

## Energy of the Oscillating Legs of a Fast-moving Cheetah, Pronghorn, Jackrabbit, and Elephant

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**ABSTRACT** Lifelike models of the oscillating legs treated as three-segment systems show the course of kinetic and potential energy over the locomotor cycle for a cheetah, pronghorn, jackrabbit, and elephant running at speeds approaching their maxima. The models can be adjusted to eliminate differences among the animals in time intervals, mass or length of limb, and joint angles. This facilitates analysis of the influence on total energy of each of these variables and of the distribution of mass among leg segments. Fast-cycling legs of the carnivore type have significantly more energy than those of the hoofed type. This may contribute to the lesser endurance that is usual for carnivores that hunt using a high-speed dash.

The first objective of this paper is to present correlations between trajectories of the limb segments of mammals running at near their maximal speeds with the time course of the kinetic energy (K.E.) and potential energy (P.E.) of their legs. The cheetah (*Acinonyx jubatus*) was selected because it is the fastest land animal, the American pronghorn antelope (*Antilocapra americana*) because it may be as fast as any hoofed mammal, the black-tailed jackrabbit (*Lepus californicus*) because it is among the smallest and most limber of fast-running mammals, and the Asian elephant (*Elephas maximus*) because its bulk forces it to adopt relatively stiff and simple leg motions which contrast with those of the other animals. Similar correlations between limb motions and energy have long been made for man and several animals moving under laboratory conditions (e.g., Manter, '38; Winter et al., '76). A recent study at Harvard University (Fedak et al., '82) included such material for three quadrupeds and four bipeds moving on a treadmill. Our unrestrained animals moved up to four times faster than the treadmill (roughly  $25 \text{ m/s}^{-1}$  for the cheetah), thus providing data for animals under more demanding conditions.

Our second objective is to introduce modeling of the cycling legs that permits variables to be controlled so that their individual influences on the total energy budget of the system can be clarified. Our final objective is to

apply this procedure to contrast the energy of oscillation for the legs of the digitigrade cheetah with that of the unguligrade pronghorn, which has a more proximal distribution of limb mass. This contrast is made important by the surprising conclusion of Taylor and associates ('74) that for the cheetah, gazelle, and goat, leg conformation does not significantly influence cost of transport.

### MATERIALS, PROCEDURES, AND LIMITATIONS

We used the best films that had been located, in extensive prior work on quadrupedal locomotion, of very fast performances of the selected animals. The film-advance speeds for cheetah, pronghorn, rabbit, and elephant were, respectively 64, 80, 200, and 24 frames per second. The precision of the elephant and rabbit films is superlative, and that of the pronghorn is good. The precision of the cheetah film is barely adequate, yet the best available. For this animal many consecutive strides were averaged to increase accuracy. The cheetah and rabbit used the rotary gallop (for a characterization of asymmetrical gaits see Hildebrand, '77), the pronghorn both rotary and transverse gallops, and the elephant the singlefoot in lateral sequence (for a characterization of symmetrical gaits see Hildebrand, '76).

Each leg was considered to have three segments, the foot being taken as an unjointed unit. Skeletal measurements were used to determine the proportionate lengths of the

