

WALKING, RUNNING, AND JUMPING

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Man has studied the walking, running, and jumping of animals since long before the first cave painters depicted the chase. So much has been learned about terrestrial locomotion that even a brief review is difficult in only a few pages.

The subject has been approached through physiology, anatomy, mechanics, and motion analysis. Noteworthy among physiologists who have studied locomotion is the British Nobel laureate, A. V. Hill (see particularly, 1949). Fundamental relationships between body size and muscle dynamics have been described. Muscle performance has been related to load, temperature, and rate of contraction. The design of muscles has received attention, and further studies are in progress.

Anatomical and mechanical approaches to the analysis of locomotion are usually combined, the emphasis falling sometimes to one and sometimes to the other. As long ago as 1873 a preacher named Houghton wrote a book on the principles of animal mechanics that is still superior to most texts on kinesiology. More recently, important contributions have come from Cambridge (e.g., Barclay, 1946; Gray, 1944) and elsewhere in England (e.g., Smith and Savage, 1956). The major work on the spine by the eminent Dutch morphologist, E. J. Slijper (1946), is exemplary. In America the most important analysis of terrestrial locomotion is by A. B. Howell (1932, 1944), but a paper by Gregory (1912) remains useful, and many other studies have been reported (e.g., Camp and Smith, 1942; Eaton, 1944; Evans, 1946; Schaeffer, 1947; Snyder, 1954).

The range of variation of structure among

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cursorial vertebrates is considerable. No one animal has all the characteristic adaptations. Some cursors have but few of them: runners of small body size need fewer adaptations to achieve performance equal to that of their larger cousins. The following is only a sketch of anatomical features that characterize cursorial animals; an adequate summary of this extensive subject is not possible here.

Runners are usually larger than rabbits, and may be as large as the giraffe; hoppers tend to be smaller than kangaroos, and may be as small as mice. Body proportions are trim to reduce weight. The spine of large runners is relatively rigid to minimize stresses resulting from oscillations. Carnivores and rabbits increase speed in several ways by flexing and extending the back as they gallop. The presacral spine of bipedal hoppers is short to increase stability, and the tail is long to serve as a counterpoise. Limbs are long to lengthen the stride. The legs have evolved relatively long metapodial (central foot) and epipodial (central limb) segments. Cursors have further increased the functional length of their limbs by changing foot posture from the heel-down, plantigrade stance of unspecialized ancestors to the digitigrade posture (some reptiles, birds, carnivores) or unguligrade posture (ungulates). Limb muscles are massed close to the body. In these ways the length of the leg has been increased without increasing the kinetic energy that must be developed and overcome each time the limb swings to and fro.

As evolution lengthened the foot, it also compacted the metapodials (cheetah), caused adjacent metapodials to fuse together (birds, artiodactyls), or discarded lateral elements (ostrich, some marsupials and rodents, ungulates). These changes in-

crease strength without increasing weight. The shoulder blade of runners tends to be oriented vertically against a deep narrow chest. With loss or reduction of the collar bone, the shoulder blade becomes free to swing in the plane of the moving forelimb. This adaptation increases both length and rate of stride. The evolution of relatively hinge-like joints provided with splines and grooves restricts limb motion to the direction of travel and prevents dislocations. As capacity for adduction and abduction of the legs and for rotation of the lower leg was sacrificed, the muscles and bones associated with these motions were modified (e.g., springing ligaments of ungulates), reduced (distal ulna), or even lost (fibula of some ungulates). Limb muscles of cursors insert relatively near to the joints they move, producing greater limb velocities but sacrificing force in proportion.

Anatomical and mechanical adaptations for terrestrial locomotion have been reviewed in a small book by Howell (1944), in special chapters in more general works (Böker, 1937; Gray, 1953; Ottaway, 1955; Slijper, 1947), and in an article by Hildebrand (1960).

The fourth approach to the study of terrestrial locomotion is motion analysis. How do living animals actually move? The human senses are virtually incapable of observing the limb actions of any but large animals that are moving slowly. Progress by this approach was therefore scant until the advent of photography. The classic photographs predating motion pictures, taken by Muybridge (1899), are still widely studied. Using a battery of 24 still cameras ingeniously triggered in sequence, he photographed the motions of more than two dozen kinds of mammals and several kinds of birds.

Motion pictures have been used to advantage to study the gaits of certain animals (e.g., Barclay, 1946; Bartholomew and Caswell, 1951; Bartholomew and Cary, 1954; Evans, 1946; Hildebrand, 1959, 1961; Snyder, 1949, 1952). Since Muybridge, how-

ever, only de la Croix (many papers in the 1920's and 30's), whose conclusions often must be questioned, has attempted a comprehensive analysis of the gaits of vertebrates, and some papers on locomotion therefore tend to be too theoretical. Limbs that do not swing as pendulums are likened to pendulums; body size is related to speed of muscle action without knowledge of actual stride rates; some factors have gone undetected that contribute to speed, support, balance, or maneuverability.

The author is analyzing the gaits of animals from motion pictures taken at 64 to 200 frames per second. Some of the films have been prepared specifically for the study; others have been obtained by purchase, rental, donation, and exchange from various private and commercial sources in several countries. A large film editor with frame counter is used to make several kinds of records including "progression diagrams" (see Hildebrand, 1960, Fig. 4) which show, on an appropriate time scale, the sequence of footfalls and duration of contact of each foot with the ground for one or several cycles of motion. One or more gaits of about 50 genera (mostly mammals, but also other tetrapods) have been analyzed. It is expected that this coverage will be doubled before results are published. It would be premature to include here even the tentative results. It is appropriate, however, to indicate the general nature of the study.

