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ANALYSIS OF ASYMMETRICAL GAITS

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ABSTRACT.—Asymmetrical gaits (that is, gallops and bounds) have the footfalls of a pair of feet unevenly spaced in time. Such gaits were studied from slow motion film for 79 genera. All information about the timing of events at the ground can be expressed by five variables. Foot contact intervals range from 16 to 70 percent of the cycle. Fore and hind contacts are nearly equal for most ungulates and carnivores; fore contacts are the shorter for most rodents and rabbits. Fore contacts are proportionately shorter at higher speeds. The size of the fore lead is less than the hind for some apes; fore and hind leads are about equal for many carnivores and ungulates; fore leads are the longer for most mammals—particularly for smaller, more agile genera when moving fast. Actions of the forefeet as a pair are related to those of the hind feet by "midtime lag." When this variable is plotted against the percentage duration of ground contact by one or both hind feet, a basic gait graph is derived on which are distinguished gaits with no suspensions, with a gathered suspension, an extended suspension, and both suspensions. The distribution of plots on the graph also correlates roughly with body size, maneuverability, and lead sequence (that is, transverse, rotary, half bound, or bound). A terminology of asymmetrical gaits is presented. The distribution on the graph of 104 identified footfall formulas is shown, and formulas characteristic of 55 genera are depicted. Asymmetrical gaits probably evolved, in amphibians and several times in reptiles, to benefit escape. Gaits with short leads or none, and an extended suspension are considered primitive. All lead sequences evolved early.

A gait is an accustomed, cyclic manner of moving in terrestrial locomotion. Although actions of the head, spine, and tail may be gait characteristics, this study is limited to the timing of the footfalls, the durations of the contacts that the feet make with the ground, and the sequences of the different patterns of support made by the feet in combination. There are two principal classes of gaits, symmetrical and asymmetrical. The former has the footfalls of a pair of feet evenly spaced in time. Symmetrical gaits include the pace, various walks and running walks, and the trot. This class of gaits has been described and analysed by me (for example, 1965, 1966, 1967, 1968, and, particularly, 1976) and by other authors (for example, Dagg and De Vos, 1968*a*; Howell, 1944; Sukhanov, 1974; Zug, 1972).

Asymmetrical gaits have the footfalls of a pair of feet unevenly spaced in time. They include the gallops and bounds. Numerous authors have described certain asymmetrical gaits (for example, Dagg and De Vos, 1968*b*; Gambaryan, 1974; Hildebrand, 1959, 1961; Howell, 1944; Magna de la Croix, 1929; Muybridge, 1899), but this paper is the first general analysis of its kind of this class of gaits.

This is a companion article to Hildebrand, 1976, which presented general considerations of tetrapod gait analysis and described and interpreted symmetrical gaits of 156 genera. The objectives of this article are as follows: (1) to present a comprehensive and integrative system of analysis for asymmetrical gaits that can facilitate the storage and recovery of data and provide a conceptual basis for the study of this kind of locomotion; (2) to present a terminology for asymmetrical gaits; (3) to describe certain asymmetrical

TABLE 1.—*Orders and genera studied, number of smoothed records, or plots, per genus, approximate body weights, and observed lead sequences. Weight group 1 = up to 4 kg., group 2 = 4.1 to 16 kg., group 3 = 17 to 65 kg., group 4 = 66 to 260 kg., group 5 = 265 kg. and over. T = transverse sequence, R = rotary sequence, B = bound, ½B = half bound, P = pronk, C = crutch walk.*

Order and genus	No. of plots	Weight class	Lead sequence
Marsupialia			
Sarcophilus	2	2	T
Isoodon	9	1	½B
Perameles	6	1	½B
Dendrolagus	1	3	B
Macropus	3	3	B
Chiroptera			
Nyctalus	–	1	B
Insectivora			
Tupaia	2	1	T, ½B
Urogale	8	1	½B, B
Primates			
Lemur	2	2	T
Galago	1	1	?
Ateles	3	2	T
Cercocebus	1	2	T
Cercopithecus	6	2	T, R
Macaca	1	2	T
Papio	3	3	T, ½B
Presbytis	1	2	T
Hylobates	4	2	T, C
Pan	3	3	T
Gorilla (juvenile)	3	3	T
Pongo (juvenile)	3	3	T, C
Homo (juvenile)	1	3	T
Lagomorpha			
Lepus	7	1	T, R, ½B
Rodentia			
Cynomys	4	1	T
Eutamias	3	1	½B, B
Sciurus	4	1	T, ½B, B
Spermophilus	3	1	½B, B
Dipodomys	2	1	B
Pedetes	1	1	B
Hypogeomys	2	1	B
Microtus	1	1	T
Mus	2	1	½B, B
Zapus	4	1	B, P
Dolichotis	6	2	T, R, ½B, B, P
Carnivora			
Canis	22	3	T, R
Ursus	1	4	T, ½B
Bassaricyon	1	1	T
Carnivora cont.			
Nasua	2	2	T, R
Gulo	3	2	T
Mustela	6	1	T, ½B, B
Mephitis	5	2	T
Spilogale	4	1	½B, B
Lutra	8	2	T, ½B
Arctogalidia	5	1	T, ½B, B
Herpestes	2	1	T, ½B
Mungos	1	1	½B
Hyaena	1	3	T
Acinonyx	7	3	R
Felis	3	1	T, R, ½B
Pinnipedia			
Zalophus	2	4	½B, B
Callorhinus	4	2	T, ½B
Hyracoidea			
Heterohyrax	4	1	½B
Perissodactyla			
Equus	46	5	T, (R)
Tapirus	3	5	R
Rhinoceros	6	5	T
Artiodactyla			
Tayassu	1	3	?
Camelus	1	5	T
Lama	15	3,4	T
Muntiacus	10	2	T, R, ½B
Hydropotes	1	2	R
Odocoileus	11	4	R, P
Giraffa	8	5	R
Okapia	1	4	R
Antilocapra	7	3	(T), R, (P)
Bison	1	5	T
Bos	1	5	R
Boselaphus	2	4	T, R, (P)
Synceros	3	5	R
Tragelaphus	1	4	R
Cephalophus	1	3	T
Alcelaphus	1	4	T, P
Connochaetes	9	4	T, R, P
Hippotragus	6	4	T, R
Kobus	3	4	R, P
Aepyceros	2	4	T, R, ½B, P
Antilope	3	3	R, ½B, B, P
Gazella	2	3	R, P
Capra	1	4	?
Hemitragus	3	4	T, R, ½B
Ovis	2	4	T, ½B, B, P

gaits of many genera of mammals; (4) to contribute to the interpretation of gait selection in relation to systematics, body size, speed, habit, and habitat.

MATERIALS

The raw material for the study is slow motion film. Most of the film was exposed at 64 frames per second (sec), and some at 18, 72, 100, or 200 frames per sec. Most is original, but use was made of certain film resources of the Institute Für den Wissenschaftlichen Film in Göttingen, the Grenada TV Network in London, Walt Disney Productions, several university film libraries, and about 20 other public and private film sources.

