AMER. ZOOL., 20:255–267 (1980)

The Adaptive Significance of Tetrapod Gait Selection[1]

MILTON HILDEBRAND

Department of Zoology, University of California, Davis, California 95616

SYNOPSIS. At the slow walk tetrapods avoid lateral couplets gaits to minimize support by ipsilateral bipods. Most of them use the lateral sequence because tripods then make larger triangles than for the diagonal sequence. Of the running symmetrical gaits, the single-foots (in each sequence) permit the smoothest and fastest travel without suspensions. The trot and pace allow two legs to thrust in unison, the former giving the most stability to animals not placing the feet well under the body, and the latter avoiding interference for long-legged runners. The bound and half bound are most used by small, agile mammals for bursts of speed and for maneuvering on rough terrain by a series of leaps. Such animals use the extended suspension. Large cursors on open terrain usually select the shorter, more economical, gathered suspension. The fastest runners use both suspensions to gain long strides. At moderate speed the transverse gallop has the advantages over the rotary gallop that both bipods and tripods are more stable, and that interference may be avoided. At high speed, using both suspensions, none of these advantages pertains. The rotary gallop may then increase maneuverability.

INTRODUCTION

In a series of papers extending over many years, but in two recent papers in particular (Hildebrand, 1976, 1977), I have presented a method for the recording, analysis, and comparison of tetrapod gaits. The principal objective of this paper is to summarize and extend my application of the method to the interpretation of gait selection, with emphasis on mammals. I shall also respond here to several questions that have been addressed to me sufficiently often at prior symposia to indicate general interest. These concern the relation between my method and those of other investigators, and the significance of gait analysis in general for neurophysiological research.

SYMMETRICAL GAITS

Representation

We begin with the symmetrical gaits (pace, walk, single-foot, slow gait, rack, jog, trot, etc.). It is neither necessary nor appropriate to repeat here such basic steps of gait analysis as filming and the preparation of gait diagrams. I must remind the reader, however, that for this class of gaits all events that relate to the timing of footfalls and the duration of the contacts of the feet with the ground can be expressed by two variables. These are expressed as percentages, and when plotted together form a *gait graph* (Fig. 1*A*) which must include all symmetrical gaits—usual, unusual, and theoretical.

Recall also that a *footfall formula* shows the succession of combinations of supporting feet occurring in one cycle of motion. Only the concept, not the stylized method of representation, is needed here. If the gait graph is divided into triangles as shown by Figure 1*B*, then each triangle encloses plots for gaits having the same footfall formula or combinations of supporting feet (additional, transitional formulas are represented by the lines and intersects). There are 16 basic formulas for symmetrical gaits (plus 28 transitional formulas). (If the duration of contacts by forefeet differs from those by hind feet, then the formulas, and also their distribution over the graph, are altered as explained in Hildebrand, 1966 and 1976. Since the durations of fore and hind contacts are about the same for wild mammals, this complication can be ignored here without altering conclusions about gait selection.)

Further, gaits can be named according to position on the graph. Since the variable

[1] From the Symposium on *Morphology and Analysis of Adaptation* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1978, at Richmond, Virginia.

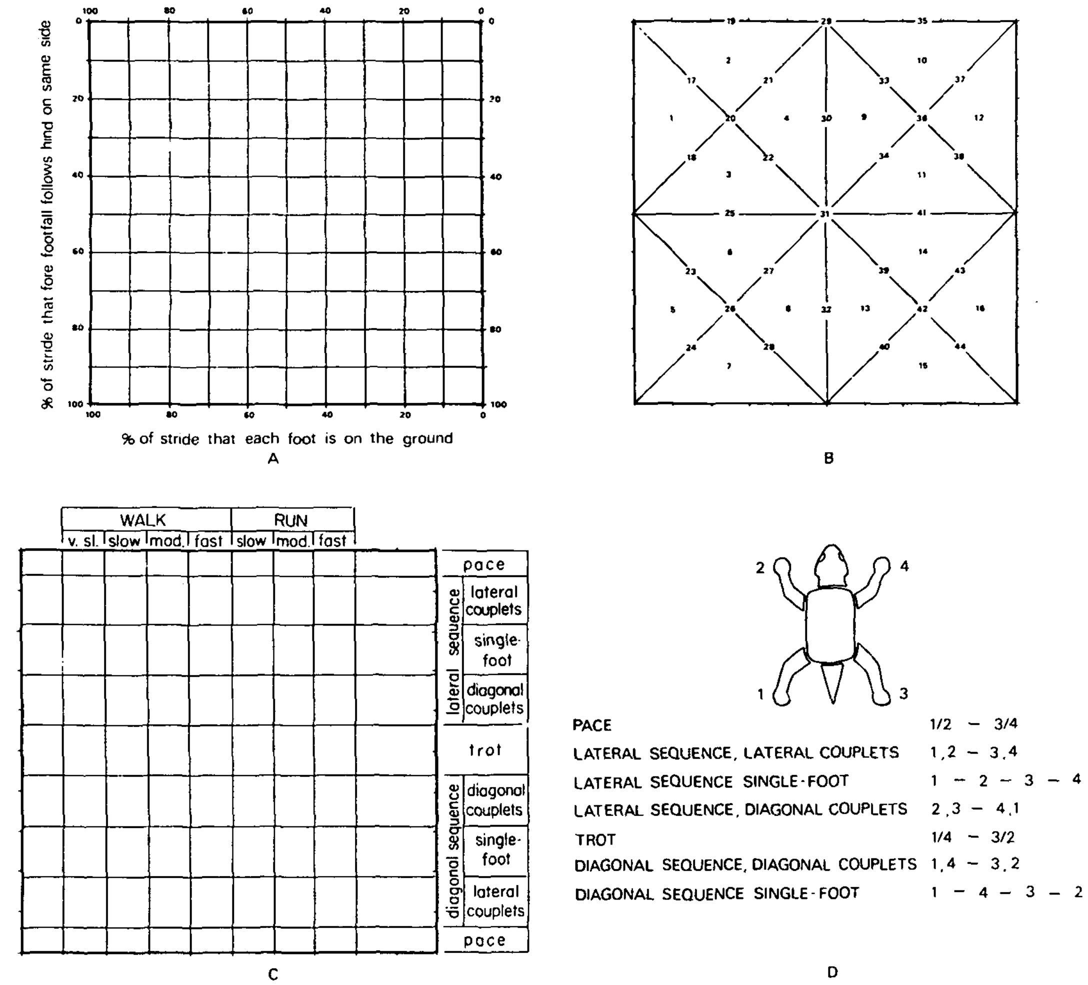

FIG. 1. *A*, gait graph for symmetrical gaits having fore and hind contact intervals the same. *B*, overlay to the gait graph showing the number and distribution of all possible footfall formulas. *C*, overlay showing scheme for naming the gaits. *D*, cadence of footfalls for symmetrical gaits.

on the horizontal axis (percent of cycle that each foot is on the ground) varies with rate of travel, the terms adopted are readily understood (Fig. 1*C*). The variable on the vertical axis (percent of cycle that fore footfall follows hind on same side) relates the action of the forefeet as a pair to that of the hind feet as a pair. If the feet of a tetrapod are numbered as shown in Figure 1*D*, then, when fore and hind feet on the same side of the body (1 and 2, or 3 and 4) strike and leave the ground about in unison, the gait is the *pace*. When fore and hind feet on opposite sides of the body (1 and 4, or 3 and 2) move together then the gait is the *trot*.

