

than for *Hippopotamus*. Are the thick legs of graviportal mammals really necessary to support them, or are these animals built to greater factors of safety (Alexander, 1981) than other mammals?

Alexander, Maloiy *et al.* (1979) measured the bones and muscles of the legs of a 2500 kg *Loxodonta* and analysed film of another *Loxodonta* running. They calculated peak stresses for the fastest run in the film, and obtained values very similar to those that had been calculated for fast locomotion of smaller mammals, including kangaroos and dogs. However, the fastest gait of the elephant was a slow run in which each foot remained on the ground for a larger fraction of the stride than in the fastest runs of the smaller animals, so the peak forces were smaller multiples of body weight. Elephants cannot gallop like greyhounds because their bones and muscles are not strong enough to withstand the forces that would be involved.

Alexander (1983*b*, 1985) used a different approach to assess the strengths of the leg bones of moas and dinosaurs. Assume that similar animals of different sizes move in dynamically similar fashion: that means that their motions could be made identical by uniform changes of the scales of length, time and force (Alexander & Jayes, 1983). The peak stresses in the shafts of homologous leg bones will then be proportional to aW^x/Z where W is body weight, a is the fraction of body weight supported by the fore or by the hind legs (as appropriate) and Z is the section modulus for bending (in a parasagittal plane) of a cross-section of the bone distant x from the distal end. The section modulus is a geometric property of the cross-section. It has two values, appropriate for calculating stresses in opposite faces of the bone, but these are not very different from each other unless the section is highly asymmetrical. We will use mean values. Since stresses in dynamically similar movement are proportional to aW^x/Z , the reciprocal Z/aW^x is a useful indicator of bone strength. An animal whose leg bones have larger values of Z/aW^x than those of another should be capable of more athletic behaviour, without breaking bones. Whether it is actually more athletic must of course depend on the dimensions of its muscles, as well as of its bones.

Materials and methods

One fore and one hind leg were removed from a female white rhinoceros (*Ceratotherium simum*) which had died in captivity at the age of 14 months. She was sexually immature, and neither of the last 2 molars had erupted. She had suffered from a debilitating illness and was very lean, with less than 0.1% of dissectable fat. In this paper we present bone dimensions but not muscle dimensions, as the appearance of the muscles suggested that some wasting may have occurred.

The moment arm of the gastrocnemius muscle about the ankle joint was measured as described by Dimery, Alexander & Ker (1986). The lengths of the long bones were measured. Sections through their shafts were transferred to paper by photocopying, and the copies were marked out in strips which were measured to determine their section moduli by numerical integration (see Alexander, 1983*a*). The section selected for measurement was halfway along the length of the bone except in the case of the femur where a slightly more distal section was taken to avoid the third trochanter, which would have given a misleading impression of the strength of the bone if it had been included. The marrow cavities contained cancellous bone but were treated as empty spaces in our calculation, because it seemed obvious that it was very much weaker than the compact bone. It was assumed that 60% of body weight is supported on the forelegs, as in horses (Björck, 1958).

We were unable to weigh the carcass on account of its size, but the zoo staff who had attended the animal estimated her mass as 700–800 kg. The following argument tends to confirm their estimate.

The unskinned carcass was 2.76 m long from the upper lip to the base of the tail, measured along the midline of the back. The foreleg was 1.55 m long from the withers to the sole of the foot, measured along the surface of the skin. We made the corresponding measurements on plastic models of rhinoceroses.

manufactured by Britain's Ltd., and calculated the ratios of carcass dimensions to model dimensions. The cubes of these ratios gave estimated ratios of volumes, and since we had determined the volumes of the models (by measuring the upthrust that acted on them, when they were submerged in water) we were able to estimate the volume of the animal. From this the mass was calculated, assuming a density of 1000 kg m^{-3} . Unfortunately, no model of *Ceratotherium* was available, so we had to use models of *Diceros* and of *Rhinoceros unicornis*. The mass estimates derived from these were 630 and 890 kg, respectively. *Diceros* seems to be more slender than *Ceratotherium* and *Rhinoceros* more portly, so we estimate the mass of the *Ceratotherium* as 750 kg, in excellent agreement with the subjective estimate.

