) and running trot (Hildebrand, 1980, 1989); meaning a symmetrical gait with diagonally synchronised limbs. Dagg (1973; also Howell, 1944) gave a basic classification of gaits in hippos, listing them as using a typical (lateral sequence) walk, but no indication of a 'running walk', and also as using a trot; but no galloping gait (stating they "cannot hoist themselves into the air"). They commented that prior studies such as Slijper (1946) classified a faster hippo gait as an 'amble' (lateral sequence), but that this term was too "ambiguous", implying it did not apply well to hippos. Dagg (1979) followed up with analysis of video data for 29 strides of a hippo that "did not use lateral supporting legs at all", concluding that the wide body and relatively short legs (e.g., Bakker, 1975) prevent balance on two ipsilateral legs (presumably due to excessive rolling momentum). Other studies of slower walking locomotion in hippos have observed lateral sequence footfall patterns (Niemitz, 2001; also see Coughlin and Fish, 2009), albeit sometimes closer to diagonal sequence (e.g., Catavitello et al., 2018). Usherwood and Self Davies (2017) obtained data for hippos using slow trotting, suggesting that this pattern minimises mechanical and perhaps metabolic energy usage (also see Smith and Usherwood, 2020). In contrast, Coughlin and Fish (2009) showed that hippos can use asymmetrical "punting" locomotion underwater (also see Niemitz, 2001; Bennett et al., 2014; Mazza, 2014; Van der

72 Greer et al., 2015; *contra* Dagg, 1973). While hippos spend much time in the water or resting
73 (~50%), their locomotion on land must remain important because they still spend around one-
74 third of their time doing so, particularly at night (e.g., Owen-Smith, 1988; Timbuka, 2012;
75 Mekonen and Hailemariam, 2016; Fernandez et al., 2020).

76 It has become at least tacitly accepted that hippos do not use gaits on land that are more extreme
77 than somewhat fast symmetrical trotting (i.e., no asymmetrical cantering or galloping), but it is
78 unclear if hippos use aerial (suspended) phases at any speeds or gaits (e.g., Christiansen and
79 Paul, 2001; Thomson, 2019; Hutchinson, 2021). Furthermore, even the basic walking patterns of
80 hippos are almost uncharacterised; do they only use slower lateral sequence walking and then
81 switch to faster trotting footfall patterns? Here, to address these uncertainties and to further
82 understanding of hippo locomotion, we use video analysis to quantify their footfall patterns and
83 stride kinematics on land.

84

85 **Materials & Methods**

86 We compiled basic kinematic data from videos of locomoting hippos from two sources: first,
87 from an internet search (not exhaustive, but particularly searching for faster running-type
88 behaviours), and second, from firsthand data collection. Each video was split into one or more
89 "trials", with a trial defined as a cyclic sequence of one or more strides from the same individual.
90 The first source of data is listed in the Supplementary Information. Empirical data for the second
91 source were obtained at Flamingo Land Resort (Kirby Misperton, North Yorkshire, UK), as
92 follows. We had access to two adult hippos: a 19 year old male (hip height ~1.3m) and 23 year
93 old female (hip height ~1.2m). Body masses were not known for any subjects. At Flamingo Land
94 Resort, a GoPro Hero 3+ (San Mateo, California) camera was set on a tripod and positioned
95 along the fence of the hippos' yard. This placement ensured the hippos would walk roughly
96 parallel to the camera's field of view. The camera was switched on (recording at 30 Hz, 1920 x
97 1080 pixel resolution) and left running for when the hippos came out of the water and walked
98 across the yard to their stable. They were also encouraged to move freely in front of the camera
99 by placing food outside. A total of 16 hours of footage across two days was recorded in this
100 manner. It was difficult to encourage the hippos to move, because it was not desirable to cause
101 the hippos any stress or use unethical stimuli to cause them to run. Thus we captured only the
102 walking data that they were willing to provide. Ethics approval was given by the Clinical
103 Research Ethical Review Board at the Royal Veterinary College; approval number CR2022-003-
104 2.