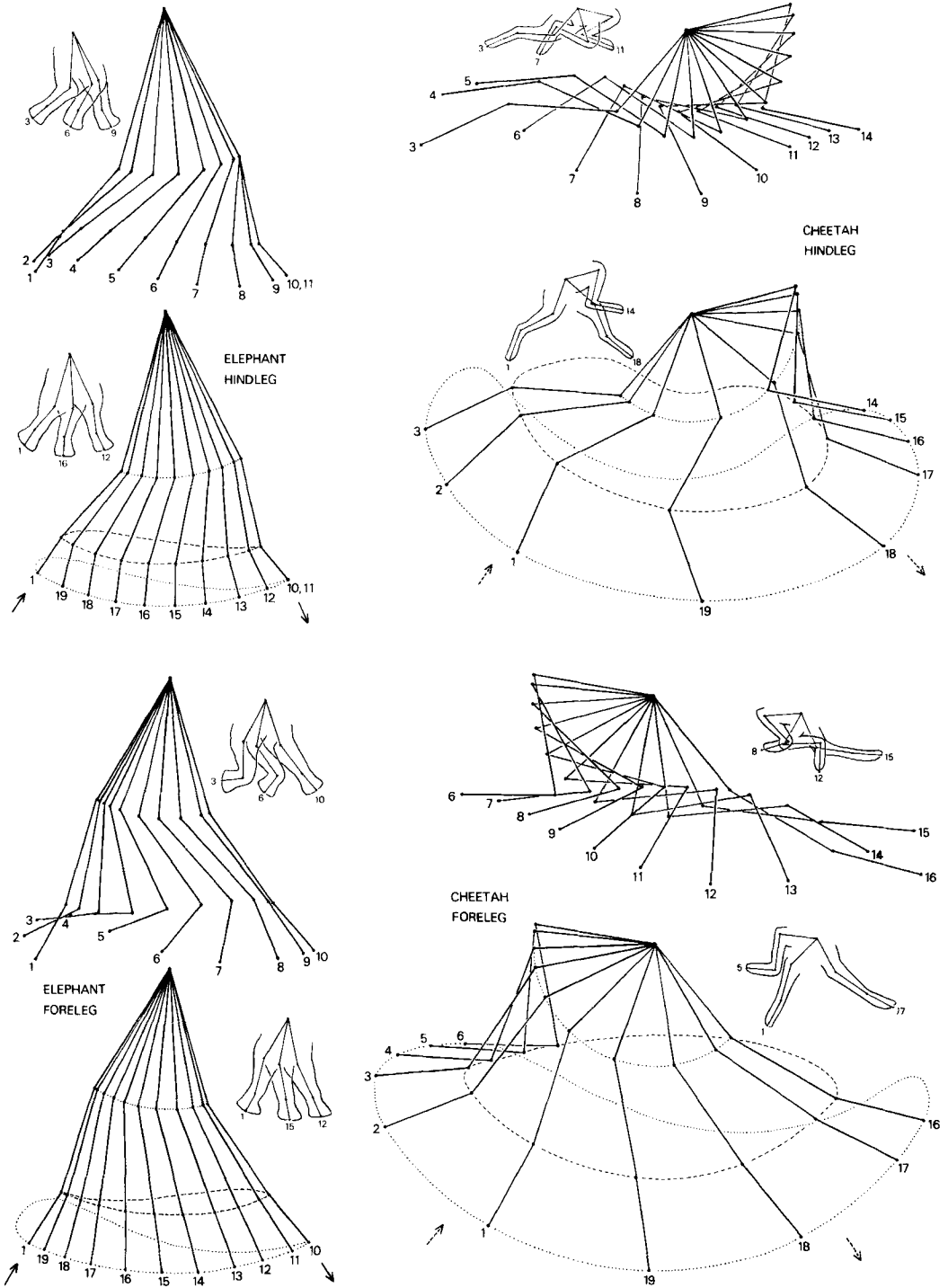


Fig. 1. Joint angles and successive positions of limb segments for a fast-moving elephant and cheetah. Arrows show the times that the feet strike and leave the ground (approximate for the cheetah).