This paper reports on 331 passes in front of the camera by animals in 79 genera. Eleven orders of mammals are represented, though five of these by only one or two genera. With the exception of *Heterohyrax*, which was photographed in an exercise wheel, all animals were in the open or in adequate enclosures; none was on a treadmill (where gaits may be altered).

The orders and genera studied are listed in Table 1. Species names are omitted because available data do not justify that level of distinction. It is not implied that all species of a genus have identical gaits, though in fact they usually do move in very similar ways. To avoid constant qualification, reference is frequently made to gaits of a genus, family, or order. It is important that it be understood that such references are only to the available data (often sketchy) for one or more species of the genera listed. It would be premature to describe *the* gaits of any tetrapod.

Except as qualified, the analysis is based on smoothed data; that is, corresponding events of three or more successive strides are averaged to mask the idiosyncrasies of individual cycles. Each smoothed record is called a "plot" in Table 1.

All film analysis is original except for all or most of the data on *Dendrolagus* (Windsor and Dagg, 1971), *Mungos* (Taylor, 1970), *Felis* (Stuart *et al.*, 1973), *Nyctalus* (Lawrence, 1969), and *Connochaetes* (Dagg, 1969).

The basic steps in gait analysis (that is, the preparation of gait formulas, footfall formulas, gait diagrams, and gait graphs) are described and illustrated in various of the papers cited above (see particularly, Hildebrand, 1966, 1976). Examples of the important gait diagram are shown in Fig. 1.

VARIABLES

A first step toward analysis is the identification of variables. Because each foot is on the ground once and off the ground once in each cycle, gaits can have a maximum of nine distinct variables. These could conveniently be expressed as the times that the feet strike the ground (the four footfalls), the durations of the contacts that the feet make with the ground (the four contact intervals), and the time interval between successive corresponding events (the duration of the cycle). (Liftoffs could substitute for footfalls, and intervals between contacts could substitute for contact intervals.)

The number of variables can be reduced by expressing them in relation to one another. Thus, if each contact interval is described as a percentage of the full cycle, one variable is eliminated. Similarly, if three of the footfalls are identified as following the fourth, or reference foot, by stated percentages of the full cycle, another variable is lost, leaving seven.

Because asymmetrical gaits have the footfalls of a pair of feet (fore or hind) unevenly spaced in time, the footfalls of a pair form couplets separated by pauses (unless they occur simultaneously). The first foot to strike in a couplet is termed the trailing foot; the second is the leading foot. It is probable that, for certain mammals, the duration of the contacts made by leading and trailing feet tend to differ–particularly when the animals are turning. This question should be studied. However, because any tendency for the contacts of leading and trailing feet of a pair to differ is usually so slight that it is masked by the idiosyncrasies of successive strides, it is as yet not sufficiently well documented to include in a general survey. By disregarding differences of this kind, the number of gait variables is further reduced to five. That is to say, five variables are both necessary and sufficient to describe all asymmetrical gaits in terms of the timing and durations of events at the ground. (Symmetrical gaits have only two or three variables.)

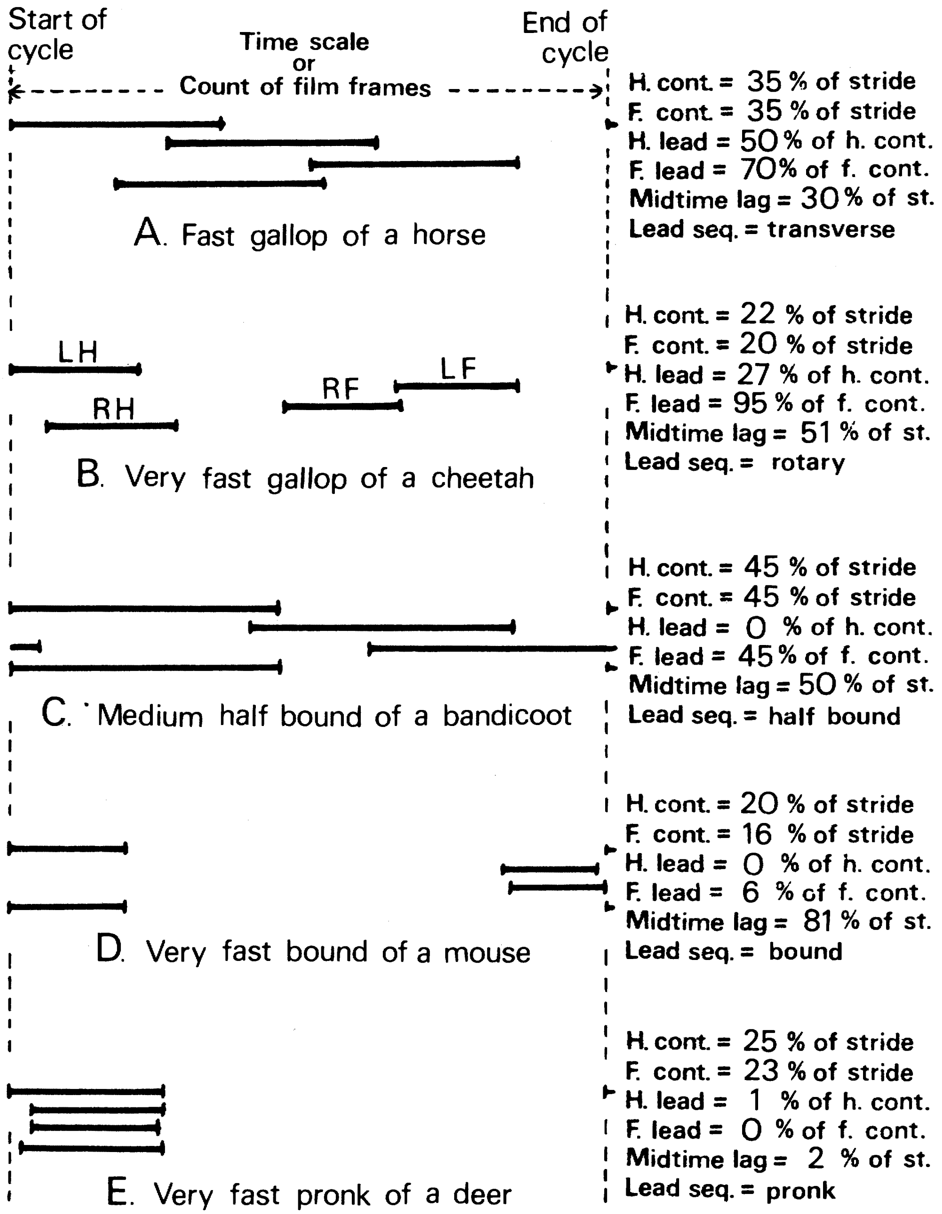


FIG. 1.—Gait diagrams of representative asymmetrical gaits. The initials, L, R, F, and H stand for left, right, fore, and hind feet; "cont." means contact interval. Horizontal lines show proportionate durations of the contacts the respective feet make with the ground.