105 GoPro light videos then were uploaded onto a laptop into GoPro Studio software (https://gopro-
106 studio.en.softonic.com/), where "fisheye" effects were removed, and the videos were converted
107 to AVI format. All videos were inspected and trials which included obvious non-steady
108 locomotion such as acceleration, deceleration, turning, or slow grazing were discarded. Each
109 video was analysed frame by frame in VirtualDub software (https://virtualdub.sourceforge.net/)
110 and the times at which each foot hit and left the ground (as long as feet approximately were
111 visible) were estimated. "Foot-on" was defined as the frame that the limb ceased travelling

112   forward; "foot-off" was defined as the frame that the limb began travelling forwards/upwards;
113   see Fig. 1. These definitions helped to reduce errors caused by blurriness, rough terrain, obscured
114   feet, or feet brushing the ground. Footfall patterns and other basic stride kinematics were
115   determined from these timing data, as follows.

116   We followed the standard approach of defining each limb's phase as the fraction of a stride
117   relative to the left hind foot contact (= 0.0). Biknevicius and Reilly (2006) suggested that trotting
118   can have (left fore and right hind) limb phases of between 0.44 and 0.56 (0.50 ± 0.06),
119   encompassing potential variation; we follow that definition here (and right fore phases should be
120   0.94-1.0). We also quantified duty factor (DF = ground contact time; i.e., stance phase duration;
121   divided by stride duration) and stride frequency (SF = 1/stride duration). Here we loosely term
122   gaits with DF≥0.5 as walking and DF<0.5 as running. As none of our videos had reliable scale
123   objects for calibrating distances, we could not calculate velocity-related parameters including
124   stride lengths. This was because distances were unknown in the internet videos, and we were
125   unable to place a scale object in the hippo enclosure during our filming. However, it provided the
126   advantage that we could obtain more trials because we did not have to rely on strides and trials
127   that were parallel to the camera's field of view and in the same plane as a scale object.

128   Our internet search for videos yielded 25 videos containing 34 trials used here. Usherwood and
129   Self Davies (2018) obtained kinematic data from 5 videos (1 no longer available; all obtained via
130   www.youtube.com) for hippos. Similarly, Lees et al. (2016) measured (again from
131   www.youtube.com; 3 videos but 1 redundant with our sample) hippos walking. We reanalysed
132   these 7 videos here as part of that sample of 23 videos. Our data collection at Flamingo Land
133   Resort provided 12 valid trials. All trials were composed of between 1 and 8 continuous strides
134   that we used for final data analyses; ultimately totalling 169 strides from the 46 trials for a total
135   of 32 individual hippos. Details on videos and trials are Table S1.

136   Our study's aims are descriptive, so we only used basic statistics. We plotted limb phases (LF =
137   left front; RF = right fore; RH = right hind) and stride frequencies (SF) against duty factor (DF;
138   which should be roughly inversely proportional to speed) using regressions in GraphPad Prism
139   10 software (Boston, Massachusetts). We also calculated stance and swing phase durations. In
140   analysing data, we took the mean values of each of these stride parameters for each trial.

141

Results

143   On average, the hippos we analysed were trotting: mean limb phases were RH = 0.51 ± SD
144   0.051, RF = 0.94 ± SD 0.040 and LF = 0.46 ± SD 0.050. No limb phases showed significant
145   changes with speed (Fig. 2: linear regressions: p values for RH, RF and LF = 0.0925, 0.155 and
146   0.153) and all phases had appreciable variation (R^2 for RH, RF and LF = 0.063, 0.045, 0.046).
147   This finding suggests that the hippos typically were demonstrating a 'walking' trot at DF≥0.5
148   and a 'running' trot at DF<0.5. Some trials marginally varied into more lateral or diagonal
149   sequence patterns overall (Fig. 2). The supplementary video (available at
150   https://figshare.com/s/99e958f4094b1cc24e80; doi:10.6084/m9.figshare.25027142) shows trials
151   for the two hippos at Flamingo Land Resort.

152   Stance durations ranged from 0.17-5.48 seconds (the latter a very slow value for a slowly grazing
153   hippo); and swing durations from 0.13-0.58 seconds (Fig. 3). SF decreased with DF, and ranged
154   from 0.17-3.2 (the highest values 2.8 and 3.2 Hz in fighting hippos) (Fig. 4). Mean DF varied
155   between 0.37-0.94. Forelimb vs. hindlimb DFs showed high variation (means 0.66 ± SD 0.18;
156   0.65 ± SD 0.17) but forelimbs had slightly (median 0.01) greater DFs than hindlimbs (median
157   0.76 vs. 0.75; Wilcoxon matched-pairs signed rank test, two-tailed: p = 0.0041, n = 46). Overall,
158   it seems that during hippo locomotion studied, speed (using DF as a rough proxy) was increased
159   by decreasing mean stance durations ~32 times and swing durations only ~4.5 times (Fig. 3),
160   thereby increasing SF ~19x (Fig. 4) while DF decreased to approximately one-third slow-
161   walking values.