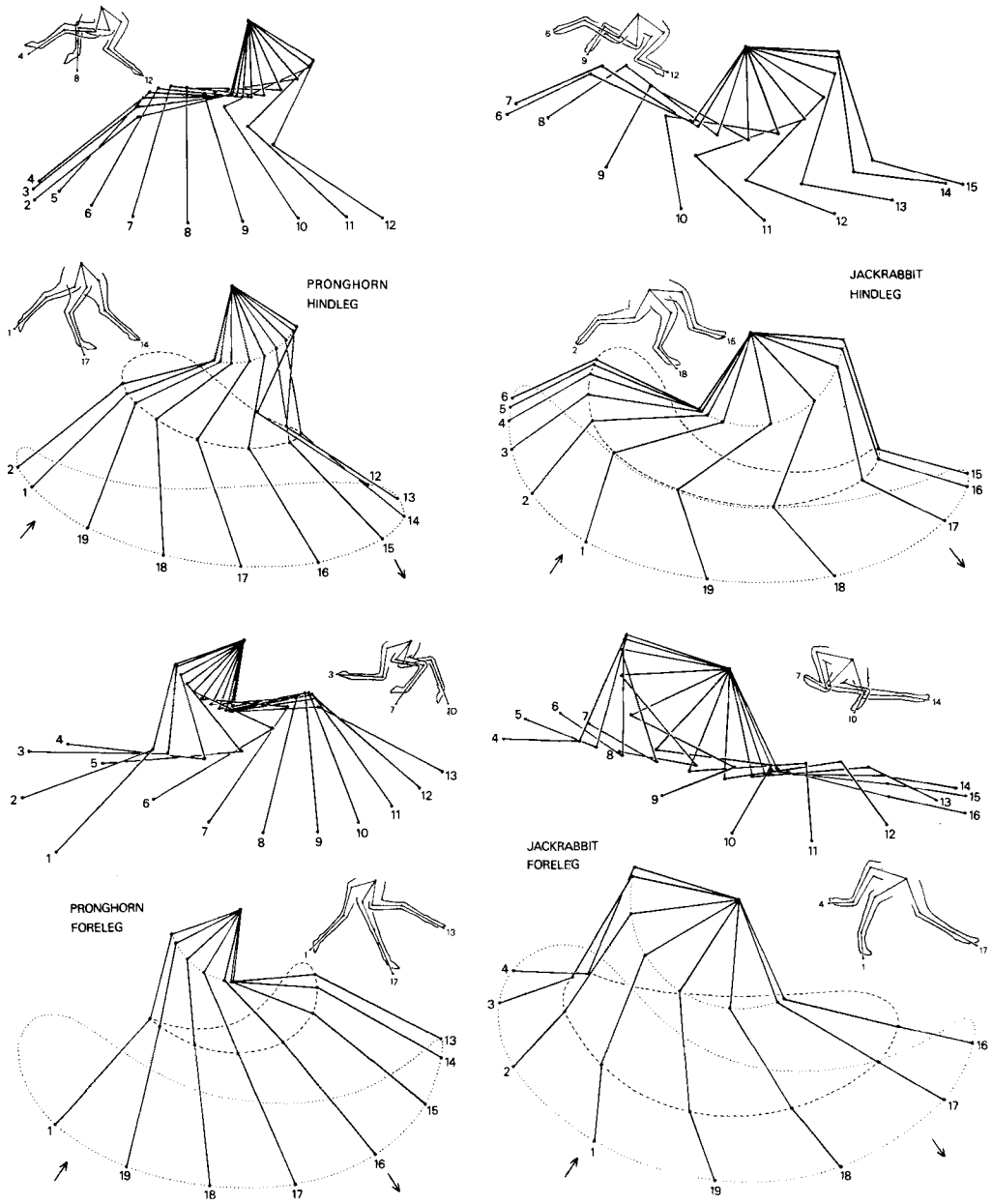


Fig. 2. Data as for Figure 1, but for the pronghorn and jackrabbit.

segments on the projected images of frames of the films. This assisted greatly in locating the more obscure joints (shoulder, hip) from the more evident joints (elbow, heel or hock). All locomotor cycles were standardized to 19 successive positions equally spaced in time (Figs. 1, 2). Joint angles were measured clockwise from the vertical to the axis of each limb segment for each position. Measurements were repeatable within  $2^\circ$ . Because errors in measuring joint angles are not cumulative, and sudden brief aberrations of joint angles are unlikely in life, minor smoothing of the progression of angles was considered to increase accuracy.

We determined for each limb segment the total length, mass, and position of mass center in relation to the joint pivots. This was done from carcasses for the pronghorn and rabbit, and from freeze-dried limbs and proportionate data from other felids for the cheetah. It was necessary to estimate the total mass of each limb of the elephant and to approximate the remaining data from models prepared using photographs and skeletal material. Limbs are severed from the body and frozen prior to measuring masses and mass centers. We judge that a principal source of error in this and related studies is the unavoidable arbitrariness in the amount of flesh that is removed at shoulder and hip. Trials showed that errors of plus or minus 5% in determining the proportionate mass of the proximal limb segment result in differences of plus or minus 7% in calculated K.E.

