The nearly columnar limbs of elephants are very different from the more flexed, spring action limbs of running mammals and birds

A review of recent research on limb posture and action in elephants indicates that their appendages are highly divergent in form and function from those of running mammals and birds.

Ren and colleagues' conclusion in a recent paper (Ren et al., 2008) that elephant limbs are significantly less columnar and much more similar to those of other animals than previously thought is an over-interpretation that discounts the highly unusual form, action and performance of elephantine limbs. Their study also incorporates under-appreciated methodological problems that inherently limit researchers' ability to understand limb function in big animals.

No recent technical study states that elephants possess perfectly straight and rigid jointed limbs even during the load-bearing, propulsive phase of the limb stroke (Gambaryan, 1974; Alexander et al., 1979; Hildebrand and Hurley, 1985; Paul, 1998; Paul and Christiansen, 2000; Christiansen and Paul, 2001), Bakker's narrative (Bakker, 1986) was a simplified analogy for a popular audience, and all illustrations in these publications show some degree of joint rotation and/or flexion.

In many mammals the forelimb is strongly flexed (Muybridge, 1957; Gambaryan, 1974; Hildebrand and Hurley, 1985; Paul, 1998; Paul and Christiansen, 2000). This posture applies to ungulates in which the humerus is short in order to prevent the forefoot from being placed too far posteriorly relative to the elbow joint with the humerus sloped strongly posterior–ventrally from the shoulder joint. The system is characteristic of modern galloping rhinos, appears to be present in hippos, which can trot, and was apparently characteristic of gigantic indricotheres, which retained a proportionally short, ungulate-like humerus and long distal segments (Granger and Gregory, 1936; Kingdon, 1979; Alexander and Pond, 1992; Paul, 1998; Paul and Christiansen, 2000). Ren and collegues confirm that all the joints of the elephant forelimb are highly extended during the entire load-bearing phase even at a fast pace, so the elephant forelimb is columnar and the humerus is elongated compared with those of ungulates (Ren et al., 2008). Even though Paul and Christiansen [see their figure 5D (Paul and Christiansen, 2000)] illustrate even more elbow flexion than do Ren and colleagues [see their figure 10 (Ren et al., 2008)], and the former also diagram significant knee flexion and rotation in an elephant, the latter stereotype Paul and Christiansen's work as consistently characterizing elephant limbs as hypervertical.

In the study by Ren and colleagues [see their figure 10 (Ren et al., 2008)] the elephant foot appears so plantigrade that it seems more flexed than the digitigrade and unguligrade feet of ungulates. The recording of foot posture and action *via* a line from the ankle to the tip of the toe in their paper makes the foot look flatter than it really is. In most cases foot posture and rotation should be measured along the long axis of the metatarsus. Even this exaggerates hindfoot flexion when a massive footpad helps support the pes along the entire length of the metatarsus to the ankle, which is held well above ground level, rather than in contact with the ground as in truly plantigrade feet [Fig. 1; see also figure 1193 in Osborn (Osborn, 1942), who notes that the elephant pes is effectively unguligrade]. In elephants the main axis of the main body of the foot is nearly vertical at the middle of the propulsive stroke when ambling [Fig. 1; see also figure 1 in Hildebrand and Hurley (Hildebrand and Hurley, 1985)], so the classic view of the foot as functionally columnar is correct.

Using the tip of the toe also exaggerates apparent rotation of the ankle because the rotation of the toe segments is being added to the total. Hildebrand and Hurley [see their figure 1 (Hildebrand and Hurley, 1985)], who do not include the toes, observed much less foot rotation in an ambling elephant. Because the elephant foot is immersed in pliable padding it is difficult to quantify the exact angle of flexion between the foot and shank. In any case it is clear that the elephant foot is too short and insufficiently flexible to produce the strong spring action that many extant mammals and birds use to achieve a fully suspended phase running gait (Paul, 1998; Paul and Christiansen, 2000; Christiansen and Paul, 2001). Reduced rotation of the elephant hindfoot results from the astragalus–tibia articulation being flatter [see figure 1193 in Osborn (Osborn, 1942)] than in other mammals with a roller-type joint.

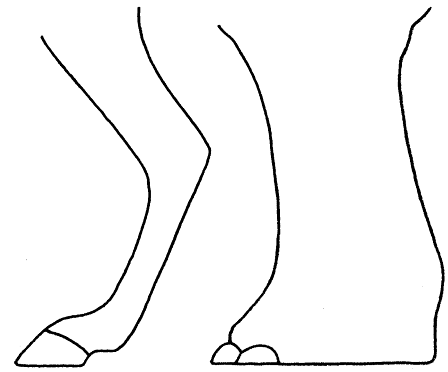

Fig. 1. Comparison of the very different hindfoot form and posture in a running horse and an ambling Asian elephant, both lower legs shown at mid-propulsive stroke, to the same approximate scale. Although there is no ready procedure to measure the exact posture of the elephant foot, its large pad results in a much more functionally columnar orientation than the easily measured strong slope of the horse metatarsus. After image 5 in plate 52 and image 14 in plate 112 of Muybridge (Muybridge, 1957).