162   Importantly, the 12 'running' trot (mean DF<0.5) videos obtained from the internet appeared to
163   (and in some cases, clearly showed) brief aerial phases (e.g., Fig. 5), although some footfall
164   patterns deviating slightly from an ideal trot seemed to prevent aerial phases. As per Hutchinson
165   et al. (2006), an aerial phase would occur if the DF was less than the greatest phase difference
166   between two consecutive footfalls (always ipsilateral limbs). This difference was a mean of 0.54
167   for LH vs. LF (= 1-0.46) and 0.43 for RF vs. RH (= 0.94-0.51), which is roughly 0.5 overall, so
168   trots with DF<0.5 would be expected to involve aerial phases, which they did.

169

170   **Discussion**

171   Our most notable findings are that hippos normally trot (whether walking or running), and do use
172   an aerial phase when running quickly; the latter to our knowledge has not been reported before.
173   Interestingly, hippos studied did not normally change their footfall pattern across gaits; instead
174   they transition from a 'walking' trot to a 'running' trot (Figs. 1, 2, 5). This is an unusual pattern
175   for large terrestrial mammals: elephant use lateral sequence gaits; rhinoceroses (as far as is
176   known, for all extant species) use a lateral sequence walk, true trot and transverse gallop; giraffes
177   use a lateral sequence walk and a rotary gallop (see Introduction). Compared with smaller
178   mammals, the gait repertoire of rhinos (and to a degree, giraffes) is more "normal" (and
179   ancestral, evolutionarily, for most mammals), raising the question of why hippos trot and never
180   gallop on land -- but have not entirely lost the ability to use an aerial phase. Two not mutually
181   exclusive hypotheses are that hippos are too large; with low strength:weight ratios; and too
182   aquatically adapted for athletic locomotion on land. However, if hippos can indeed obtain speeds
183   of ~7 ms^{-1}, they would match the performance of elephants, and their lowest DF observed here
184   (0.37) is identical to DFs of elephants of any size or species (minimal observed DF 0.37;
185   Hutchinson et al., 2003, 2006). Intriguingly, elephants also have evolved with some aquatic
186   adaptations as members of the clade Tethytheria (e.g., Gaeth et al., 1999), so the evolutionary
187   and biomechanical explanations for hippo and elephant maximal locomotor performance may be
188   similar to some degree. The maintenance of lateral sequence (not trotting) footfall patterns across
189   all speeds in elephants helps explain why, kinematically, they do not use aerial phases at DFs
190   similar to those of fast-running hippos, because that footfall pattern evenly spaces out ground
191   contacts whereas trotting involves (near-)synchronous limb pairs.

192   Our fastest hippos were using extreme behaviours (in the wild or in captivity) that may be near-
193   maximal performance: avoiding lions or rhinoceroses or aggressive behaviour toward each other
194   or humans and their vehicles. Maximal measured athletic capacities for stride parameters for
195   elephants vs. hippos are: in elephants, maximal SF 1.9 (hippos = 3.2) and minimal stance and
196   swing durations of 0.20 (hippos = 0.17) and 0.28 (hippos = 0.13) seconds (Hutchinson et al.,
197   2003, 2006). Unlike elephants, hippos appear to change speed mainly by decreasing stance
198   duration (and thus DF; and increasing SF) rather than swing duration. Thus overall, while it
199   remains unclear if hippos can achieve faster speeds than elephants do, they clearly reach greater
200   SFs and smaller DFs and swing durations (with slightly smaller stance durations), and thus show
201   relatively greater athleticism.