As a check on the method, we used the *Diceros* model to estimate the masses of 3 of the *Diceros* listed by Meinertzhagen (1938), from the linear dimensions given by him. The estimates were 1.02, 0.91 and 0.96 times the actual masses.

Adult *Ceratotherium* were pursued by a vehicle to make them run in a very large paddock at Whipsnade Park. They were filmed from behind the fence, by means of an electrically-driven cine camera that was shown (by filming a digital clock) to run at 62 frames per second. The film was analysed as described by Alexander, Langman & Jayes (1977), except that the linear dimensions of the animals were obtained from it by using the vehicle as a scale of length. Some of the data from this film have already been published (Alexander & Jayes, 1983).

Stresses in leg bones were calculated by the method used for buffalo and elephant by Alexander, Maloiy *et al.* (1979).

Results and comparisons

Film analysis

Figure 1 shows an adult *Ceratotherium* galloping at 6.1 m/s. Other sequences (also of adults) show speeds up to 7.5 m/s. This is slightly above the maximum speed of 7.0 m/s recorded for buffalo (*Syncerus caffer*) by Alexander, Langman & Jayes (1977), but well below the 11 m/s which they recorded for giraffe. The highest speed shown for *Loxodonta* in the film analysed by Alexander, Maloiy *et al.* (1979) was only 4.5 m/s, but this may not have been a maximum speed. Other records of elephant speeds seem to be subjective estimates rather than measurements (Garland, 1983).

The duty factor of a foot is the fraction of the stride duration for which it is on the ground. Peak forces are proportional to (body weight/duty factor) so low duty factors imply large forces. The lowest duty factor we observed for *Ceratotherium* was 0.39 (both fore and hind). This is less than the minimum of 0.49 for *Loxodonta* (Alexander, Maloiy *et al.*, 1979) but considerably above the minima of 0.27 and 0.23 for buffalo and giraffe, respectively (Alexander, Langman & Jayes, 1977).

Previous analysis of our film by Alexander & Jayes (1983) showed that *Ceratotherium* change from trotting to galloping at about the same Froude number (a dimensionless speed parameter) as other cursorial mammals. At any particular Froude number they use about the same duty factor and relative stride length as other cursorial mammals. They are restricted to fairly low Froude numbers but, within the range available to them, move very much like smaller mammals.

Bone dimensions

The strength indicators for the major limb bones of *Ceratotherium* are a little higher than for *Syncerus* and much higher than for *Loxodonta* (Table I). A high value implies that a bone is short or thick or both. Table II compares bone lengths, taking account of the different sizes of the animals by expressing them relative to the lengths predicted by allometric equations obtained from