Although all the various time factors of a stride can be derived from the variables stated (four footfalls, four contact intervals, and duration of cycle), it might be preferable, according to one's purpose, to directly combine and express the factors in other ways. Thus, one might record the duration of support by hind feet only, or by one or more feet in any combination. The investigator must choose, therefore, which, and how many variables to use. What factors, and what combinations of factors best serve the objectives of the analysis?

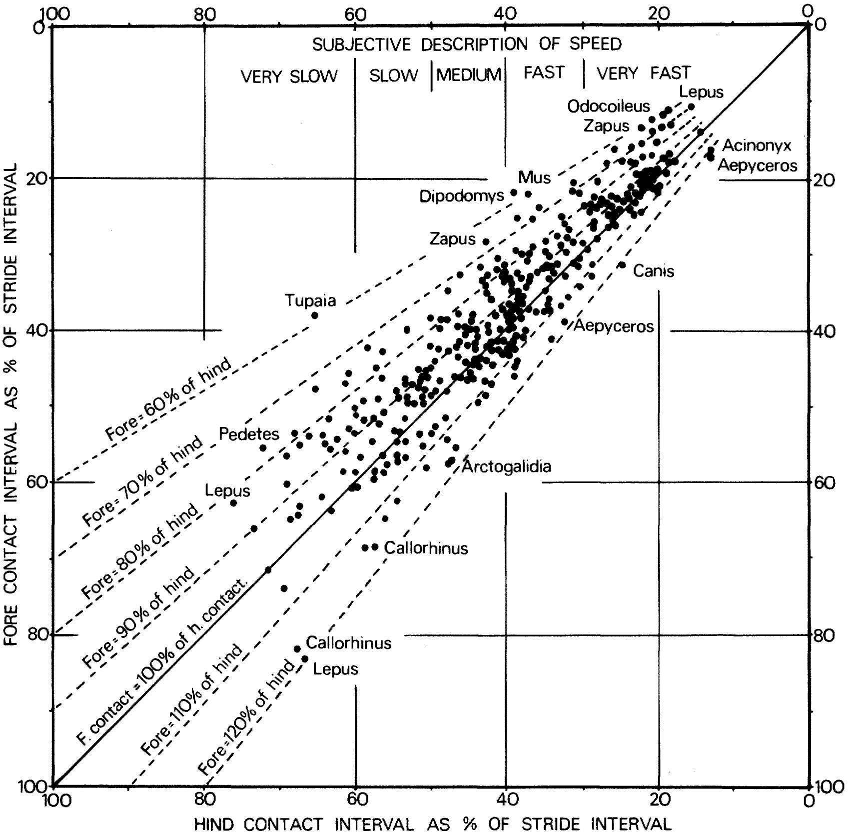


FIG. 2.—Durations of fore and hind contact intervals as percent of the stride interval, and duration of the fore contact interval as percent of the hind contact interval.

As a preliminary and exploratory step, five pairs of variables were identified that were thought to be likely to have positive correlations. For each pair, data from the 331 available filmed performances were plotted separately (by computer) by nine of the orders represented, by weight (in five increments having a logarithmic relation to one another), and by body proportions (in six categories according to relative length of legs to body, and of fore to hind legs). This procedure produced 100 bivariant graphs. Certain combinations of three or more variables were also tested. Study of the results, and intuitive judgement based on long examination of hundreds of gait diagrams, are the basis for the procedures adopted.

CONTACT INTERVALS

The durations of fore and hind contact intervals, expressed as percentages of the stride interval (or full cycle), and the duration of the fore contact interval as a percentage of the hind contact interval are shown by Fig. 2. The wide variation from cycle to cycle, and from individual to individual that characterizes asymmetrical gaits is in evidence; nevertheless, conclusions can be drawn.

The hind contact interval approaches 20 percent of the cycle for various fast runners ranging from the horse, dog, and cheetah to the jumping mouse and rabbit. It is less than 18 percent only for individual strides of exceptional cursors. Likewise, the fore contact interval approaches 16 percent of the cycle in various fast-moving mammals, but is

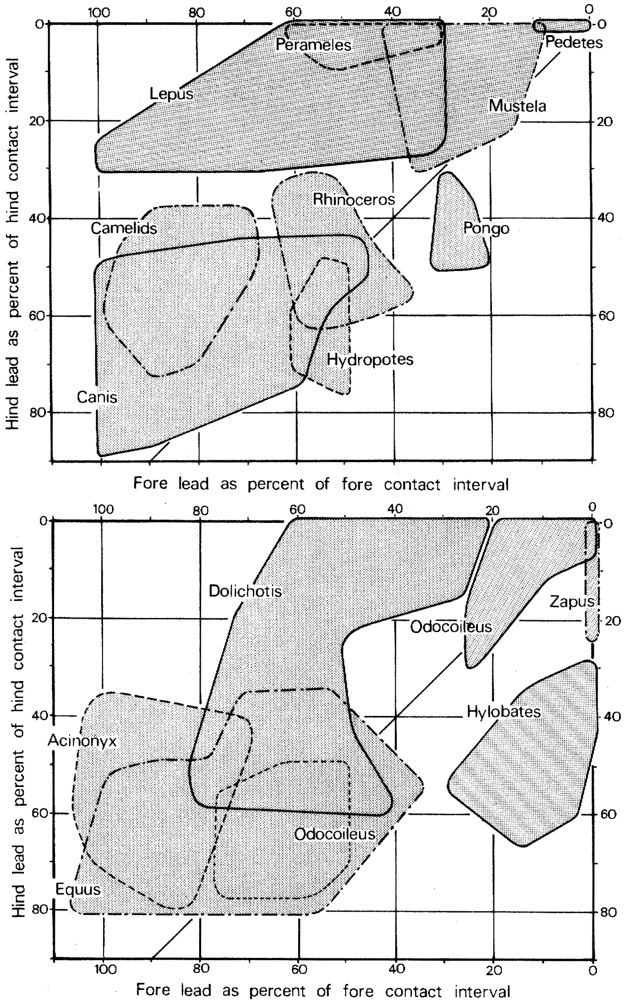


FIG. 3.—Fore and hind leads of representative genera as percentages of the respective contact intervals. Shaded areas show range of variation. The number of records per genus ranges from 5 to 84.

rarely less than 13 percent for consecutive strides. In steady progression, neither the fore nor the hind contact interval is likely to be greater than 70 percent of the stride interval.

The duration of the contact intervals (particularly of hind contacts) varies inversely with rate of travel. Actual speed cannot be derived from contact intervals, but the subjective terms shown at the top of Fig. 2 would be considered appropriate by most observers.

The duration of fore contacts is about the same as that of hind contacts for perissodactyls (except show horses), most artiodactyls (but not some of the smaller or faster ones), most carnivores (but with more scatter around the norm than for ungulates), and for nearly half of the primates studied. For most of the other primates, fore contacts are about 90 percent of hind contacts, but other values are also observed.

Fore contacts scatter near 80 percent of hind contacts for most rodents, several carnivores (including *Acinonyx* when moving fast), many show horses, and some artiodactyls (*Antilocapra, Antilope, Hemitragus, Odocoileus,* and *Ovis dalli*). Fore contacts drop to 70 percent or less of hind contacts for *Lepus* at speed, *Zapus*, *Dipodomys*, and *Pedetes*.