202   The absence of clear lateral sequence walks in our data, vs. several claims that these exist in
203   hippos (Slijper, 1946; Dagg, 1973; Niemitz, 2001; Coughlin and Fish, 2009; Catavitello et al.,
204   2018), is perplexing, but strongly concurs with numerous prior studies, including quantitative
205   ones (see Introduction). Lateral sequences might be used for some very slow walking (e.g., while
206   grazing); as Hildebrand (1976) intimated; yet we did not observe that pattern in our slow trials.
207   Compared with Common hippopotamuses, pygmy hippopotamuses spend less time underwater
208   and more time on land (Walker, 2008). This might explain why Hildebrand (1989) found that
209   they used more lateral sequence walking, but the circumstances under which he collected both
210   species' data remain unknown; the differences might purely be variation. Usherwood and Self
211   (2018) analysed 5 videos of hippos using slow (DF 0.76) trotting (RH and LF limb phases
212   ~0.45), in agreement with our findings. Lees et al. (2016) studied 3 videos that we also find to
213   involve slow trotting, and with stance and swing durations of 1.12-1.48 and 0.41-0.52 seconds,
214   DF 0.73-0.74 and SF 0.50-0.65; which our re-analyses of these data concur with. Dagg (1979)
215   studied hippos with DF ~0.79. All of these published data fit within variation of our other trials
216   (Figs. 2-4).

217   We found small (~0.01) differences in hippo forelimb and hindlimb DFs but we deem these
218   probably to not be of much biomechanical significance. However, the expectedly greater
219   antigravity supportive roles of the forelimbs (typical of quadrupedal mammals; e.g., Basu et al.,
220   2019a) would benefit from greater forelimb DFs to moderate ground reaction forces.

221   Our study was limited by inability to measure velocity-related parameters, which would be
222   particularly valuable to have for fast-moving hippos. Furthermore, no kinetic data exist for
223   hippos. Such data would reveal limb forces and mechanical energy fluctuations; the latter being
224   crucial for testing biomechanical gait transitions (i.e., vaulting to bouncing gaits; see Biknevicius
225   and Reilly, 2006; Struble and Gibb, 2022). Almost all of our data involved 25-30 Hz videos,
226   which inevitably would introduce more imprecision and noise into the fastest trials (e.g., one
227   frame at 0.04 seconds is ~31% of swing phase duration at 0.13 seconds). Thus surely some of the
228   variation in our results is due to human error and resolution of hardware; and absence of
229   quantitative data on steady-state locomotion. Similarly, no hippos were moving over ideally
230   smooth, level terrain and few were moving in straight forward directions. However, some of
231   these problems could be seen as benefits, too. Our measurements are for hippos either in their
232   natural environments (most of the internet videos used) or else in fairly natural terrain in

233   captivity. Thus the kinematic patterns we measured should better reflect normal locomotion
234   overall. Our study's decent sample size of 169 strides from 46 trials of 32 individual hippos,
235   across a broad (qualitative) speed range defends its value.

236   Our data and conclusions are relevant to clinical veterinary care of hippos, especially detection
237   of lameness via comparison of an animal's gait to a "normal" patterns (e.g., Hilsberg-Merz,
238   2008; Ross and Dyson, 2010; Dadone, 2018; Panagiotopoulou et al., 2019; Turner et al., 2023).
239   Flacke et al. (2015) analysed 43% of all pygmy hippos that had died in captivity and concluded
240   that musculoskeletal or neuromuscular degenerative diseases (e.g., Hittmair and Vielgrader,
241   2000; Regnault et al., 2013; Jones et al., 2018; Dadone et al., 2019) were common or the most
242   common causes for euthanasia of adult or geriatric individuals. These hippos likely would have
243   presented with clinical signs of lameness. Improved detection of lameness would aid
244   identification and monitoring of hippo foot/limb pathology and development of treatments such
245   as appropriate flooring of enclosures or ideal environments for encouraging exercise in captive
246   animals.

247   New information on hippo locomotion that we provide here is also useful for understanding the
248   evolution of locomotion, body size, habitat usage and ecology in Hippopotamidae (e.g., Sondaar,
249   1977; Boisserie et al., 2011; Mazza, 2014; Van der Greer et al., 2015; Rozzi et al., 2020;
250   Houssaye et al., 2021; Georgitsis et al., 2022). It is conspicuous that there is one recorded
251   instance of a young pygmy hippopotamus at Tampas Lowry Park Zoo (Florida) using a
252   transverse gallop (https://www.youtube.com/watch?v=nmsZwwWYJkE; includes an adult
253   quickly trotting) which could have important implications for the biomechanics of
254   hippopotamuses across ontogeny and size variation, and through evolution. A fascinating
255   question is how (and when) hippos seem to have lost their ability to use asymmetrical gaits and
256   now only trot -- how tightly were changes in athleticism linked to aquatic habitats, body size and
257   morphology in different hippopotamid lineages? This is an excellent example of where
258   integration of biomechanics and evolution could be powerful and exciting.