If the foot to move after a hind foot is the forefoot on the *same* side of the body, then the gait has *lateral sequence* (1,2,3,4), whereas if the foot to move after a hind foot is the forefoot on the *opposite* side of the body, the gait has *diagonal sequence* (1,4,3,2). Also, if the footfalls are evenly spaced in time, the gait is a *single-foot,* either in lateral or diagonal sequence. Finally, if the footfalls on the same side of the body are coupled in time, the gait has *lateral couplets* (1,2—3,4); whereas, if foot-

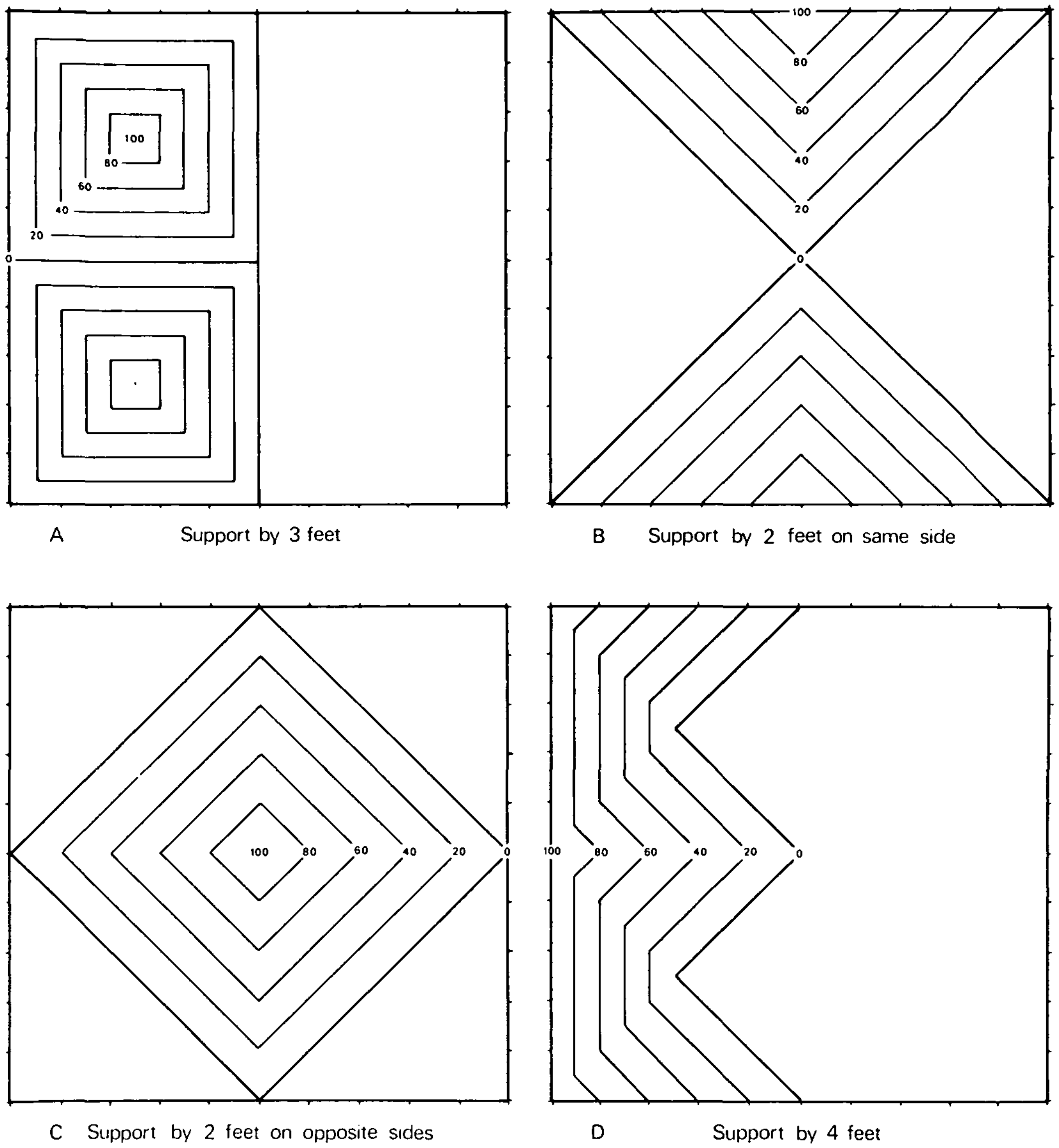

FIG. 2. Overlays to the gait graph showing the percentages of the locomotor cycle that the body is supported by two, three, and four feet.

falls on opposite sides of the body are coupled in time, the gait has *diagonal couplets* (2,3—4,1).

Combining the terms that are descriptive of variation along the two axes of the graph (Fig. 1*C*) provides terms for the gaits which, though unfamiliar to laymen, are descriptive and accurate, *e.g.*, moderate, running trot; fast, lateral sequence, lateral couplets walk.

This background serves as a basis for the study of gait selection.