Fore contacts are 110 percent or more of hind contacts in some available records for two pinnipeds (*Callorhinus* and *Zalophus*), and for *Bos gaurus* and *Aepyceros*. This was expected for *Bos*, because fore contacts tend to be the longer in symmetrical gaits of some heavy-shouldered artiodactyls; it is less clear why the relationship holds for the impala.

The ratios of fore to hind contact intervals that characterize available records for various specific genera are shown in Figs. 10 through 17. In general, fore contacts tend to be a lesser percentage of hind contacts for smaller, lighter animals than for their counterparts, particularly at higher speeds. The scatter of individual plots around the norm for a genus also tends to be greater for the smaller animals, reaching extremes in *Lepus* and *Dolichotis*. Variability in this regard seems to correlate with agility, maneuverability, and rough terrain (relative to body size). The ratio of fore to hind contact intervals tends to incraase during deceleration and to decrease during acceleration.

LEADS

The trailing foot is the first of a pair to strike the ground in each couplet of footfalls; the second to strike is the leading foot. The magnitude of the lead (for each pair) is best expressed as the time interval between the two footfalls as a percentage of the contact interval for that pair (which is here assumed to be the same for trailing and leading feet). Thus, the resulting percentage lead is 0 if the two feet strike the ground simultaneously, and 50 if the leading foot strikes half way through the contact interval of the trailing foot.

In Fig. 3, the fore and hind percentage leads, and the relation between them, are shown for 16 representative genera. In preparing the figure, separate plots were made for individual strides, that is, successive cycles were not averaged as for most records in this paper. Consequently, the number of plots per genus is about three times the number of plots listed in Table 1. In every instance, the shaded areas representing the scatter of the plots by genus would be increased, and their borders made more regular, by additional data.

Fore percentage leads are again plotted against hind percentage leads in Fig, 4. Solid lines encompass the maximum range of all typical plots. Sixteen genera are identified for which plots include marginal records. Black spots show not individual plots, but the visual centers of weight of all of the plots of each genus–a way of representing approximate averages.

Dotted lines on Fig. 4 show percentage leads for one conspicuously atypical canter of a show horse (higher on the graph), for the slightly asymmetrical walk of a monkey (to the right), and for the asymmetrical trots of several ungulates.

A terminology for length of lead is shown along the two axes of Fig. 4. The percentage leads represent proportionate time intervals, not distances: nevertheless, the values correlate with the length of the step taken by the leading foot in relation to length of leg. The terms describe the subjective impression of the observer. (When small cursors, such as cats and rabbits, cover much distance per cycle, then even though a lead may be an appreciable percentage of the respective contact interval, it may be a small percentage of the full cycle. The unskilled observer may then judge the lead to be less than it is.)

As Fig. 3 makes clear, there is wide variation in lead within a genus. Nevertheless, some generalizations can be made about the available data. The fore lead tends to be less than the hind lead only for most apes (notably for *Hylobates*), several artiodactyls, several jumping rodents, and some show horses. The fore lead tends to center between equality with the hind lead and about 1¼ times the hind lead for most carnivores, most artiodactyls, and most horses. The fore lead centers between 1¼ and 1½ times the hind lead for some agile artiodactyls (*Antilocapra*, *Aepyceros*, and *Gazella*), the cheetah at

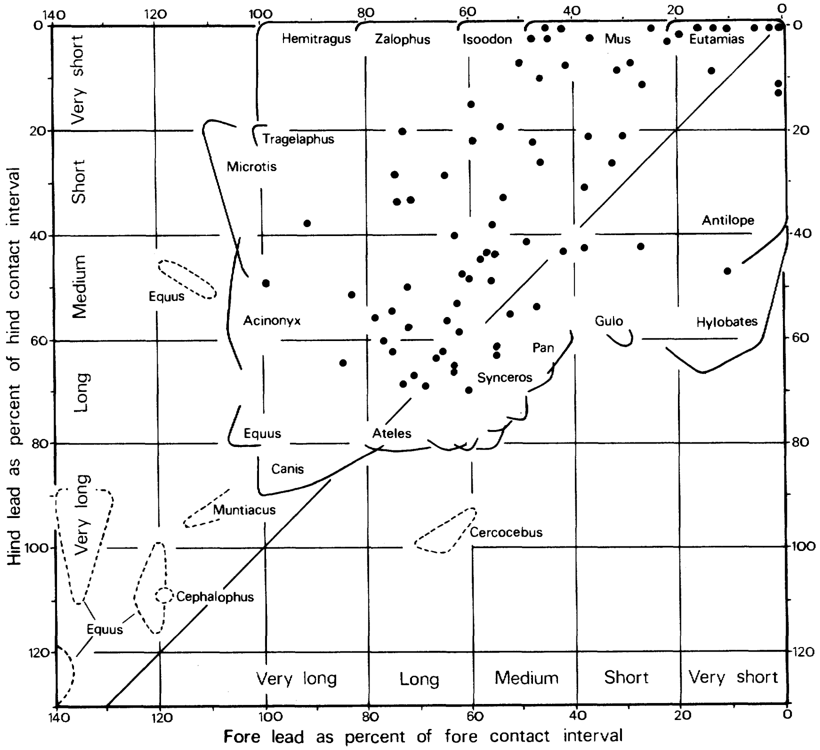


FIG. 4.—Summary of fore and hind leads. Solid lines encompass the range of all typical plots; many genera are identified for which plots include marginal records. Black spots show visual centers of weight of all plots of each genus. Dotted lines show atypical records and performances transitional with symmetrical gaits.

moderate speed, the horse at high speed, the rhinoceros, and some sciurids. The fore lead tends to center between 1½ and 2 times the hind for the cheetah at high speed, camelids, and tapir. It centers between 2 and 3 times the hind lead for a miscellany of mammals including *Lepus* (in part), *Giraffa*, *Muntiacus*, and *Hemitragus*. Finally, it is more than 3 times the hind lead for various marsupials, carnivores, rabbits, rodents, and the hyrax which perform the bound or halfbound (defined below). Characteristic values for fore and hind leads of various genera are shown in Figs. 10 through 17.

With various exceptions, the fore lead tends to increase in relation to the hind lead as body size decreases (the giraffe and camelids notwithstanding), as agility and maneuverability increase, as speed increases for a given genus (examples: *Acinonyx*, *Dolichotis*, and *Equus*), as the respective contact intervals decrease, and as the fore contacts become a lesser percentage of hind contacts. The variation in lead from cycle to cycle is greatest for medium-sized mammals capable of high speed or great agility (*Papio*, *Canis*, *Dolichotis*, *Antilocapra*, *Muntiacus*, *Antilope*, *Hemitragus*, and *Ovis*).

MIDTIME LAG AND SUSPENSIONS

Thus far, the analysis has presented four variables–hind contact interval and hind lead, and fore contact interval and fore lead. This provides all needed information about the actions of the hind feet as an isolated pair and the forefeet as an isolated pair. It remains to relate the actions of the two pairs. This will be done by adding two more variables, one in this section and one in the next.