259

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Figure 1

Footfall patterns and foot-on/foot-off definition examples for hippo locomotion data analysis.

Footfall patterns and foot-on/foot-off definition examples for hippo locomotion data analysis. Sequence from left to right, top to bottom is: left hind foot-on, right hind foot-on, left front foot-on, left front foot-off, right front foot-on, right front foot-off. Here, the footfall pattern deviates slightly from an ideal trot, but the foot contact sequence still is [left hind, right fore], [left fore, left hind]. Images captured and cropped from internet video at: https://www.youtube.com/watch?v=ej6DrFpnJrk . Image credit: Victoria Wallace, Director, Zikomosafari. CC-BY 4.0 license.

Figure 2

Hippos' limb phases plotted vs. mean duty factor (DF).

RH = right hind; RF = right front; LF = left front. All phases are the fraction of a stride for foot contact timing vs. left hind's.
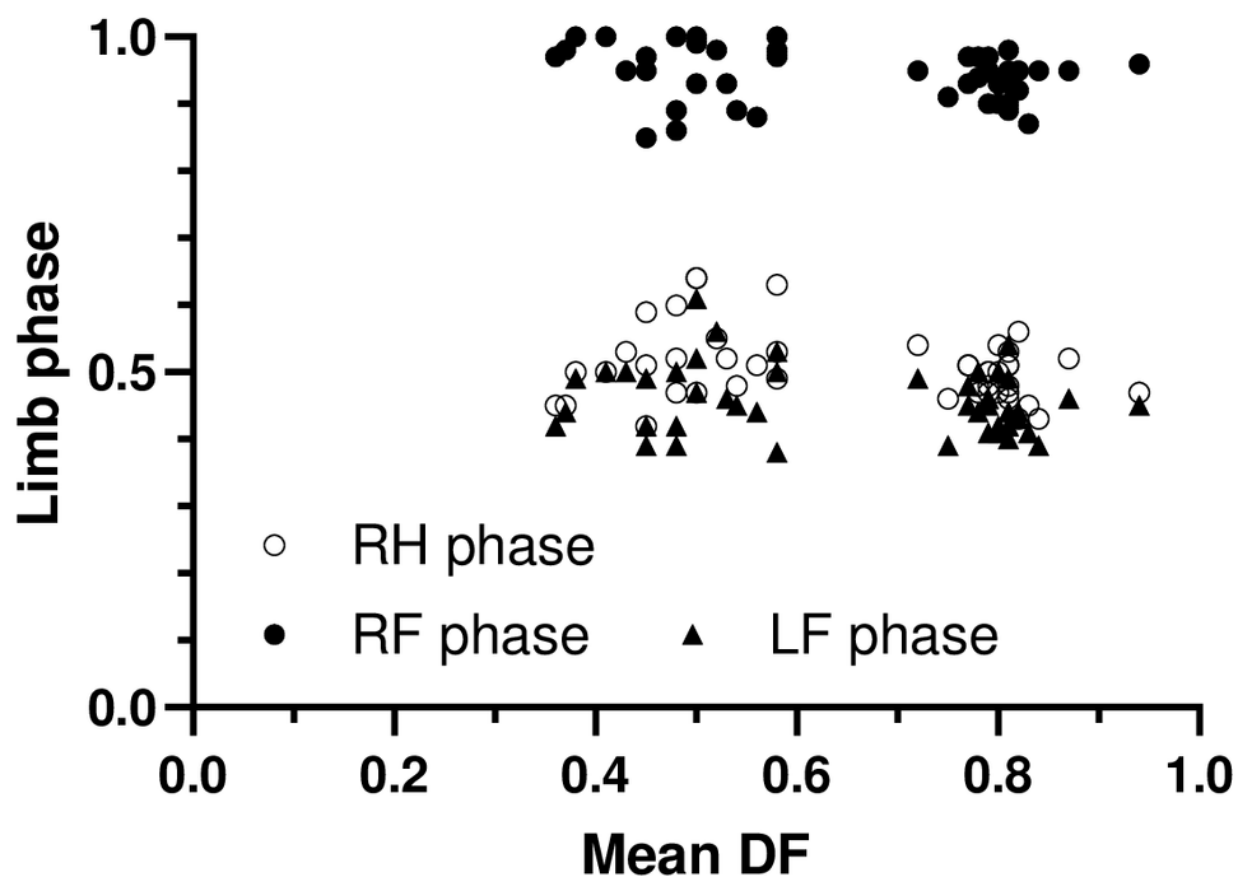
Figure 3