Our analysis is limited to motion in the sagittal plane. Since we treat the foot as a rigid unit, the model does not take into account the flexion that occurs at the fetlock of the pronghorn or footpads of cheetah and rabbit. These sources of error were ignored because they were judged to contribute less error than inevitable inaccuracies in measuring masses, mass centers, and joint angles. We do not know the actual rates of travel of our animals, and the time intervals between the positions represented were approximated from the rated film-advance speeds of the cameras, which can be in error (but see below for an adjustment of the model in allowance for this uncertainty).

Our results show the energy course of the oscillating leg as a system without regard to muscular input, support or propulsion, wind resistance, or storage and release of energy. We show the energy that the system *has*, not where it comes from or the efficiency of its production or recovery. We characterize models closely resembling our animals as

they undergo typical fast motion. Clearly, we do not (nor could anyone) describe *the* fast motions of *the* cheetah, pronghorn, jackrabbit, or elephant.

#### ENERGY CURVES FOR THE INDIVIDUAL ANIMALS

With the data for masses, mass centers, and joint angles described above, J.P. Hurley used the usual application of Lagrangian equations to calculate the K.E. (translational plus rotational) for the 19 transitions between the 19 positions drawn for each leg in Figures 1 and 2. Successive values for P.E. were calculated using the condition that the minimum potential energy be zero (see Appendix).

The K.E. and P.E. cycles of the oscillating limbs of the four animal models are quantified and contrasted by Figure 3. The following examples show that the energy curves closely follow the trajectories of the limbs. The K.E. has one peak on the forward swing of the leg (maximal rearward extension to maximal forward extension) and another on the backward swing. For the elephant model, the forward swing is a little the faster, and hence has higher peak K.E. For the other animals the backward swing is much the faster, and the K.E. peak is then correspondingly greater. For all of the animals, the K.E. peak is greater for the hind leg than for the lighter foreleg, though least so for the elephant, for which the foreleg was estimated to be nearly as heavy.

The elephant has virtually no follow-through (from lift-off of the feet to maximal rearward extension), and no down-swing (from maximal forward extension to ground contact); accordingly, lift-off and touch-down come when K.E. is minimal. This is not so for the other animals. On the forward swing, relatively rapid movement of the thigh is initiated sooner in the cycle (as numbered on the figures) for the cheetah than for the pronghorn; consequently, peak K.E. comes earlier in the cycle for the cheetah. The most rapid movement of the arm, in contrast, comes later in the foreswing for the cheetah, so peak K.E. is later for cheetah than pronghorn. Since P.E. varies with position, not velocity, it peaks with the great follow-through of the cheetah arm after lift-off, and with the high lift of the knee much later in the respective cycle.