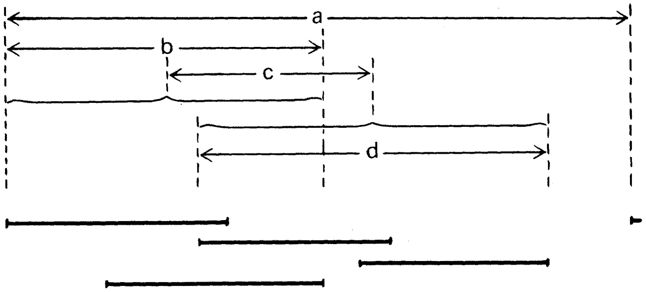


FIG. 5.—Gait diagram showing some measurements used in analysis. Representation as in Fig. 1.

In symmetrical gaits, the two feet of a pair function independently; the contact interval of either taken alone is a satisfactory reference. In asymmetrical gaits, by contrast, the two feet of a pair function more or less as a unit. Consequently, in the next step of the analysis it is desirable, from a functional viewpoint, to use the time interval that one or both feet of a pair are on the ground. This is expressed as a percentage of the stride interval, or in Fig. 5, 100 b/a for the hind feet and 100 d/a for the forefeet. (These intervals are the sums of contact intervals and leads; they merely combine variables already introduced.) Now, in relating the contacts of one or both forefeet to those of one or both hind feet, what datum best serves as referent?

Because the contact interval of hind and forefeet commonly differs, and because the length of the step, or lead taken by hind and forefeet commonly differs, the time intervals between footfalls of hind and forefeet are usually not the same on the right as on the left. Also, the intervals between footfalls usually differ from the intervals between the respective lift offs. A referent that is practical, and has the desired functional value, is to identify the instant in time that is half way through the duration of contact by one or both hind feet (the hind midtime), and the same for the forefeet (the fore midtime), and then to record the percentage of the stride interval that the fore midtime follows the hind midtime, or 100 c/a in Fig. 5. (Actions of the forefeet are related to those of the hind, rather than the reverse, because the hind feet play the greater role in propulsion and commonly have longer contact intervals.)

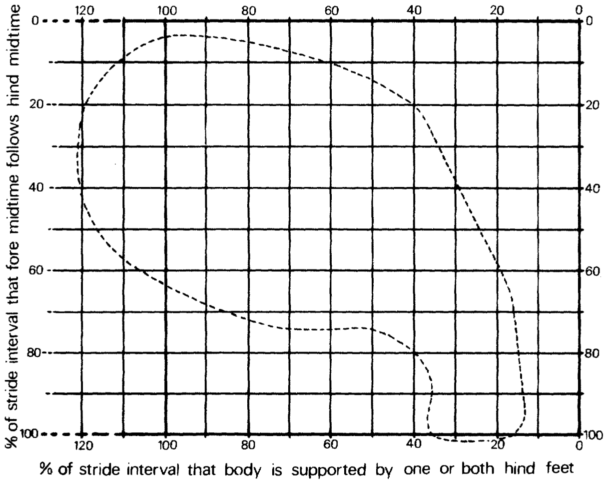


FIG. 6.—Basic gait graph relating hind support to midtime lag. The smoothed range of 331 plots is shown. Figs. 8 through 18 are overlays to this graph.

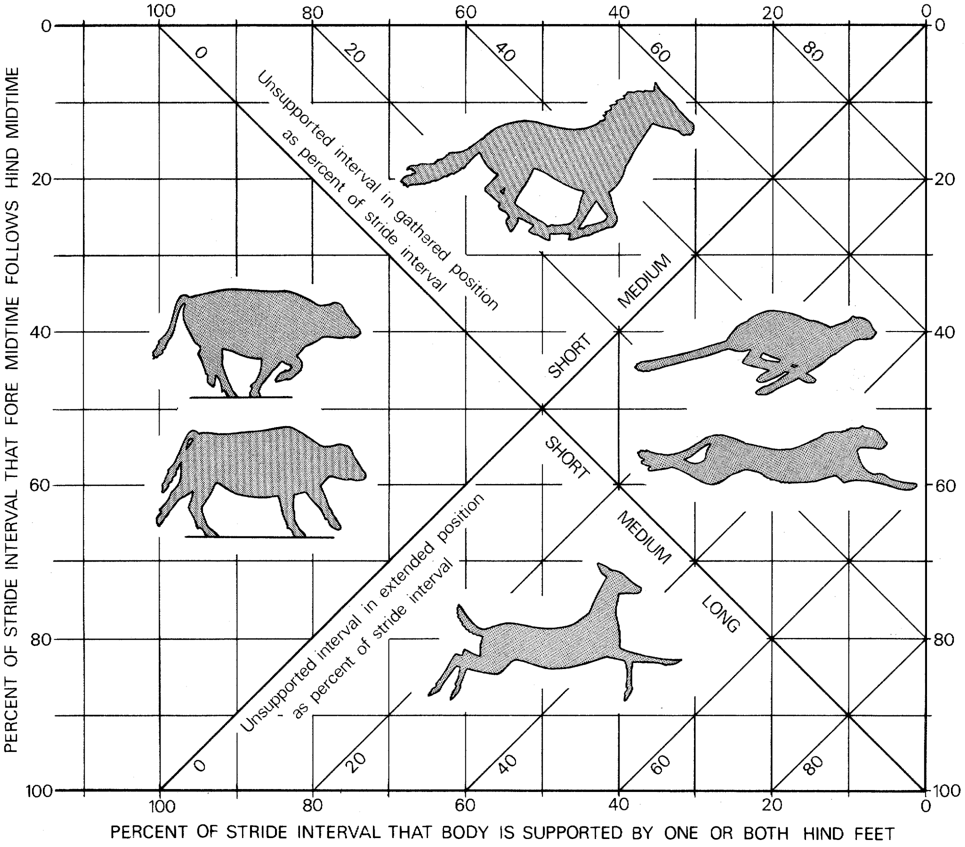


FIG. 7.—Gait graph relating hind support to midtime lag, and showing distribution and relative durations of gathered and extended suspensions when fore contact and lead equal hind contact and lead.

A very useful gait graph is made by a grid having hind support (contact by one or both hind feet) on the abscissa and midtime lag (interval between hind midtime and fore midtime) on the ordinate, both expressed as percentages of the stride interval (Fig. 6).

The right border of the graph is an absolute limit; there, the hind feet cease to touch the ground. The left border is also absolute because there each hind foot is always on the ground and locomotion ceases. If the hind contact interval and hind lead were both very long, the left border might, in theory, extend to nearly 200 percentage points on the abscissa. Actual values range only to about 125 percentage points. The top and bottom borders of the graph are identical; it is the same for the fore midtime to follow the hind midtime by 0 or 100 percent of the stride interval. It is as though the graph were rolled into a cylinder such that top and bottom borders coincide. The range of observed plots, somewhat smoothed, is shown by the dotted line in Fig. 6.