Hippos' stance and swing phase durations plotted vs. mean duty factor (DF).

Equations: stance duration = $8.506\ DF^{7.188}$ (R^2 = 0.934); swing duration = $0.4817\ DF^{0.7119}$ (R^2 = 0.391); n = 46 and df = 44.
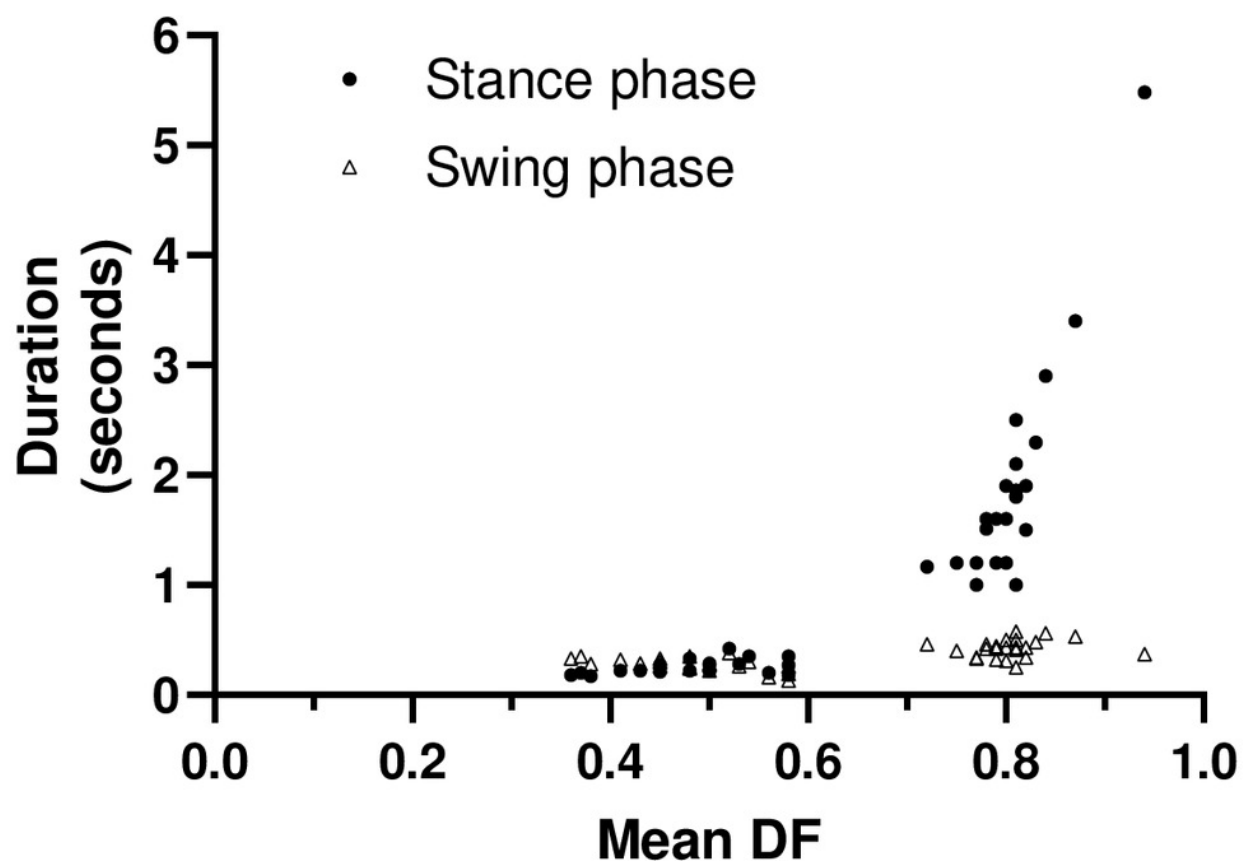
Figure 4

Hippos' stride frequency (SF) plotted vs. mean duty factor (DF).