Walking gaits: Stability

Gaits represented by the left side of the graph have each foot on the ground more than half of the time and are called walking gaits. For walking gaits, the principal criterion for gait selection is usually stability. The body is always supported by two,

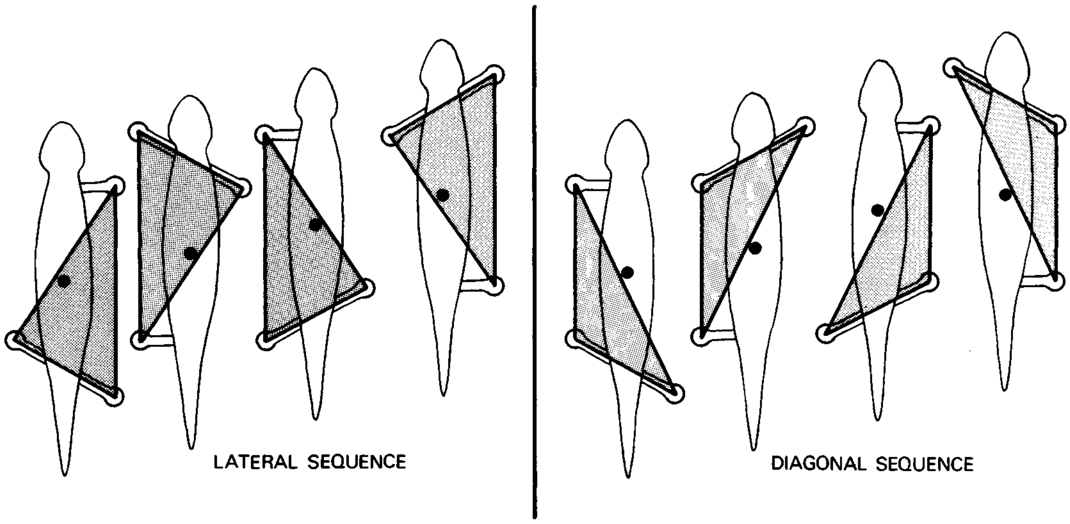

FIG. 3. Support provided by tripods for walking symmetrical gaits, in lateral and diagonal sequence. The spot is the center of gravity.

three, or four feet at a time, so stability is increased by (1) maximizing support by four feet, (2) minimizing support by two feet, and, in particular, by (3) selecting the combinations of two and three feet that are favorable to balance.

All walking gaits except the exact pace (top line, Fig. 2*A*) and trot (line separating lateral-sequence gaits from diagonal-sequence gaits) have at least some support by tripods. The stability of a tripod depends on the area enclosed, and on the position of the tripod relative to the animal's center of gravity. Long ago, Sir James Gray (1944) showed that the tripods for lateral-sequence gaits are more stable than those for diagonal-sequence gaits.

Figure 3 shows that when a tetrapod (*e.g.*, salamander) walks with a straight spine, the supporting tripods for the lateral sequence are indeed larger, and more favorably placed under the animal's center of gravity, than those for the diagonal sequence. Also, lateral sequence facilitates undulation of the spine, which rotates the girdles and lengthens the step, thus further enlarging the supporting triangles. In addition, undulation of the spine may move the animal's center of gravity back and forth across the midline of travel and toward the centers of the supporting triangles. The same benefits are not possible with the diagonal sequence because undulation then cannot rotate the girdles so as to increase the length of the step. (Hence, Fig. 3 shows an animal with a straight spine so that the two modes of travel will be comparable.)

We conclude that the slow gaits of most tetrapods, including all tippy ones like turtles, should fall in the upper left quadrant of the gait graph. Any exceptions may be expected to be animals for which stability is assured by large feet or a wide stance. This expectation is realized: Animals known to walk in diagonal sequence are primates and the giant armadillo, aardvark, and kinkajou.

Figure 2*B* shows the distribution on the gait graph of support by the two feet on the same side of the body—an unstable combination at low speeds, because there is then a tendency for the body to roll unless it is swayed from side to side, or the legs are long and the feet small enough to be placed under the midline of the body. Consequently, we would expect animals to avoid gaits that fall near the upper left and lower left corners of the graph, and this is, in fact, the case.

Support by the two feet on opposite sides of the body (Fig. 2*C*) is much more

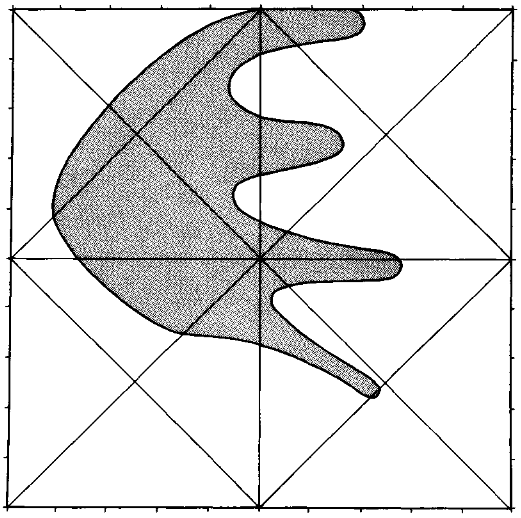

FIG. 4. Distribution on the gait graph of more than 1,000 plots for 156 genera of tetrapods. Scattered marginal records (about 5½% of the total) have been deleted to give focus to the pattern.

stable because the line of support then passes diagonally under the body in such a way as to come approximately below the center of gravity.

Support by all four feet (Fig. 2*D*) is, of course, the most stable combination. The figure shows that the duration of such support is greatest relative to rate of travel in the areas of the graph numbered 2, 3, 6 and 7 on Figure 1*B*.

To summarize for walking gaits, areas 1 and 5 (Fig. 1*B*) are favorable at very slow rates of travel because support by four feet is good and support by bipods is eliminated. The slowest performances of small and unsteady animals might fall here. Areas 2 and 7 are unfavorable because of the relative instability of support by the two feet on the same side of the body. This difficulty becomes less serious, however, as speed increases (*i.e.*, in the right hand portions of these areas), because then, although the percent of the time that the body is supported by bipods increases, the duration of each such phase decreases, and the motion of the body contributes dynamic stability. Long-legged and agile animals might, therefore, use gaits falling to the right in areas 2 and 7, particularly on open terrain.

Areas 3 and 6 are favorable because there support by four feet is maximum and the bipods are the more stable diagonal opposites. The portions of these areas that lie adjacent to areas 1 and 5 would have only very short bipods and would be nearly as stable as gaits in areas 1 and 5.

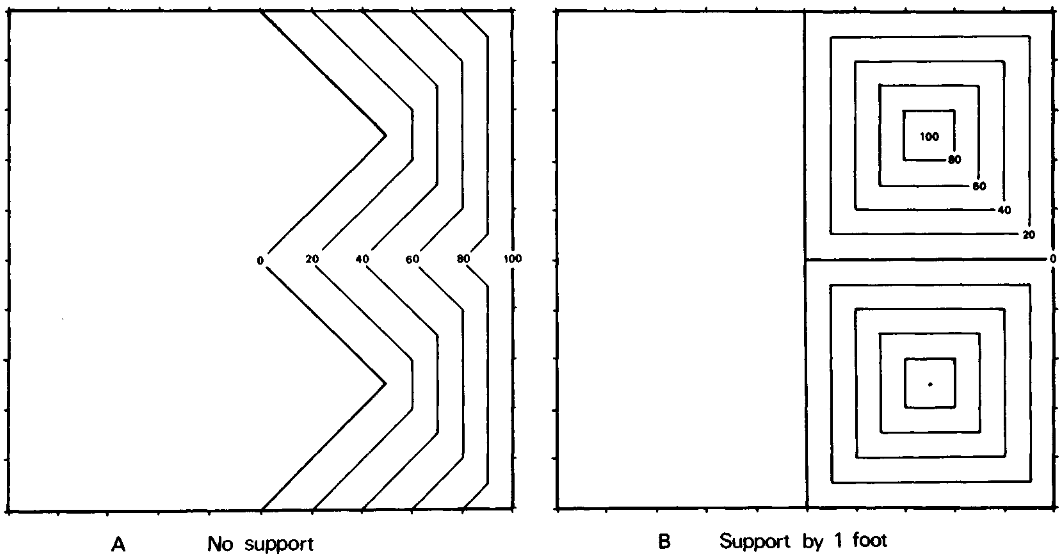

FIG. 5. Overlays to the gait graph showing the percentages of the locomotor cycle that the body is unsupported, and supported by only one foot.