If fore contacts and leads equal hind contacts and leads (conditions often approximated), then, as shown in Fig. 7, diagonal lines divide the graph into four triangular sections which represent gaits that are visually quite distinct. On the left are gaits having no periods of suspension; the body is always supported by at least one foot, as is common for the slower gallops of many mammals and usual for faster efforts of some (for example, giraffe).

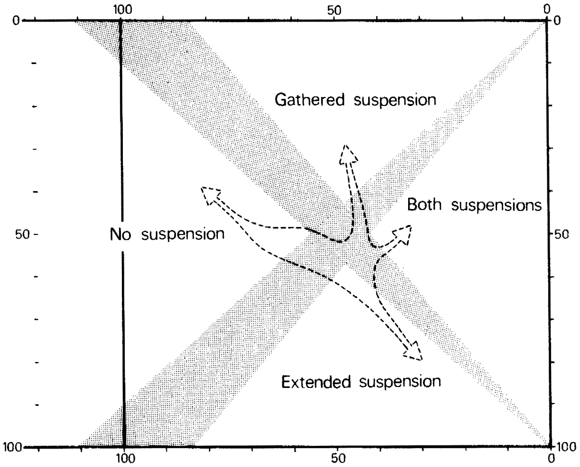


FIG. 8.—Overlay to the gait graph of Fig. 6 showing distribution of periods of suspension. Plots falling in the shaded areas represent gaits that may have the suspension of either adjacent area depending on relative contact intervals and leads of fore and hind feet. Dotted lines show possible evolutionary relationship of the gaits.

In the upper section are found plots for gaits having one interval of suspension in each cycle that comes when the legs are gathered under the body, as is typical of the faster gallops of perissodactyls and camelids. This kind of unsupported interval is termed flexed suspension by Dagg and De Vos (1968*b*) and crossed flight by Gambaryan (1974). Because the feet cross little or not at all for some such animals (for example, many horses), and the legs do not flex notably for some (for example, giraffe), I prefer the term *gathered suspension*; the legs are always relatively collected under the body. The duration of the suspension, as percent of stride interval, can be read on the graph for a given plot using the scale of diagonal lines. The subjective impression of the length of this suspension (in time or distance) is as shown by the terms on the graph.

In the lower section of the graph are found plots for gaits having one interval of suspension in each cycle that comes when the spine is dorsoflexed and the legs extended forward and backward, as for deer and some rodents. All authors call this the *extended suspension*. Again, Fig. 7 shows its magnitude, both as percentage of the stride interval and as the observer's impression, for the stated conditions.

Finally, plots falling in the right section of the graph represent gaits having two suspensions in each cycle, one gathered and one extended. Fast gallops of the rabbit, and of various carnivores and artiodactyls are representative.

Fig. 7 pertains only when fore contacts and leads equal hind contacts and leads. When fore contacts are the shorter, the intersect of the diagonal lines shifts left, and the right triangular section enlarges at the expense of the others. When fore lead is the shorter, the intersect shifts right, and the right section is reduced. Because the fore contacts tend to be relatively short when the fore lead is relatively long, the factors tend to compensate. Within the combinations of relative contacts and leads represented by Figs. 9 to 17, section boundaries shift over the shaded areas on Fig. 8.

(As seen by Fig. 4, the fore lead exceeds the fore contact for some strides of some fast-running carnivores and ungulates. This introduces another period of suspension between the fore contact intervals, but it is exceedingly short.)

A final variable must be introduced before we return to the basic gait graph.

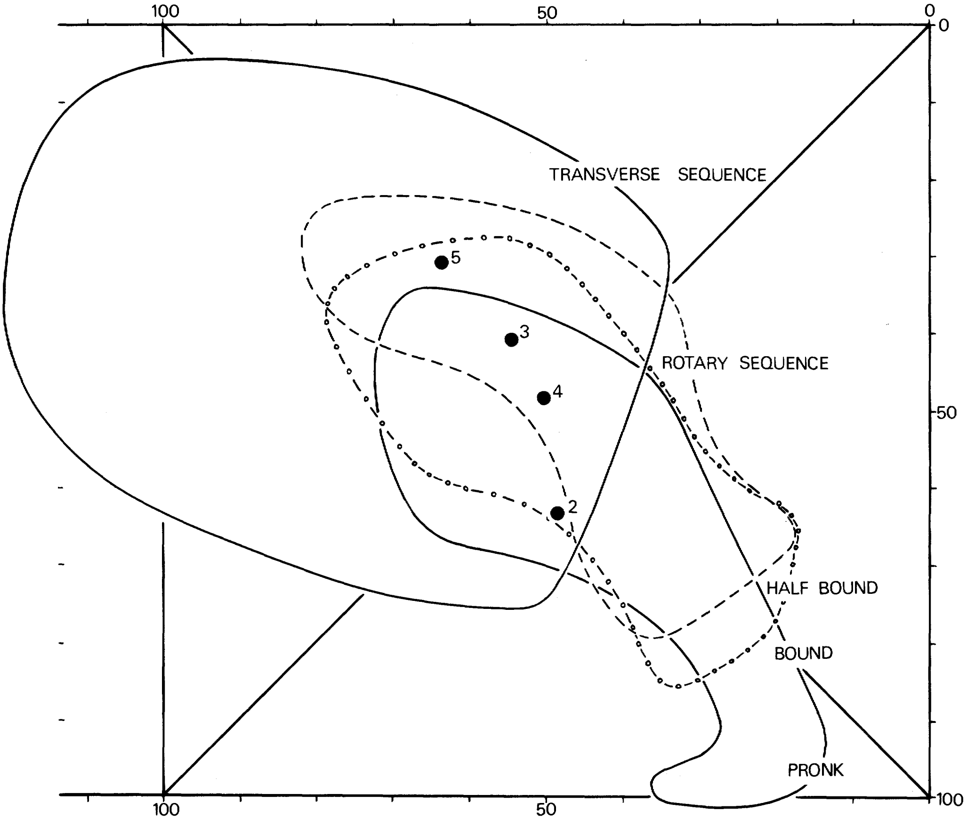


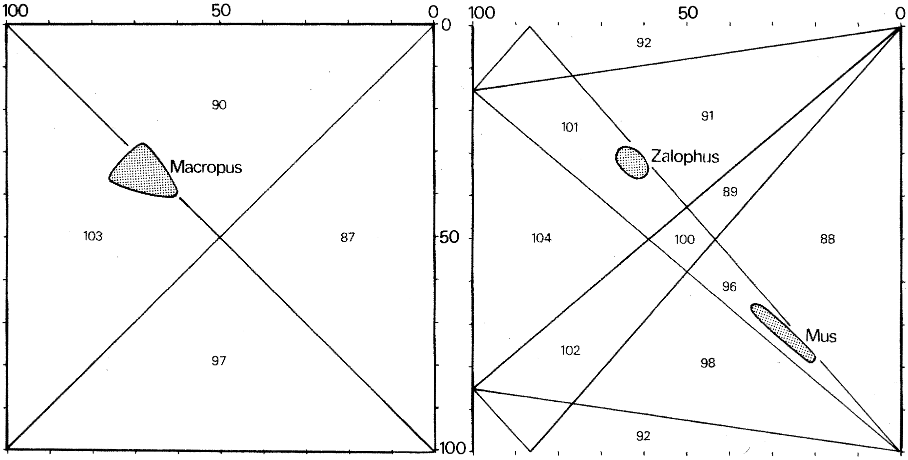
FIG. 9.—Overlay of the gait graph of Fig. 6 showing distribution of lead sequences and, for ungulates, mean values for the weight classes of Table 1.