#### COMPARISON OF CHEETAH AND PRONGHORN

Functional morphologists have long noted that mammalian cursors have longer legs

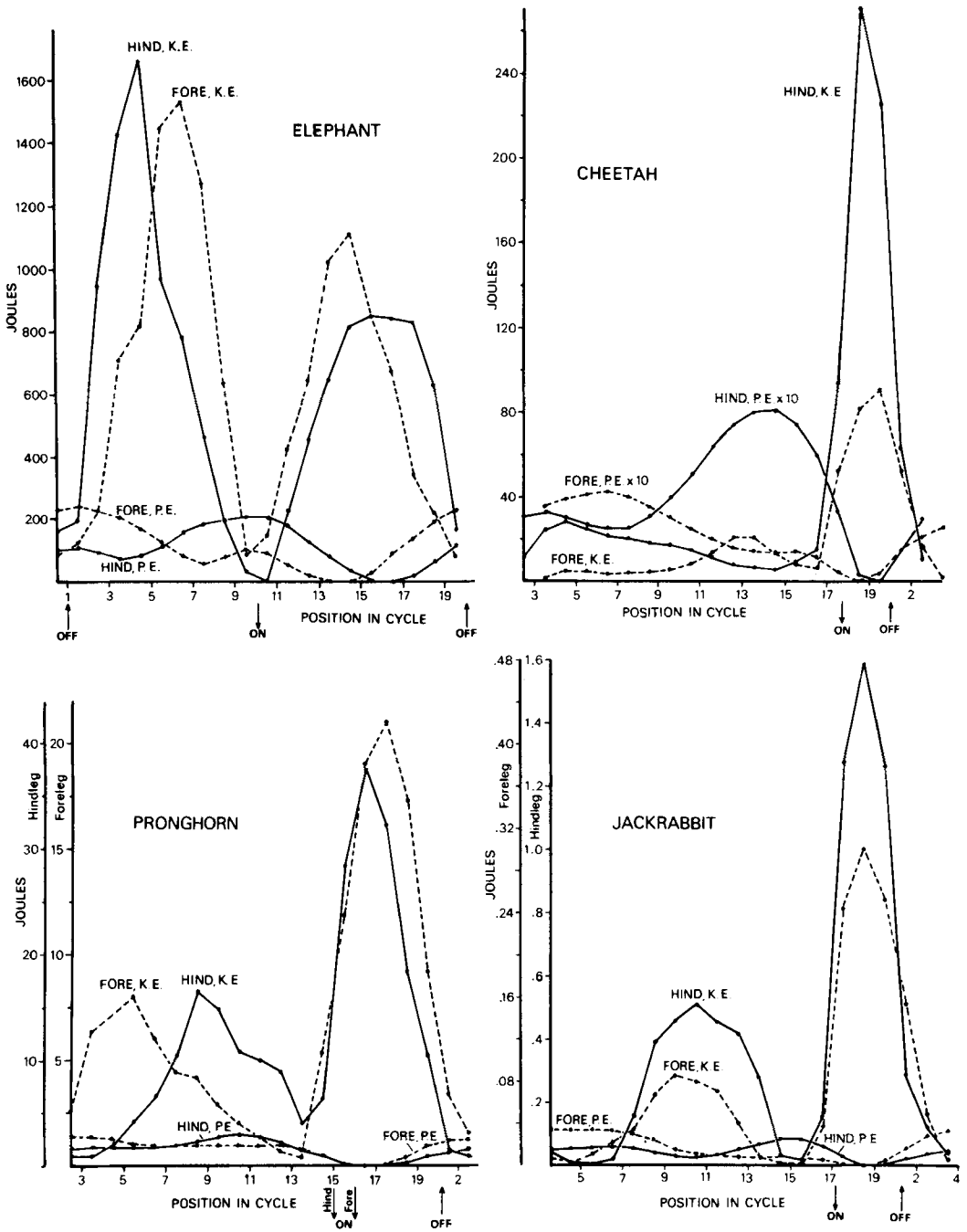


Fig. 3. The K.E. and P.E. cycles of the hindlegs (solid lines) and forelegs (dashed lines) of the respective animals. Positions in the cycles are keyed to Figures 1 and 2. Note that the P.E. of the cheetah model is shown  $\times 10$  and that the energy of hind- and forelegs is shown on different scales for the pronghorn and jackrabbit.

relative to body length than do their less swift cousins but that the proximal segments lengthen least, or not at all. The relative lengthening of distal segments is particularly marked for slender artiodactyls (e.g., deer, pronghorn, and small antelope). Thus, femur length is 39% of total leg length for the cheetah model but only 31% for the pronghorn model, whereas hindfoot length is 24% of leg length for the former, but 31% for the latter. Corresponding percentages for the humerus are 38 (cheetah) and only 28 (pronghorn), but for the forefoot, 25 and 39, respectively. It has been assumed that by keeping the more fleshy, heavier proximal segment relatively short, the center of mass of the leg is held closer to the body where it oscillates more slowly, thus conserving energy.

Quantitative data have not been available, however, and some relevant factors have been disturbing. Cursorial reptiles, living and extinct, have relatively long hindlegs, but their distal limb segments lengthen scarcely more than the other segments (Coombs, '78; Reiser, '77). Furthermore, when C.R. Taylor and associates ('74) studied the oxygen utilization of cheetahs, gazelles, and goats running on a treadmill, they concluded that "... the relationship between body weight and energetic cost of running apparently applies to animals with very different limb configurations ...," suggesting that "... most of the energy expended in running at constant speed is not used to accelerate and decelerate the limbs."