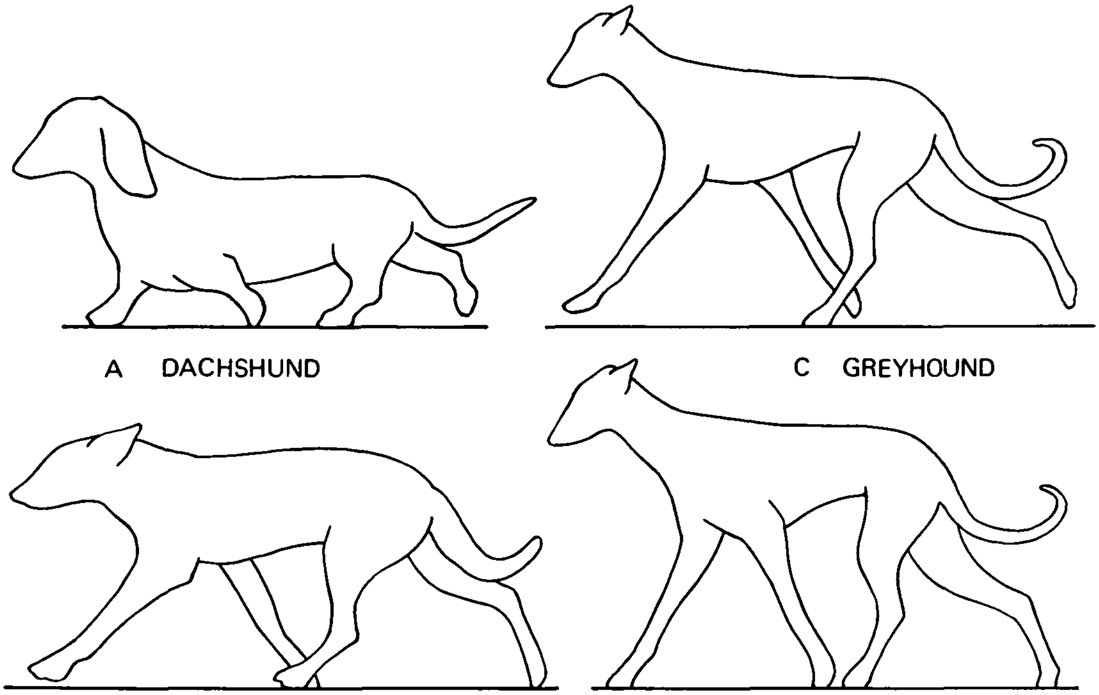

FIG. 6. The relation of the pace and trot to interference, body build, and speed.

Areas 4 and 8 are favorable because, although support by four feet is lost, increased speed compensates, and the bipods are of the more stable kind. Finally, however, despite the above considerations, areas 5, 6, 7, and 8 are unfavorable because of the relative instability of gaits using the diagonal sequence. Overall, therefore, one can predict that many tetrapods select the gaits represented by areas 1, 3, and 4, and that some animals, having good balance because of their conformation, may select gaits of areas 2, 6, and 8. Area 7 is rejected for the nature of both its bipods and tripods. These expectations are, in fact, realized, as shown by Figure 4. (For further details of gait selection by specific species see Hildebrand, 1976.)

Running gaits: Economy and interference

At faster rates of travel—on the right side of the graph—stability remains important if the legs are short or splayed to the sides of the body, but economy of effort and avoidance of interference among the legs (which are now swinging in wider arcs) are added as criteria in gait selection.

Suspensions (periods in the locomotor cycle when all feet are off of the ground) may be costly in terms of effort. Figure 5*A* shows the distribution on the gait graph of gaits having suspensions, and also the relative durations of the suspensions. It is at the levels on the vertical axis where the two single-foots fall that greatest speed can be obtained before suspensions are introduced. Further, since these gaits have the footfalls evenly spaced in time, loads are about evenly distributed among the four legs. The single-foots, therefore, have advantages for economy of effort.

An alternative strategy for an animal is to run at the pace or trot, each of which has the disadvantage of longer suspensions, but the advantage that two legs work together in absorbing impact and imparting thrust. (Compare Figs. 1*C*, 2*B*, 2*C*, and 5*A*.) These gaits avoid (or nearly avoid) the strain of supporting the body by one foot at a time (Fig. 5*B*).