One complete cycle of motion is called a "stride." Each stride is arbitrarily considered to start with the placement of a hind-foot on the ground; the duration of a stride is called the "stride interval." Strides of quadrupeds can have nine variables that relate to timing. These can be expressed in various ways, depending on the references and definitions used. It is convenient to use as references the stride interval and the duration of contact with the ground by a given hindfoot (= "given hindfoot contact interval"). The "leading foot" is the second of a pair to strike the ground in each couplet of footfalls when the footfalls are not

evenly spaced in the stride interval. The variables are then as follows:

1. Stride interval.
2. Percent of stride interval occupied by a given hindfoot contact interval.
3. Percent of given hindfoot contact interval that other hindfoot is on the ground.
4. Percent of given hindfoot contact interval that a given forefoot is on the ground.
5. Percent of given forefoot contact interval that other forefoot is on the ground.
6. Percent of stride interval that placement of second hindfoot lags behind placement of given hindfoot.
7. Percent of stride interval that placement of second forefoot lags behind placement of given forefoot.
8. Lead of forefeet in relation to lead of hindfeet.
9. Percent of stride interval that placement of given forefoot lags behind placement of given hindfoot.

This appears to be a discouragingly long and complicated list of variables to correlate with one another, yet the problem is not so desperate as it seems. Consider first a family of gaits having the footfalls of each pair of feet (fore and hind) evenly spaced in time. The walk, trot, and pace are of this nature. The animal then cannot be said to lead with any foot; variable 8 (above) is not applicable. Variables 6 and 7 are equal and a function of variables 1 and 2. Further, observation shows that for these gaits the four feet are on the ground for equal periods, so variables 3, 4, and 5 need not be considered. (This simplified analysis disregards random variations among consecutive strides, which may be of considerable magnitude.) A graph can now be prepared to relate the two principal variables of these gaits: the percent of the stride interval during which each foot is on the ground (variable 2, which correlates roughly with speed) and the relation in time of the fore footfalls to the hind footfalls (variable 9).

Such an analysis shows that there are va-

rious ways of walking which merge into one another. The crawling walk permits turtles and infant mammals to move only one limb at a time. One type of four-beat walk having each fore footfall follow the hind footfall on the same side of the body provides a smooth continuity of support and is used by elephants and most ungulates. The pacing walk enables such long-legged, agile animals as the cheetah and gerenuk to avoid interference among their limbs. The trotting walk of short-legged animals such as the weasel and hippopotamus gives maximum stability. With speeding-up, the pacing walk, the above four-beat walk, and trotting walk respectively become, without any break in stride, the pace, running walk, and trot. A fifth kind of walk is a four-beat walk having each fore footfall follow the hind footfall on the *opposite* side of the body. It is used by few animals. Some reasons for its relative inferiority are evident, but further analysis is desirable.

Another family of gaits has the footfalls of each pair of feet (fore and hind) unevenly spaced in time: the intervals between left and right feet differ from the intervals between right and left, and the animal is said to run with a given lead. The various gallops are of this nature. Fore- and hindfeet may use the same lead (transverse gallop) or opposite lead (rotatory gallop). The body may be supported all of the time, or there may be one or more unsupported intervals in the stride. Contact intervals of left and right feet of a pair tend to be equal (so variables 3 and 5 may be disregarded), but fore contact intervals often differ from hind contact intervals, and the interval between footfalls of a pair of feet (fore or hind) (variables 6 and 7) is not determined by the stride interval and foot contact interval, as was the case for the other family of gaits.

In spite of seeming complexity, meaningful correlations are easily made by plotting on one axis of a graph the per cent of the stride interval that one or *both* hindfeet are on the ground (thus combining vari-

ables 2 and 6), and on the other axis the per cent of the stride interval by which placement of the forefeet as a pair lags behind placement of the hindfeet as a pair (thus combining variables 7 and 9). From such a graph one can read directly the per cent of the stride interval that the animal is supported by the hindfeet, supported by the forefeet, unsupported with feet collected under the body, and unsupported in the extended position. Appropriate symbols distinguish transverse and rotatory gallops, and also the related half-bound (hindfeet placed simultaneously, forefeet alternately) and bound (feet placed simultaneously by pairs). The type of gallop or bound used correlates well with body size, speed, and maneuverability. It is usually possible to predict the gaits that a particular animal uses.

The duration of unsupported intervals tends to increase with speed and maneuverability, but large animals are in contact with the ground more of the time at maximum speeds than at near maximum speeds. Maximum stride rates range from about 1.4 strides per second, for the elephant, to 10 or 12 strides per second, for certain lizards and mice. As speed of travel increases, ungulates and carnivores increase stride distance considerably but increase stride rate only slightly. Small rodents also increase stride distance as speed increases, but they decrease stride rate. As speed increases, the forefoot contact interval tends to become shorter in relation to the hindfoot contact interval (variable 4).

Other kinds of analyses that can be made from high-speed motion pictures include determination of the paths followed by various parts of the limbs in relation to the ground or to other parts of the body, contributions to speed made by flexion and extension of the spine (Hildebrand, 1959), contributions to performance made by motions of the head, neck, and tail, and sequence and magnitude of various coordinated motions.

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