Accordingly, we contrasted the energy of oscillation for our model of the digitigrade cheetah with that of the unguligrade pronghorn, which has particularly stiltlike distal limb segments and proximal distribution of mass. Begin with the K.E. of the forward swing. For the hingleg and foreleg, respectively, peak energy for the cheetah is 171% and 260% that of the pronghorn (Fig. 4). However, this striking disparity cannot be attributed to differences in limb conformation unless related variables are minimal; thus, refinement of the data is necessary before interpretation is made. The time interval between successive limb positions is shorter by .0025 s for the cheetah model than for the pronghorn, which increases the relative K.E. of the former. (This is the equivalent of convergent errors of 10 frames per second between the actual and rated film-advance speeds of the cameras, which is possible but unlikely.) Accepting the time difference as accurate, the model was altered to give the cheetah the same interval as the

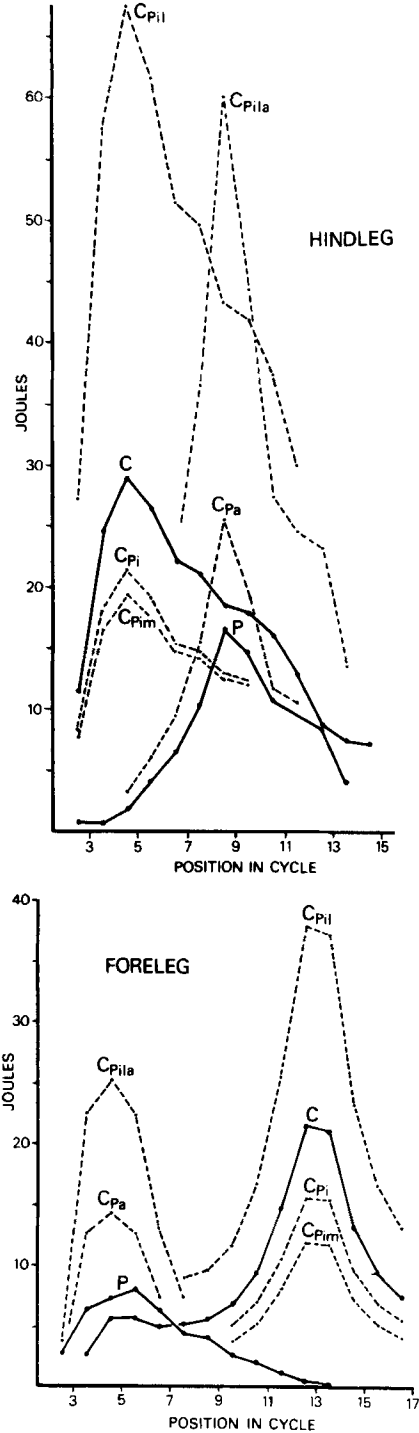


Fig. 4. Contrasts between the K.E. of the cheetah and pronghorn models for the forward swing of the legs. C, cheetah; P, pronghorn; i, time interval between successive leg positions; m, mass of leg; l, length of leg; a, joint angles. Thus, curve C<sub>Pim</sub> models a cheetah adjusted to have pronghorn intervals and mass.

pronghorn (curves  $C_{Pi}$  on Fig. 4). This reduces the peak K.E. of the hind- and forelegs of the cheetah to 127% and 194% that of the pronghorn. (In slowing its stride the living cheetah would also alter the trajectories of its limbs, probably reducing K.E. slightly more.)

Moreover, the hind- and forelegs of the cheetah weigh 106% and 120% as much as the respective legs of the pronghorn, which also increases their K.E., regardless of conformation. When the cheetah model is further modified so that its legs have both the interval and total mass of the pronghorn legs (curves  $C_{Pim}$ ), the values for its peak K.E. drop further to 116% and 147% those of the pronghorn.

The hind- and forelegs of the cheetah, however, are only 79% and 84% as long, respectively, as those of the pronghorn, and in reducing the masses of this carnivore's legs to equal those of the ungulate, the model's leg lengths are diminished to 78 and 80% those of the pronghorn. A "cheetah" with both reduced intervals and shortened legs would probably not be able to keep up with its intended prey.

Seeking to balance the reduced interval of the cheetah by increasing the length of its legs to equal the lengths of pronghorn legs also increases their masses so much that K.E. escalates beyond reasonable comparison (curves  $C_{Pil}$ ). The energy is reduced if the cheetah model is made to have not only the interval and leg lengths of the pronghorn but also its joint angles (curves  $C_{Pila}$ ), but the comparison remains unrealistic.