Problems in marking actual points of joint rotation in large animals chronically hinder understanding of their limb function. True limb action can be measured only with motion x-rays, which are not practical above a modest body size. Placing markers on the skin is potentially misleading because the marker may not be accurately placed, and because it may float relative to the joint's center of rotation as the skin slides over the musculature during limb action. A casual examination of humans shows that the latter is the case. So external markers are not necessarily precise measurements of locations of internal joint rotation, they are estimates that may in part be measuring skin rather than joint movement. Whether Ren and colleagues have established that elephant knees are about as flexed and flexible as those of horses using external markers is therefore open to question. Likewise, the motion diagrams in the studies by Paul and Christiansen [see their figure 5B–D (Paul and Christiansen, 2000)] and Hildebrand and Hurley [see their figure 1 (Hildebrand and Hurley, 1985)] cannot be verified or refuted.

Ren and colleagues have not shown that elephant limbs are not markedly more columnar and otherwise distinctive from those of running mammals and birds. At most they have provided additional but not definitive evidence that elephant knees are significantly flexed especially when fast ambling, and that minor foot rotation occurs during the propulsive stroke. This does not alter the fact that elephant limbs are radically divergent from those of other extant large land animals, being overall less flexed and having short, massive distal segments, with the hindfoot especially short and limited in flexibility. As a result of this uncommon limb form elephants are restricted to an exceptionally slow ambling gait that does not include an entirely suspended phase. Conversely, elephant joint flexion during the propulsive stroke is limited because their limb excursion arcs are modest due to their combination of slow speed and large size. All ungulates and large birds use their more flexible limbs to achieve a full-suspended phase run, which in turn requires more extensive joint flexion and rotation during the propulsive stroke because limb excursion arcs are higher. Although ancient authors exaggerated the columnar rigidity of elephant legs, they correctly recognized that their limbs are dramatically different from those of faster animals. Conversely Ren and colleagues exaggerate the commonality of large animal limb form and function based on data that – although useful – is less reliable than they present because unavoidable data-gathering limitations prevent a truly detailed examination of large animal locomotion; only improved technologies for imaging large animal interior anatomy can solve the problem. When it comes to restoring peak locomotary performance, morphology continues to matter.

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Response: Of ideas, dichotomies, methods, and data – how much do elephant kinematics differ from those of other large animals?

Gregory Paul's reply demonstrates that our study's critique (Ren et al., 2008) of how previous studies have dichotomized animal limb function into 'flexed *vs* columnar' categories was on the mark. He again divides limb configurations into either 'strongly flexed' or 'highly extended' but where do the boundaries between these categories lie? Do large animals supposedly representing such categories, such as horses and elephants, differ appreciably from each other?

A quantitative approach is needed to shed light on this question, as postures are best described in terms of joint and segment angles. For example, the angles of limb joints/segments at mid-stance (approximately corresponding to maximal limb loading) in ambling elephants and trotting horses at equivalent size-normalized speeds are shown in Table 1. The data shown for horses are firmly validated with radiographic studies, as we cited. Horse and elephant thigh limb segment angles at mid-stance are quite similar whereas humerus segments may be slightly more protracted in horses (we repeat that elephant scapular motion remains to be measured). Furthermore, the wrist joint angles of running horses and elephants are almost identical. Elephants have ~30–60 deg. more flexed elbows, knees and ankles than horses do. Similar results hold for other instances in the stride cycle or other speeds. Where then do the supposed sharp divisions between 'flexed' and 'columnar/extended' limb orientations lie?

Table 1. Mid-stance joint angles for ambling elephants and trotting horses at Froude numbers ~1

Segment or joint	Elephant angle	Horse angle
Humerus	–32	–50
Elbow	144	175
Wrist	189	185
Thigh	11	2
Knee	135	180
Ankle	108	170

Average values from Ren et al. [Tables S1 and S2 in supplementary material in Ren et al., 2008 (Ren et al., 2008)] and Back et al. [fig. 4 in Back et al., 1995a (Back et al., 1995a); fig. 4 in Back et al., 1995b (Back et al., 1995b)], respectively.

Quantitative data (Table 1) show that such dichotomies have no legs to stand on. Indeed, elephants' limbs could be said to be more flexed than horses' limbs during running – although we took a more cautious approach and described them as being roughly similar.

Paul repeats many of our points about the technical problems that face interpretation of elephant (and other large animal) locomotion. His approach (fitting a skeleton inside Muybridge's images of a single stride) is not equivalent to ours (in which six digital cameras captured 240 images per second at 1 mm accuracy, for 288 complete strides of 15 elephants, with joint landmarks palpated and visualized, and thorough statistical analysis). Our 3-D motion analysis approach is well accepted and validated as a reasonable standard (e.g. Back et al., 1995a; Back et al., 1995b) despite the technical flaws we discussed; his is unvalidated. Because Paul simply used Muybridge's data and did not provide a reliable method or quantitative results (unlike the other studies we discussed), we did not cite his small illustrations of an elephant in Paul and Christiansen [fig. 5D in Paul and Christiansen, 2000 (Paul and Christiansen, 2000)]. Likewise, we did not cite countless images of moving elephants in popular books. We felt all of these potential sources of data were too unreliable.