LEAD SEQUENCE

All mammals that gallop use both right and left leads (though some individuals do show a preference). When turning, the inside forefoot leads. When describing a given gait, therefore, it is immaterial which lead is adopted for the reference pair of feet. To standardize my gait diagrams (Figs. 1 and 5) and footfall formulas (Figs. 19–21) I always depict a right hind lead. For the opposite lead, the diagram or formula is simply reversed. However, the forefeet can either have the same lead as the hind, making the sequence of footfalls *transverse* (diagonal of Gambaryan, 1974) as in Fig. 1A, or the opposite lead, making the sequence *rotary* (lateral of Gambaryan 1974) as in Fig. 1B.

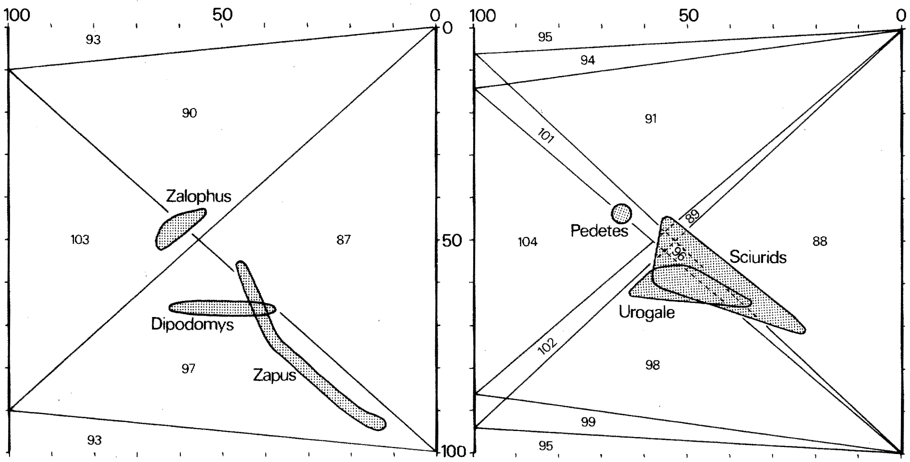
If the two hind footfalls are simultaneous, (or the hind lead is not more than about 10% of the hind contact) and the equivalent is true of the fore footfalls, then the gait is termed a *bound*. Bounds cluster at the upper right corner in Figs. 3 and 4. If the hind footfalls are simultaneous, or nearly so, but there is an evident fore lead, then the gait is a *half bound*. Such gaits fall along the upper margin in Figs. 3 and 4. If the fore footfalls only are simultaneous, the gait is a *crutch walk*. If all footfalls occur at about the same instant, the gait is a bound of the kind termed the *pronk* (or stott). The pronk has one long suspension that is transitional between gathered and extended.

The observed lead sequences of the various genera are shown in Table 1. Many mammals use more than one sequence, and additional data would surely prove some animals to be more versatile than these records indicate. The transverse sequence is



F. contact = 100% of h. contact.
H. lead = 0 % of h. contact. F. lead = 0 % of f. contact.

F. contact = 100 % of h. contact.
H. lead = 0 % of h. contact. F. lead = 30 % of f. contact.



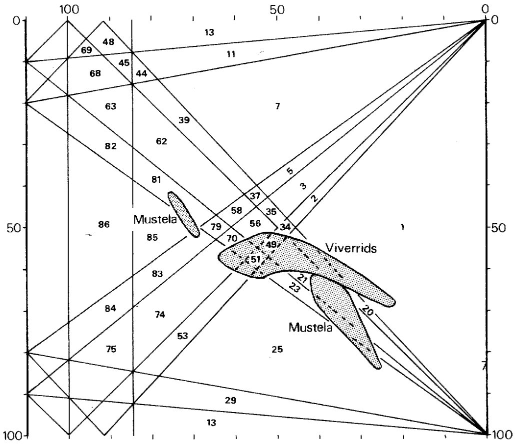
F. contact = 80 % of h. contact.
H. lead = 0 % of h. contact. F. lead = 0 % of f. contact.

F. contact = 80 % of h. contact.
H. lead = 0 % of h. contact. F. lead = 10 % of f. contact.

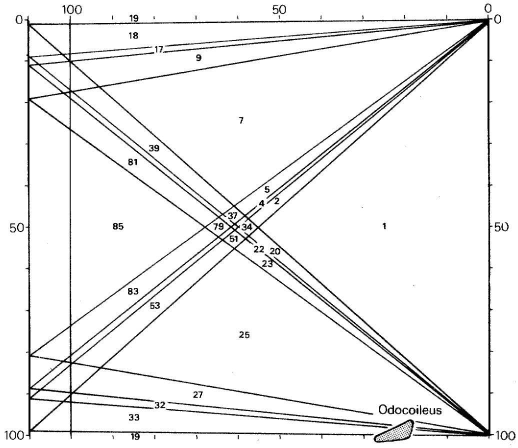
FIG. 10.—Overlay to Fig. 6 showing the ranges of available plots for the genera indicated, and the distribution of footfall formulas under the stated conditions. The numbers are keyed to the respective formulas in Figs. 20 and 21 (and to the equivalent rotary gallops.)

characteristic of primates, most carnivores, perissodactyls except the tapir, and camelids. The rotary sequence is preferred by the tapir and giraffids. The half bound and bound are typical of most of the marsupials studied, tupaiids, a bat, rodents, small carnivores, pinnipeds, and hyrax. The pronk is not the usual gait of any mammal, but is used by *Zapus*, *Dolichotis*, and at least 15 genera of artiodactyls (Dagg, 1973). The crutch walk may be used by *Pongo* (Tuttle, 1967) and *Hylobates*, and probably by other apes.

Fig. 9 shows that lead sequence relates to the distribution of suspensions on the gait graph. No correlation was found between lead sequence and either absolute or relative magnitude of the leads of fore or hind pairs of feet; that is, sequence of lead between pairs seems independent of size of lead within pairs. The bound and half bound tend to correlate with short fore contact interval in relation to hind contact interval.



F. contact = 100% of h. contact. H. lead = 10% of h. contact. F. lead = 30% of f. contact.



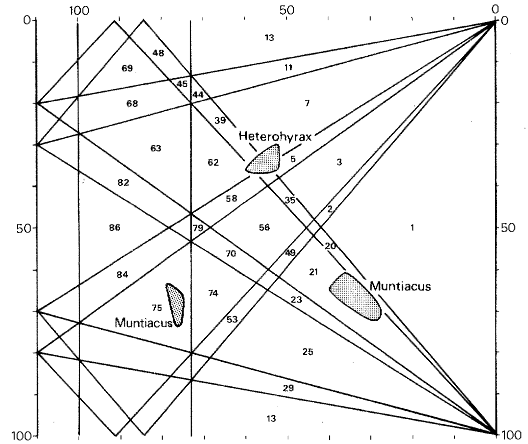
F. contact = 80% of h. contact. H. lead = 10% of h. contact. F. lead = 10% of f. contact.