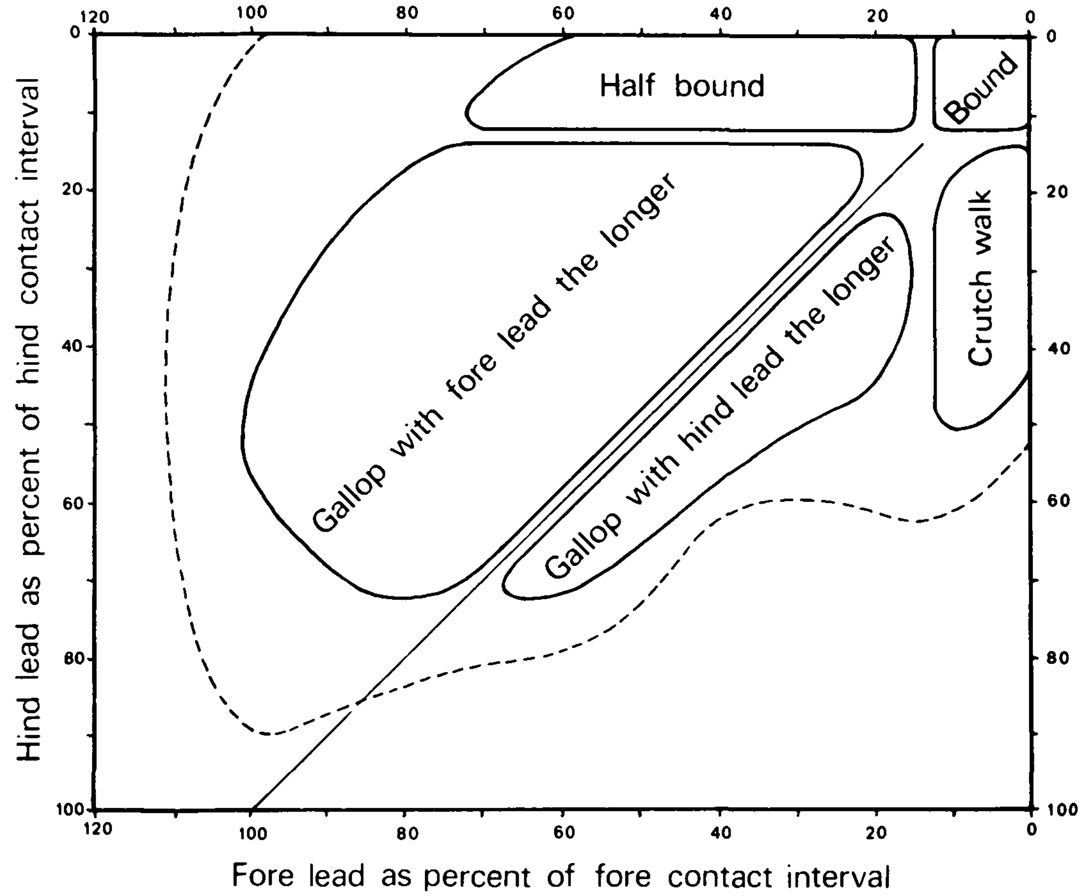

FIG. 7. The length of fore and hind leads in relation to the terminology of asymmetrical gaits. Usual records shown by solid lines; marginal records shown by dashed line.

Figure 4 shows that these four gaits (pace, trot, and the two single-foots) are, in fact, the symmetrical gaits selected by running animals. All alternative gaits (which would have lateral or diagonal couplets) would be more stressful. Which of the four gaits is selected depends on considerations of stability and interference, and thus also on body build and speed.

The short-legged dachshund (Fig. 6*A*) is unable to kick itself, even at a fast trot. Accordingly, it uses the trot and avoids the pace, which, as explained above, is less stable for an animal of that build. With the same leg angles, the German shepherd must either pace (Fig. 6*B*) or crab (*i.e.*, track the hind feet to one side of the respective fore feet). The long-legged greyhound commonly paces to avoid interference (Fig. 6*C*) and can trot without crabbing only if moving relatively slowly (Fig. 6*D*).

Following these considerations, most tetrapods trot (if they run at all), and those with short to medium legs (most rodents, most carnivores), stocky build (bovids, rhinoceros, hippopotamus), or legs splayed to the side (lizards) have no other running symmetrical gait. The long legs of camelids and certain breeds of dogs provide both the necessity to pace (to avoid interference) and the capacity to do so steadily on open terrain without loss of balance. The horse paces slightly faster than it trots.

The elephant uses the lateral sequence single-foot because that gait is smoother than the pace or trot and avoids suspensions, matters of importance to so huge an

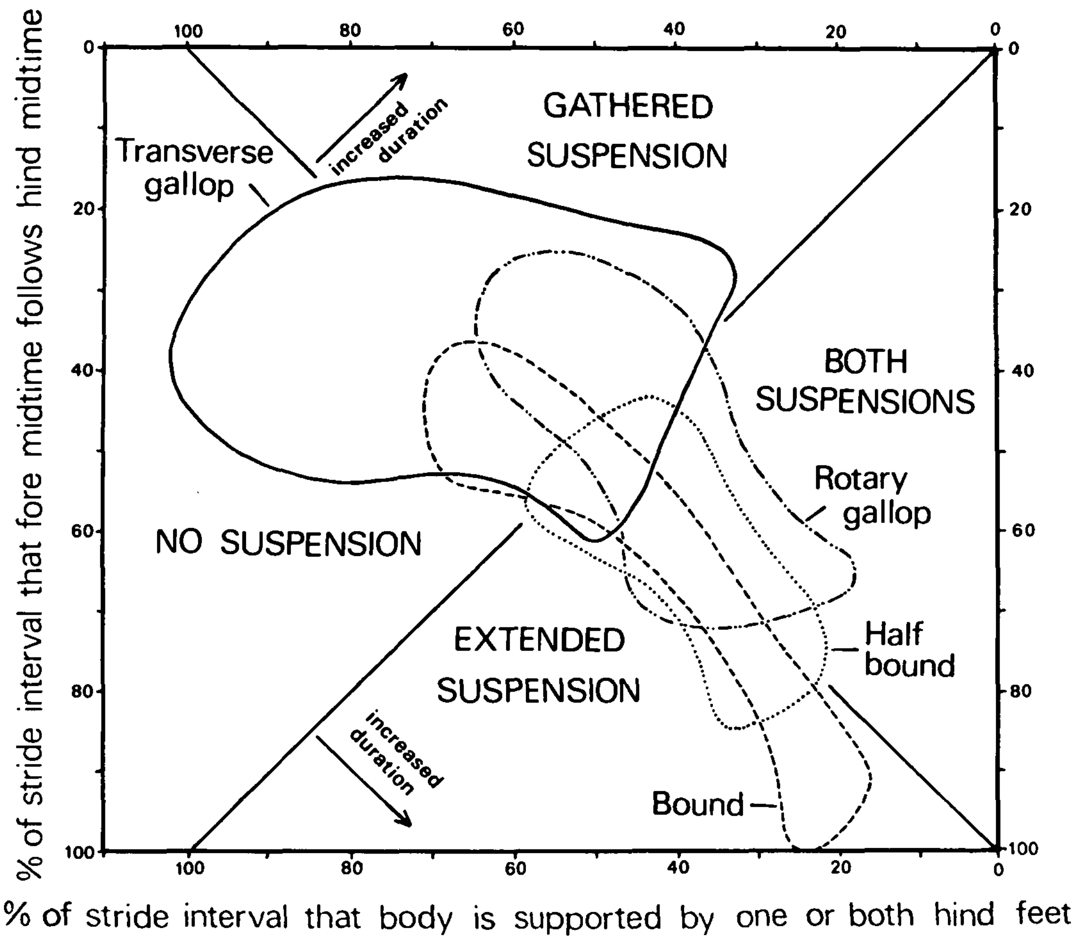

FIG. 8. Gait graph relating lead and suspensions to hind support and midtime lag. Marginal records have been deleted to give focus to the pattern.

animal. Some horses are trained to use this gait (also called slow gait, rack, and running walk) because the smoothness pleases riders. One German shepherd dog demonstrated its versatility by using this single-foot when burdened with a load that would have bounced uncomfortably at a pace or trot.