Paul has provided no new information on the problem of skin motion for experimental studies whereas we treated the subject cautiously with a statistical analysis of marker placement and a restraint from quantifying proximal joint angles, which are expected to have the worst artifacts. In addition, we used defleshed cadavers, which lacked such artefacts, to show that horse and elephant limbs have broadly similar flexibility.

Paul tries to argue that the two methods are more or less equivalent and the problems so difficult that it's anyone's guess how elephant limbs move; the issue is 'open to question' and 'cannot be verified or refuted.' We find this attitude disturbingly anti-scientific and quite misleading as it implies comparably accurate methodology.

Our method of quantifying foot skeletal joint angles was not flawed for the purposes of our analysis that was to estimate skeletal joint and segment angles, not to estimate the centre of pressure, which essentially all researchers have assumed would be more caudally positioned along the foot. Paul appears to conflate where the centre of pressure is with where the axis of foot motion is. The former is probably near mid-foot (our unpublished data); the latter is along the third digit. Estimating skeletal motion from the lateral side of the foot would underestimate ankle joint flexion and confuse ankle abduction and flexion. Motion of the short digits of elephants would not greatly change our results. Indeed our unpublished *in vitro* and radiographic data support the assumption that the toes move very little and that our markers were positioned on skeletal landmarks that enable approximation of ankle joint motion. Paul repeats descriptions of the same foot (and footpad) anatomy and function that we have described in three papers on that subject (Weissengruber et al., 2006; Hutchinson et al., 2008; Miller et al., 2008), so we do not see what he is critiquing. Again, he is providing no new information.

We showed how elephant ankles dorsiflex, then plantarflex during the stance phase (as in most other mammals with spring-like ankles), exhibiting classic spring-like kinematics. Paul provides no evidence or coherent argument to falsify our measurements; the statement that elephant ankles are ‘too short and inflexible’ is a non-sequitur. Precisely how long would they need to be and what kind of quantitative motion would they need to exhibit to be spring-like? Specifically, how much more ‘functionally columnar’ is an elephant’s foot than a horse’s foot, if the skeletal kinematics are less columnar in elephant feet? Certainly more data on foot mechanics for elephants and other large animals would be useful and our ongoing studies are fulfilling this need.

Whereas few studies have provided reliable new data, we cited numerous studies (e.g. Paul and Christiansen, 2000) that have talked about elephant locomotion without measuring or carefully considering empirical data. Some studies hung elaborate ideas about broader patterns in animal locomotor evolution on tidy categories like ‘flexed’ and ‘columnar.’ In our introduction, we first cited some antiquated notions about elephant limbs as being inflexible or simply column-like and then noted ‘ridiculous as those fallacies may seem to contemporary scientists, elephant posture and gait remain misunderstood, partly because of their strange anatomy and partly because of little rigorous measurement of elephant locomotion’ [p. 2735 in Ren et al. (Ren et al., 2008)]. That sentence summarizes the current dialogue quite well.

Morphology can matter; indeed we agree with Paul that the locomotor differences between elephants and other animals may hinge upon anatomy and other factors, so we suspect that there is much more to the mystery than simple dichotomies and qualitative anecdotes. For example, Fig. 1 supports the inference that previously perceived differences in posture between ‘cursorial’ horses and ‘graviportal’ elephants are largely due to different limb proportions, i.e. relative lengths of the proximal and distal limbs, not more flexed limbs in horses.

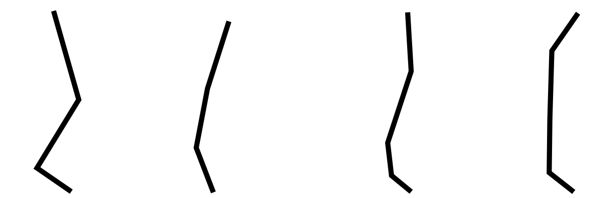

Fig. 1. Mid-stance limb orientations for ambling elephants and trotting horses at Froude numbers ~1; individual data (not averaged, thus joint angles do not perfectly match those presented in Table 1), respectively, from Ren et al. [see fig. 11 in Ren et al., 2008 (Ren et al., 2008)] and Back et al. [see fig. 4 in Back et al., 1995a (Back et al., 1995a); see fig. 4 in Back et al., 1995b (Back et al., 1995b)].

Gait analysis of elephants and other large animals needs more data but Paul offers none. Ideas about animal locomotion are not enough, especially when weighed down with ponderous conceptual baggage and antiquated methodology. To contribute to animal locomotor science, researchers must generate novel data with reliable methods. We stand by our original methods and data.

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