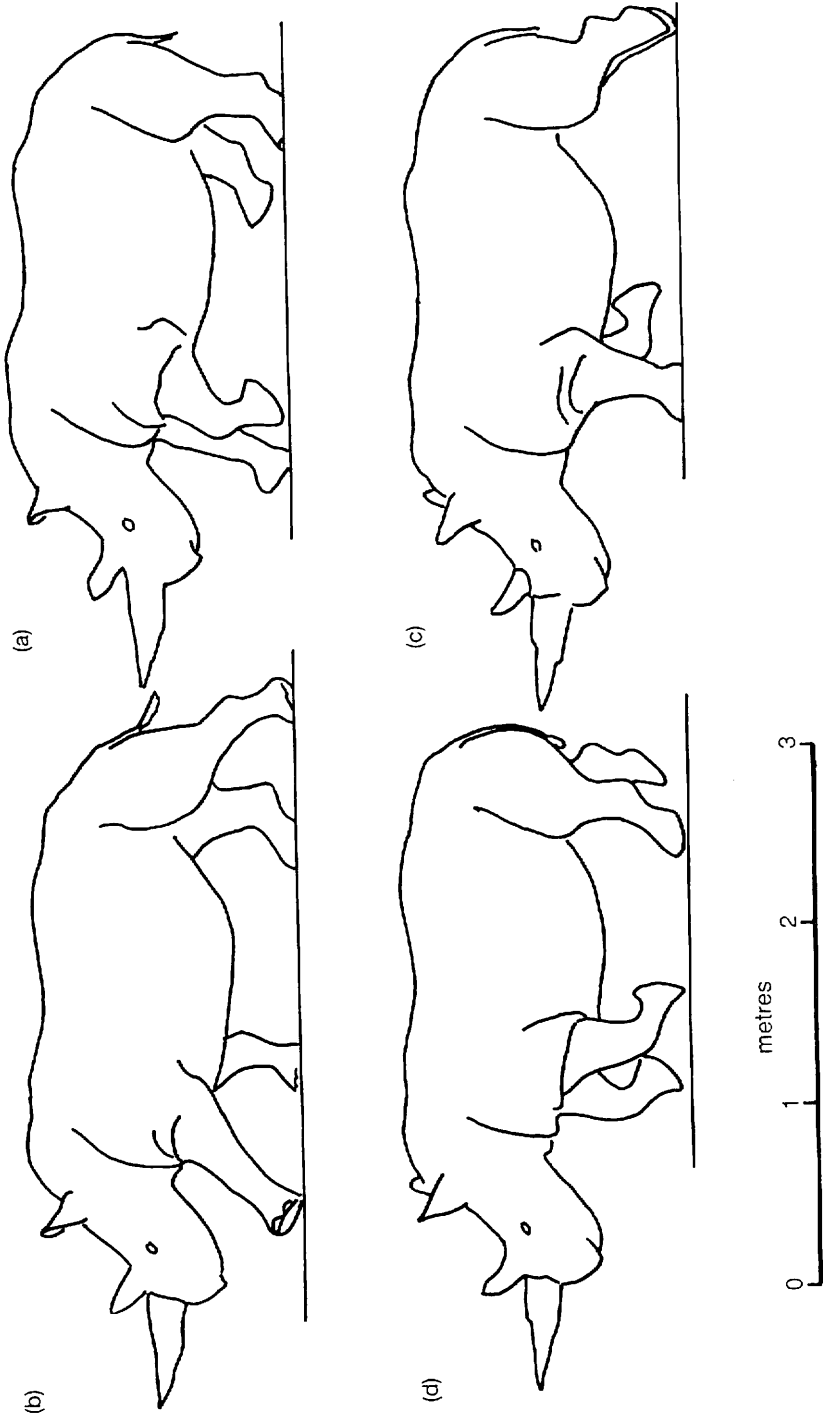


FIG. 1. Outlines traced from a film of an adult *Ceratotherium simum* galloping at 6.1 m/s. The time interval between successive outlines is 0.128 s.

TABLE I
Strength indicators (Z/aWx) for leg bones of *Ceratotherium* and other large mammals

	Mass (kg)	Strength indicator (GPa ⁻¹) for		
		humerus	femur	tibia
<i>Loxodonta africana</i> *	2500	11	7	9
<i>Ceratotherium simum</i>	750	31	26	33
<i>Syncerus caffer</i> *	500	21	22	27

* Data from Alexander (1985)

a selection of mostly smaller mammals. Economos (1983) suggested that very large mammals tend to have shorter bones than the equations predict, and most of the bones in Table II are only about 0.7 times the predicted length. The elephant humerus and femur, however, are much longer than this and some of the rhinoceros bones a little shorter. These differences contribute to the differences in strength indicators.

Estimates of stresses

Table III shows calculations of stresses in the humerus and tibia. Calculations for trotting are shown because these gave higher values than galloping. The duty factors in the two gaits were very similar (0.39 to 0.49 for galloping; 0.43 to 0.54 for trotting) but in trotting the bones made larger angles with the vertical at mid stance. Similarly, Biewener & Taylor (1986) found larger bone stresses in fast trotting than in slow galloping, in goats and dogs.

The stresses shown in Table III are rather lower than were calculated for buffalo and elephant by Alexander, Maloiy *et al.* (1979). Their values were for the buffalo, -113 to +93 MPa (humerus) and -58 to +36 MPa (tibia); and for the elephant -85 to +69 MPa (humerus) and -57 to +45 MPa (tibia). The buffalo stresses are higher than for rhinoceros, because the duty factors and strength indicators are both lower. The elephant's straight-legged gait (with humerus and tibia making angles of only 18° and 20° with the presumed direction of the force on the foot) tends to reduce stresses, but is not enough to compensate for its very low strength indicators (Table I).