Several small artiodactyls (duiker, muntjak) use the diagonal-sequence single-foot. Why they select this graceful, tripping gait is not clear.

ASYMMETRICAL GAITS

Length of lead: Body size and agility

Asymmetrical gaits have the footfalls of each pair of feet unevenly spaced in time. The feet of a pair either strike the ground in unison, or in quick succession followed by a pause before they strike again. The first foot of the pair to strike is termed the trailing foot; the second is the leading foot. The size of the step between these footfalls, or the magnitude of the lead, is written as the time interval between the footfalls expressed as a percentage of the duration of the contact of each foot. It can range from 0% (feet of a pair moving in unison) to more than 100% (long lead).

On Figure 7, fore lead is plotted against hind lead. If both leads are very short or absent, the gait is termed the *bound*. If there is scarcely any hind lead but an evident fore lead, the animal is doing the *half* *bound.* In the opposite circumstance, scarcely any fore lead but an evident hind lead, the gait is the *crutch walk.* All other asymmetrical gaits have at least some lead, both fore and hind, and are called *gallops.* There may be much variation in the magnitude of the two leads among individual galloping animals, and between successive cycles of the same individual. Nevertheless, Figure 7 shows that although fore and hind leads are usually similar, the fore lead tends to be the longer. What factors control gait selection in regard to length of lead?

When the hind feet function in unison, or nearly so, they can impart a much stronger thrust to the body than when they move independently. Paired action is to be expected, therefore, among animals that move by a series of leaps. Such animals would be those that are otherwise capable of leaping (body of medium or small size, legs strong and of at least moderate length), and that can most benefit from such progression (terrain rough in relation to body size, need to maneuver above, or to see over, ground vegetation, need to accelerate quickly or to dodge). Since a series of leaps may be costly in terms of energy, the hind feet would be most used in unison by animals that run only moderate or short distances.

The bound and half bound are, in fact, used by just such animals: the more slender and long-legged marsupials, insectivores, and rodents, and by hyraxes, rabbits, many carnivores, and (though not exclusively) the smaller artiodactyls. The forelimbs are better able to absorb impact (as of a long leap) when they function together. Hence the bound is favored by the longest jumpers (squirrels, jumping mouse, impala). However, the duration of the support role of the forefeet is increased by their independent action, so the half bound is commonly favored when the leaps are of moderate length. The crutch walk is used (though not regularly) by apes as a consequence of their relatively long arms.

The most common running asymmetrical gaits are the gallops, *i.e.,* both fore and hind pairs of feet take at least a small lead. Figure 7 shows that, although there is wide variation in the relative lengths of the two leads, the fore lead tends to be the longer. As for the half bound, this is the consequence of the greater propulsive role of the hind feet and greater supportive role of the forefeet.

Representation

Although symmetrical gaits can be expressed by only two percentage figures (assuming that all contact intervals are the same), it is not reasonable to describe most asymmetrical gaits by fewer than five variables. Fore and hind leads have already been considered. Two variables (or, in a sense, combinations of variables) that are of particular utility for the analysis of gait selection will be described as our next step. (For a more detailed account of the variables, see Hildebrand, 1977.)

Since, in this class of gaits, the hind feet function more or less as a unit in propelling the animal, it is useful to determine the duration of the contact that both hind feet make with the ground in each cycle. (This is the contact interval of one foot of the pair plus the lead.) The duration of this combined contact, as a percentage of the cycle, diminishes as speed increases.

A second useful variable is what I have called midtime lag. The midtime is the point half way in time between the strike of the trailing foot of a pair of the lift off of the leading foot (*i.e.,* half way through the combined contact noted in the preceding paragraph). Midtime lag is simply the interval between the hind midtime and the fore midtime. This variable relates the action of the forefeet to that of the hind feet.

A useful graph is derived by plotting these two variables together (Fig. 8).

Suspensions: Gathered, extended, or both

Plots that fall in the upper triangular quadrant of the gait graph (Fig. 8) represent gallops having one suspension in each cycle, and this occurs when the feet are gathered under the animal and the back (if it is limber) is ventroflexed.

Plots in the lower quadrant represent gaits having one suspension in each cycle,

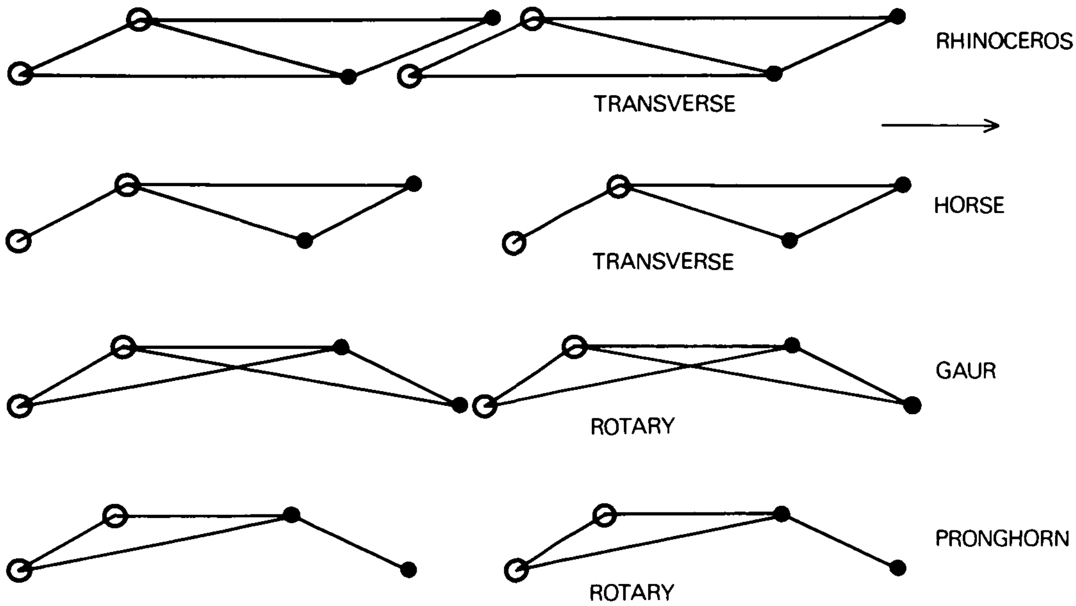

FIG. 9. Comparison of triangles of support between representative transverse and rotary gallops. Open circles show positions of hind feet, black spots show positions of forefeet. Motion is from left to right. Spacing of feet transverse to line of travel (*i.e.*, straddle) is exaggerated and standardized.

and it occurs when the feet are extended, forward and backward, and the back is dorsoflexed.