The unmodified cheetah model now looks more comparable to the pronghorn than first thought, its shorter interval and greater mass increasing K.E., but its shorter leg length reducing K.E. Perhaps the best comparison is a cheetah model converted to have the same joint angles (i.e., limb trajectories) as the pronghorn. Peak hind- and foreleg K.E. is then 152% and 176% that of the pronghorn (curves  $C_{Pa}$ ).

We have focused this comparison on the K.E. of the forward swing for several reasons: First, our data are less reliable for the backward swing (elephant excepted), where small errors in measuring joint angles are accentuated by the greater velocities. Second, interpretation of the course of the energy for the backward swing is complicated by ground forces acting on the system, and third, there are more constraints on the backward swing (i.e., the leg must be kept straight enough to support the animal), thus

making it more difficult to correlate the evolution of limb conformation and action with energy cost.

Nevertheless, because peak K.E. for fast-running mammals is so much greater on the backward swing, any evolutionary change in the limb conformation of cursors resulting from selection for reducing the energy of oscillation has probably been responsive to that part of the cycle. Accordingly, we contrast peak K.E. for the backward swing also, but the figures must be taken as approximations. It is evident from Figure 3 that this peak in K.E. exceeds the peak of the forward swing proportionately more for the cheetah than the pronghorn. Thus, the peak K.E. for the backward swing of the hind- and forelegs, respectively, of the cheetah model is 750% and 430% that of the pronghorn. Giving the former the joint angles of the latter reduces the values proportionately more than for the forward swing, but peak hind- and foreleg K.E. remains 128 and 169% that of the pronghorn.

A similar analysis for P.E. gives similar results. Details are not presented because the energy levels are so much lower (Fig. 3).

These data make it evident that relating energy utilization to limb conformation is more complicated than has been thought. Nevertheless, by all of the above comparisons, the oscillating legs of the fast-running cheetah model have considerably more K.E. than those of the pronghorn. Total energy has long been recognized (Cavagna et al., '77; Fedak et al., '82; Heglund et al., '82b; Manter, '38) to be the sum of the kinetic plus potential energy needed to lift and reaccelerate the center of mass of the body relative to the ground (external energy, or  $E_e$ ) and the K.E. needed to move parts of the body relative to the center of mass (internal energy, or  $E_i$ ). Researchers at Harvard have shown (Fedak et al., '82; Heglund et al., '82a) that  $E_e/M_b = 0.685 v_g + 0.072$ , and  $E_i/M_b = 0.478 v_g^{1.53}$ , where  $M_b$  is body mass and  $v_g$  is ground speed in  $m/s^{-1}$ . It follows that  $E_i = 0.8 E_e^{1.55}$ . Accordingly,  $E_i = 2.3$  times  $E_e$  when  $v_g = 10$  (approximate for elephant model), and 3.8 times  $E_e$  when  $v_g = 25$  (approximate for cheetah model). Most of  $E_i$  can be ascribed to oscillation of the legs (Fedak et al., '82). Since at the high speeds that must have most influenced the evolution of the special attributes of the master cursors, most of the total energy is internal, and since most of this energy is associated with oscillation of the legs, we believe that, contrary to the conclusion of the Taylor group ('74), the chee-

tah's limb configuration and manner of running are significantly more costly than are those of slender ungulates. We note, however, that the influence on the ratio of internal-to-external energy of wind resistance and the recovery of spring energy are not yet known.

Cheetahs and pronghorns are native to different continents. The impala or gazelle that escapes the cheetah's dash (successful chases average about 200 m) runs on to safety as the cat gives up pursuit (Eaton, '70). These animals show us that marked proximal distribution of the mass centers of the legs, with extreme lengthening of slender distal segments, is *not* essential for bursts of superlative speed but *does* correlate with capacity to maintain great speed. Perhaps no cursorial dinosaur had the limb proportions of ungulate mammals because none escaped predation by superior endurance in open chase.