Equation: SF = -4.14 DF + 3.89; p<0.0001; R^2 = 0.763.
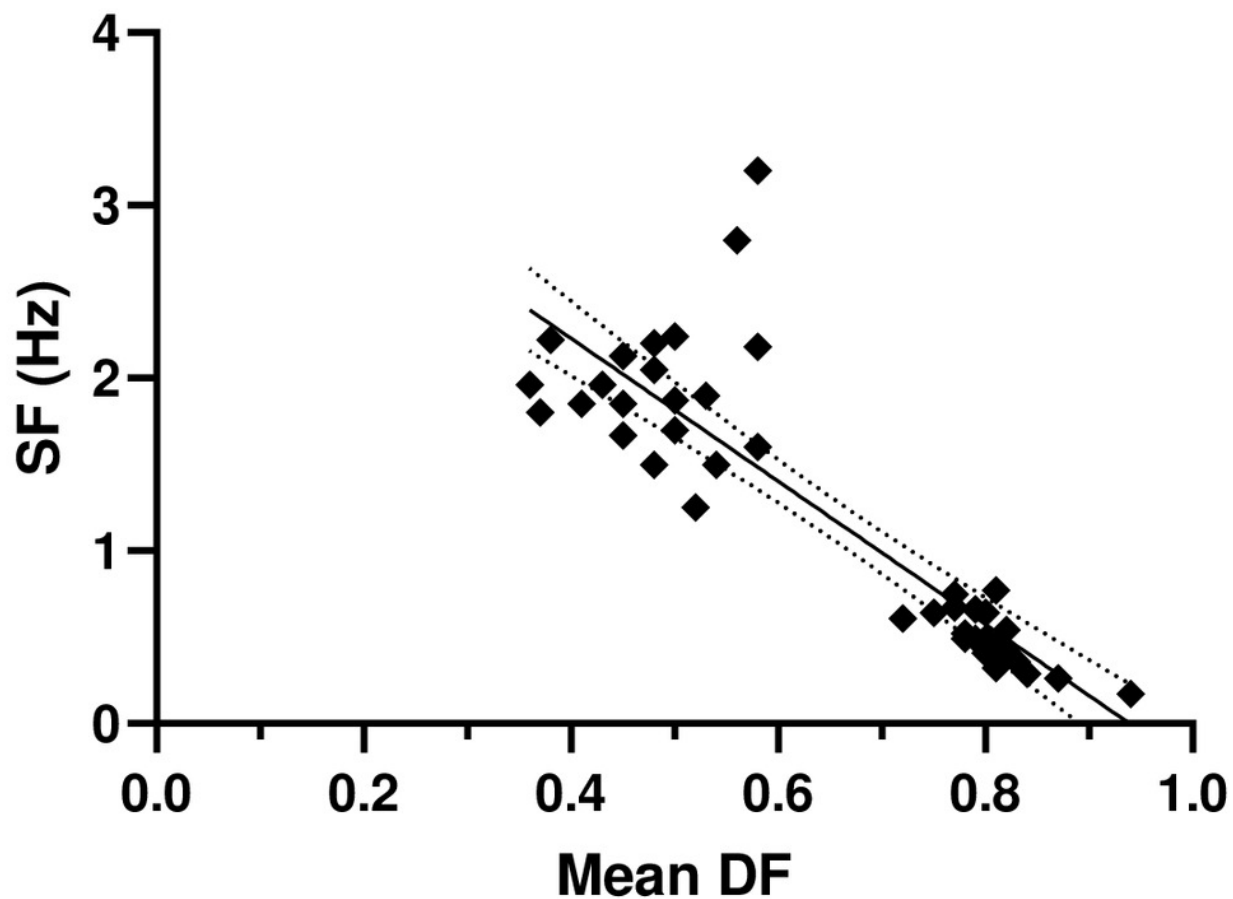
Figure 5

Example of an aerial phase in a hippo.

From internet video:

https://www.shutterstock.com/video/clip-1015076347-hippos-chasing-each-other-riverbed ,

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