Plots in the left quadrant represent gallops having no suspension, and plots in the right quadrant represent gaits having both a gathered and an extended suspension. An extended suspension is a necessary part of leaping, and hence is characteristic of small and medium-sized, agile mammals that leap to clear obstacles or as a part of maneuvering. As noted above, the faster cursors among such animals tend to incorporate the suspensions into a gallop (deer, sheep) whereas the smaller and most agile mammals tend to incorporate the suspension into the bound or half bound (rodents, many mustelids, and felids). The suspension is commonly 50% of the cycle, and may range up to 80% (pronking deer, Patagonian cavy, jumping mouse).

A gathered suspension is rarely so much as 25% of the cycle. It is little more than a provision for delaying the advance of the hind legs sufficiently to distribute support over time, and avoid or reduce the problem of interference between fore and hind feet. The animal is, in fact, minimizing suspensions for the given rate of travel. Gathered gallops reduce effort and are desirable for the larger cursors that run for long distances. Since the body is usually large (horse, rhinoceros, camelids, larger bovids), strides of adequate length can be achieved without longer suspensions. Smaller cursors may conserve energy by using only the gathered suspension when moving at less than top speed (dog, antelope), or if they are not particularly fast at best (primates).

The fastest cursors must use both suspensions in order to reach top speed, particulary if body size is otherwise too small to achieve adequate stride length (hounds, cheetah, pronghorn, antelope, rabbit). (Length of stride increases more than rate of stride as cursors gain speed.)

Many mammals are sufficiently versatile so that, at less than top performance, they can choose among gathered, extended, or both suspensions, or between two of them (bandicoots, some carnivores, some artiodactyls). (Some of these factors in gait selection have been noted by Dagg, *e.g.*, 1973, and Gambaryan, 1974, and by other workers.)

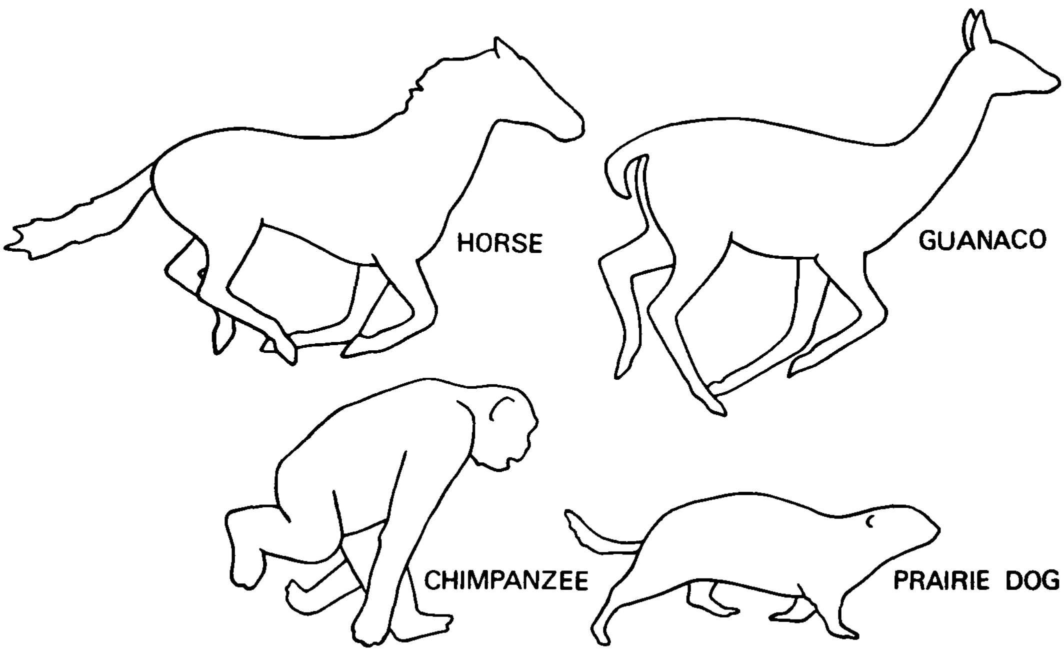

FIG. 10. The transverse gallop in relation to interference.

Transverse gallop: Stability, endurance and interference

If a mammal runs with both pairs of feet having a lead, then the gait is a gallop. If it has the same lead, fore and hind, the gallop is said to be transverse; if it has opposite leads, fore and hind, the gallop is rotary. Why would an animal select the transverse gallop over the rotary gallop?

Stability is a major factor in the selection of this gait. It is seen (Fig. 8) that the transverse gallop is the only gallop used at slow rates of travel (*i.e.*, to the left on the graph) when other sources of stability must compensate for reduced dynamic stability. All but the fast gallops by fleet cursors include one or two phases of support by tripods. These are shown in Figure 9, where spacing of the feet in the line of travel has been taken from films. The triangles of support are larger (and hence more stable) for transverse than for rotary gallops.

Further, at slow and moderate speeds, the bipods that combine support by a fore and a hind foot are more often contralateral (more stable) than ipsilateral (less stable) for the transverse gallop than for the rotary gallop.

The transverse gallop is also relatively favorable for economy of effort. It is, in general, selected by large cursors running long distances over open terrain. Figure 8 shows that this gallop correlates with the gathered suspension, which tends to be relatively short. Transverse gallopers stay close to the ground and move evenly.

Finally, the transverse gallop provides many animals with a way to avoid interference. Thus, in Figure 10, the fast-running horse and guanaco would kick themselves if the positions of one pair of feet, only, were reversed, thus changing the gallop to rotary. (The prairie dog and chimpanzee also use the transverse gallop, although the former avoids interference by having short legs, and the latter can avoid interference only by passing the feet to one side of the hands.)