The stresses calculated for the rhinoceros tibia lie well within the range measured for the tibia of cantering horses by Biewener, Thomason & Lanyon (1988).

TABLE II
Lengths of leg bones of the mammals listed in Table I, expressed as fractions of the lengths predicted by the allometric equations (for mammals in general) of Alexander, Jayes *et al.* (1979):

	Humerus	Ulna	Femur	Tibia
<i>Loxodonta</i>	0.97	0.68	0.93	0.63
<i>Ceratotherium</i>	0.69	0.62	0.63	0.52
<i>Syncerus</i>	0.70	0.67	0.68	0.69

TABLE III

Calculation of stresses in bones of a 750 kg rhinoceros trotting with a duty factor of 0.4 (fore and hind). The calculation is explained by Alexander, Maloiy *et al.* (1979)

		Humerus	Tibia
Length (m)	L	0.38	0.32
Cross-sectional area (m ²)	A	2.4×10^{-3}	2.1×10^{-3}
Section modulus (m ³)	Z	2.7×10^{-5}	1.6×10^{-5}
Estimated force on foot (N)	R	7400	4900
Angle of force to bone (°)	ϕ	50	39
Force exerted by muscle (N)	Q	10200	13700
Angle of muscle to bone (°)	ψ	-10	0
Max. stress due to bending moments (Pa)	(L/2Z)(Qsin ψ - Rsin ϕ)	5.3×10^7	3.2×10^7
Stress due to axial force (Pa)	(Qcos ψ - Rcos ϕ)/A	0.6×10^7	0.7×10^7
Range of stresses (MPa)		-59 to +47	-39 to +25

Discussion

The stresses calculated in Table III for a young female rhinoceros are rather lower than those calculated (also for fast running) for buffalo and elephant. They are similar to the stresses for cantering horses, but the horses were capable of more strenuous activities such as jumping (which imposed stresses in the tibia up to -114 and +64 MPa; Biewener, Thomason & Lanyon, 1988) which the rhinoceros could not have performed. This suggests the possibility that rhinoceros skeletons may be built to higher factors of safety than those of other mammals. Similarly, Alexander (1983*b*) suggested that the remarkably robust leg bones of a moa (*Pachyornis*) might have unusually high factors of safety. He noted that moas were herbivores that were not threatened by predators, so had no need either to pursue prey or to run from enemies. This might increase the optimum factor of safety by relaxing selection for speed.

Low stresses in rhinoceros bones imply high factors of safety only if rhinoceros bone is about as strong as bone from the other animals with which it is being compared. Professor J. D. Currey of the University of York has tested samples from the humerus of the rhinoceros carcass used in this paper. He tells us that it was more porous than bone from long bones of cattle, and about 20% less strong. We do not know whether this is typical of healthy rhinoceros, or an effect of ill health. Also, we have no measurements of bone strength for elephant or buffalo. However, if it were assumed that rhinoceros bone generally is weaker than that of the other species, and if the strength indicators for rhinoceros in Table I were reduced by 20% to take account of this, they would still be close to the values for buffalo and much larger than the values for elephant.

The elephants, rhinoceroses and hippopotamus are generally thought of together as the graviportal mammals, but the relatively long legs of the elephants are very different from the shorter legs of the others. Because their leg bones are so long without a compensating increase in thickness, they have very low strength indicators. The stresses in them are kept within acceptable limits by keeping the legs much straighter than in rhinoceros, so that the bones make much smaller angles with the force on the foot. Biewener (1983) showed that large mammals avoid having excessive stresses in their bones by keeping their legs straighter than small ones, but there is a striking difference among the largest mammals between the very straight legs of running elephants and the much less straight (but also much shorter) legs of rhinoceros and hippopotamus.

Both the filming and the dissection were made possible by the kind cooperation of the staff of the Zoological Society of London at Whipsnade Park. In particular, we would like to thank Mr V. J. A. Manton and Ms Alison Beasey.

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