#### APPENDIX

The masses of the proximal, middle, and distal leg segments are designated  $m_1$ ,  $m_2$ , and  $m_3$ , respectively. For the foreleg these values are 158, 72 and 20 K (elephant); 1075, 790, and 300 g (cheetah); 957, 520, and 332 g (pronghorn); and 30.4, 12.4, and 7.0 g (jackrabbit). Corresponding values for the hind leg are 208, 44, and 16 K (elephant); 2810, 1105, and 390 g (cheetah); 2832, 855, and 384 g (pronghorn); and 134.0, 38.5, and 19.4 g (jackrabbit). Joint angles, measured clockwise from the vertical, are designated  $\phi_1$  for hip and shoulder,  $\phi_2$  for knee and elbow, and  $\phi_3$  for ankle and wrist. The functional lengths of the proximal, middle, and distal leg segments are  $L_1$ ,  $L_2$ ,  $L_3$ . For the forelimb these are 93, 71, and 48 cm (elephant); 23.3, 23.2, and 14.6 cm (cheetah); 13.7, 21.3, and 35.0 cm (pronghorn); and 8.1, 8.6, and 5.2 cm (jackrabbit). Corresponding values for the hindleg are 120, 63, and 22 cm (elephant); 25.8, 24.3, and 16.0 cm (cheetah); 22.2, 28.0, and 33.0 cm (pronghorn); and 9.5, 11.5, and 11.6 cm (jackrabbit). Finally, the distances of the centers of mass of the respective segments from their proximal ends are  $a_1$ ,  $a_2$ ,  $a_3$ . For the foreleg these are 46.5, 30, and 24 cm (elephant); 11.3, 10.1, and 7.8 cm (cheetah); 8.5, 8.4, and 17.5 cm (pronghorn); and 4.0, 4.1, and 2.6 cm (jackrabbit). Corresponding values for the hindleg are 60, 30, and 11 cm (elephant); 12.4, 11.0, and 8.0 cm (cheetah); 11.1, 13.7, and 16.5 cm (pronghorn); and 4.7, 5.0, and 5.8 cm (jackrabbit).

In calculating the moment of inertia ( $I$ ) about the center of mass of each limb segment it was assumed that mass density varies linearly with distance from the proximal end of the segment, so that  $\rho = Ax + B$ , where  $x$  is linear distance and  $A$  and  $B$  are constants determined from the total mass of the limb and the position of its mass center. (This is the equivalent of converting the leg, which has irregular shape, to a rod having the uniform taper that gives the measured values for  $L$  and  $a$ .) We find for each segment that

$$I = m(aL - L_2/6 - a_2).$$

The K.E. (rotational plus translational) of a limb of three segments is

$$\text{K.E.} = \sum_{i=1}^3 (1/2 I_i \dot{\phi}_i^2 + 1/2 m_i v_i^2)$$

where  $v_i$  is the velocity of the center of mass of the  $i$ 'th segment. The velocities are determined from the joint angles using the following relations:

$$v_1^2 = a_1^2 \dot{\phi}_1^2$$

$$v_2^2 = L_1^2 \dot{\phi}_1^2 + a_2^2 \dot{\phi}_2^2 + 2L_1 a_2 \dot{\phi}_1 \dot{\phi}_2 \cos(\phi_2 - \phi_1)$$

and

$$\begin{aligned} v_3^2 = & L_1^2 \dot{\phi}_1^2 + L_2^2 \dot{\phi}_2^2 + a_3^2 \dot{\phi}_3^2 \\ & + 2L_1 L_2 \dot{\phi}_1 \dot{\phi}_2 \cos(\phi_2 - \phi_1) \\ & + 2L_1 a_3 \dot{\phi}_1 \dot{\phi}_3 \cos(\phi_3 - \phi_1) \\ & + 2L_2 a_3 \dot{\phi}_2 \dot{\phi}_3 \cos(\phi_3 - \phi_2) \end{aligned}$$

The potential energy is

$$\begin{aligned} \text{P.E.} = & m_1 g a_1 \cos \phi_1 + m_2 g (L_1 \cos \phi_1 \\ & + a_2 \cos \phi_2) + m_3 g (L_1 \cos \phi_1 \\ & + L_2 \cos \phi_2 + a_3 \cos \phi_3) \\ & + \text{constant,} \end{aligned}$$

where the constant is determined by the condition that the minimum potential energy be zero.

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