Rotary gallop: Speed and versatility

Moderate rates of travel are less demanding than slow rates in terms of sta-

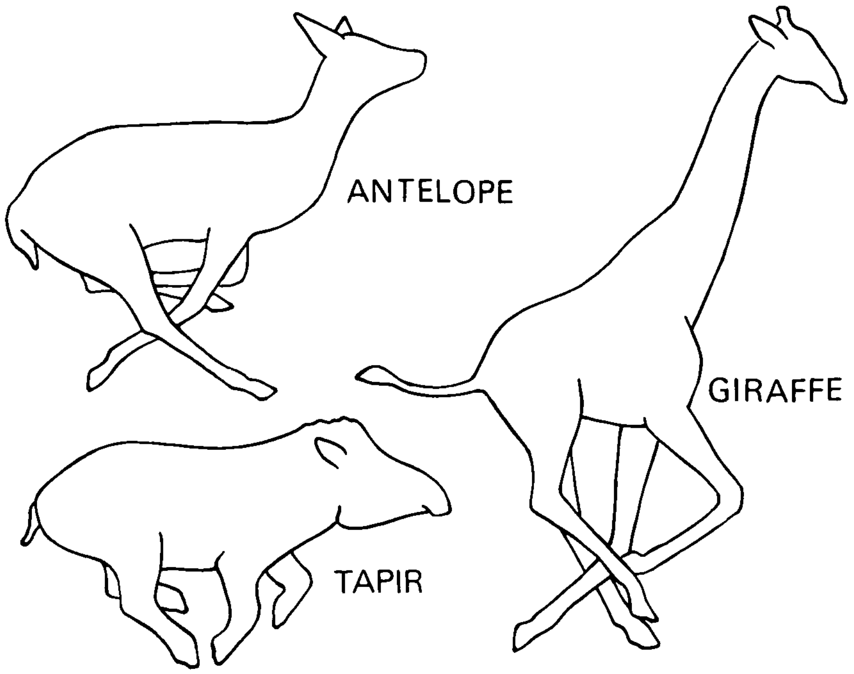

FIG. 11. The rotary gallop in relation to interference.

bility, and less demanding than fast rates in terms of exertion. Accordingly, there is versatility as to suspensions and leads, in gait selection at moderate rates (see overlap at center of graph, Fig. 8).

At maximum and near maximum performance by fleet cursors, the advantages noted for the transverse gallop no longer pertain. There are usually two suspensions, and the total time that the animal is suspended is relatively great. With two suspensions there are no tripods of support, so which type of tripod is the more stable (Fig. 9) is irrelevant. Further, there are no bipods of support that combine a forefoot with a hind foot, so the relative stability of contralateral and ipsilateral bipods is also irrelevant.

Avoidance of interference is, for some cursors, an advantage of the transverse gallop. Several rotary gallopers avoid interference, at least at usual rates of travel, by having short legs (see the tapir, Fig. 11). Most, however, have such long legs (giraffe), or long legs coupled with flexion and extension of the back (antelopes, cheetah) that interference cannot be avoided at either the transverse or rotary gallop unless the hind legs straddle wider than the fore, thus passing around them as they cross (Fig. 11). Another advantage of the transverse gallop is economy of effort. Rotary gallopers, with their longer suspensions, tend to have less endurance, but a little more speed. They are usually sprinters, of medium body size, that must use the double suspension in order to achieve a sufficiently long stride.

Explaining why fast-running rotary gallopers would not benefit from the advantages some other cursors derive from the transverse gallop does not explain their selection of the rotary gallop. After all, a double-suspension gallop is also possible in the transverse sequence. I suspect that preference for the rotary gallop may derive from subtle advantages of timing, balance, and "feel" when running at speed. There is also another probable factor.

Transverse gallopers must lead with the inside legs when turning. The inside lead of the foreleg is probably the more important to balance, yet in changing leads, the feet are usually repositioned during the gathered suspension, so it is the hind feet that first assume the new support pattern. The benefit of the change is, therefore, a little delayed. If there is an extended suspension of sufficient duration (less common for transverse than for rotary gallopers), then the feet can alternatively be repositioned during that suspension. The forefeet are then the first to assume the new support pattern—possibly an advantage in dodging quickly. Since the rotary galloper (only) has a different lead, fore and hind, it may have an advantage in swerving without changing lead at all, although, in fact, most rotary gallopers are agile animals that change leads frequently and smoothly. The transverse gallop is the more stable, and stability and maneuverability tend to have an inverse relationship.

COMMENTS

Despite the comment by Zug (1972), there is some confusion about the relation between my method for the analysis of symmetrical gaits (called the gait-formula method by Zug) and that of some other workers (called walk-pattern method by Zug). I use two percentage figures (the gait formula) to describe symmetrical gaits, and usually plot them graphically. However, *all of the support patterns and their relative durations, can be derived from these figures*. Thus, no parameter is excluded.

The walk-pattern method tabulates various support patterns numerically (*e.g.*, Dagg and de Vos, 1968, Table I). If the tabulation is adequate, then all other support patterns (and the gait formula) can be derived from those listed.

Further, although I usually average the events of several cycles to eliminate the idiosyncracies of individual strides, this is *not* a necessary part of the method, as has been implied.

Accordingly, the two "methods" deal with the same data, are essentially interchangeable, and certainly not in conflict or competition. I merely find that, having the overlays of Figures 1*B*, 2, 5, and 8 in mind, the graphical plotting of gait formulas enables me to interpret them at a glance, which I cannot do from a table of numbers.

Noting my emphasis on the frequent variation of successive strides, and on the locomotor versatility of many vertebrates, various neurophysiologists have asked what use gait analysis can be to them. If gaits are so inexact, how can their description be valuable?

When a cold turtle walks on uneven ground, the marked variation from stride to stride may well result from noise in the system. It can do no better for want of fine tuning of its sensory-neuromuscular system. However, when a cheetah chases a blackbuck at 100 km/hr over low vegetation and scattered small rocks, instantly matching every swerve of the prey, the marked variation from stride to stride is evidence of fine tuning almost beyond belief. Such tuning can hardly be studied using experimental cats on treadmills, so gait analysis may well have limited application to neurophysiology today. Ultimately, however, gait analysis must be included if we are to learn the neuromuscular secrets of the master cursors.

REFERENCES

Dagg, A. I. 1973. Gaits of mammals. Mammal Rev. 3:135–154.

Dagg, A. I. and A. de Vos. 1968. The walking gaits of some species of Pecora. J. Zool. (London). 155:103–110.

Gambaryan, P. P. 1974. *How mammals run: Anatomical adaptations.* John Wiley & Sons, New York. (Originally published in Russian, 1972.)

Grey, J. 1944. Studies in the mechanics of the tetrapod skeleton. J. Exp. Biol. 20:88–116.

Hildebrand, M. 1966. Analysis of the symmetrical gaits of tetrapods. Folia Biotheoretica 6:9–22.

Hildebrand, M. 1976. Analysis of tetrapod gaits: General considerations and symmetrical gaits. *In* R. M. Herman, S. Grillner, P. S. G. Stein, and D. G. Stuart (eds.), *Neural control of locomotion*, pp. 203–236. Plenum Press, New York.

Hildebrand, M. 1977. Analysis of asymmetrical gaits. J. Mammal. 58:131–156.

Zug, G. R. 1972. A critique of the walk pattern analysis of symmetrical quadrupedal gaits. Anim. Behav. 20:436–438.