FIG. 11.—Overlay to Fig. 6 showing the ranges of available plots for the genera indicated, and the distribution of footfall formulas under the stated conditions. The numbers are keyed to the respective formulas in Figs. 20 and 21 (and to the equivalent rotary gallops).

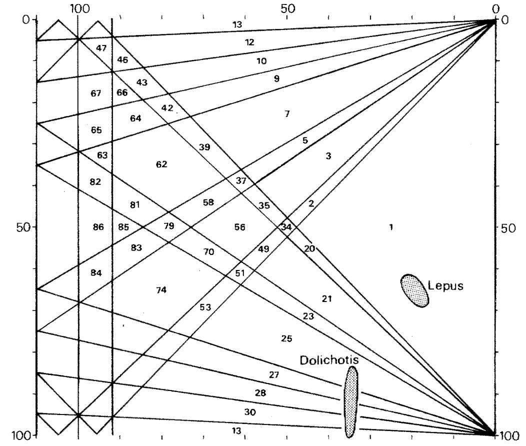
The rotary sequence tends to be preferred to the transverse sequence by the fastest and most maneuverable cursors (*Acinonyx, Antilope,* and *Gazella*), and limited evidence indicates that some artiodactyls may tend to change from the transverse to the rotary gallop as speed increases. Also, some mammals seem to tend from transverse or rotary sequence to the half bound or bound as speed increases (*Sciurus, Dolichotis, Mustela, Lutra,* and *Muntiacus*).

Fig. 9 also shows, by black spots, the mean coordinates for all ungulates of each of four weight classes as listed in Table 1. Although classes 3 and 4 are "reversed," it is seen that there is a trend in weight that correlates with the trend in lead sequence. (Because sampling, though chance, is far from random, these data are indicative but inexact.) Further, most mammals that use the half bound and bound are small and agile.

In summary, there is wide variation within genera, and overlap among genera, yet gait selection according to type and duration of suspension correlates roughly with lead sequence, body weight, speed, agility, and maneuverability. Heavier, less agile



F. contact =100% of h. contact. H. lead = 10% of h. contact. F. lead = 50% of f. contact.



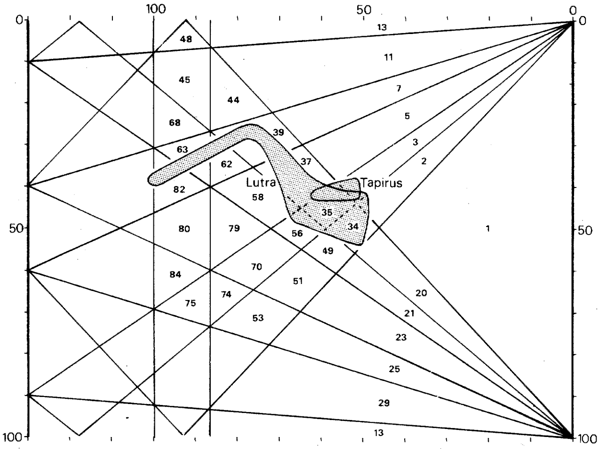
F. contact = 80 % of h. contact. H. lead = 10 % of h. contact. F. lead = 50% of f. contact.

FIG. 12.—Overlay to Fig. 6 showing the ranges of available plots for the genera indicated, and the distribution of footfall formulas under the stated conditions. The numbers are keyed to the respective formulas in Figs. 20 and 21 (and to the equivalent rotary gallops.)

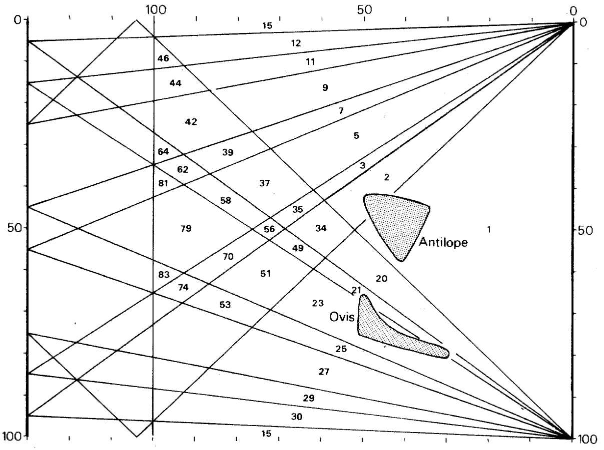
animals, and slower performances go with transverse sequence, and with either absence of suspension or a gathered suspension. Lighter, more maneuverable animals, and faster performances, go with an extended suspension or with both suspensions, and with rotary sequence or (particularly for the smallest, most maneuverable mammals moving on terrain that is rough in relation to body size) the half bound or bound. (Observations of Gambaryan, 1974, on flexibility of the spine, length of distal limb segments, and musculature correlate roughly with these factors.)

TERMINOLOGY

There are few lay terms for asymmetrical locomotion. Transverse and rotary gaits are termed the *gallop* (particularly when performed at good speed) and the word is used in that sense here. Horsemen use *canter* for a slow, collected gallop; in the show ring it is "high" or animated and often rocking. A *lope* is a moderate, sustained gallop that is "low," or not animated; the term is applied to ungulates or canids. The layman might



F. contact = 100% of h. contact. H. lead = 30% of h. contact. F. lead = 50% of f. contact.



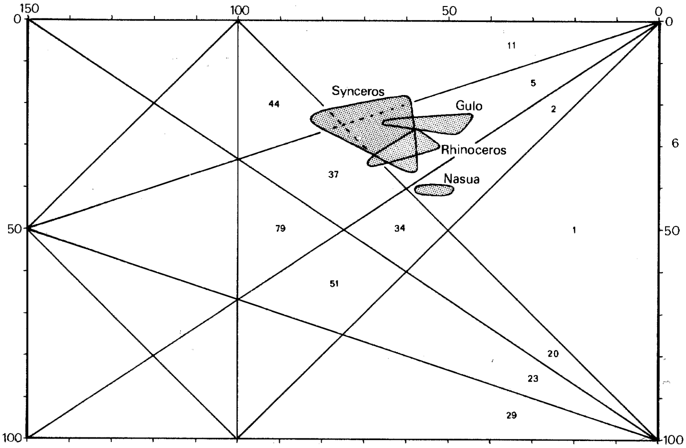
F. contact = 80 % of h. contact. H. lead = 30% of h. contact. F. lead = 50% of f. contact.

FIG. 13.—Overlay to Fig. 6 showing the ranges of available plots for the genera indicated, and the distribution of footfall formulas under the stated conditions. The numbers are keyed to the respective formulas in Figs. 20 and 21 (and to the equivalent rotary gallops).

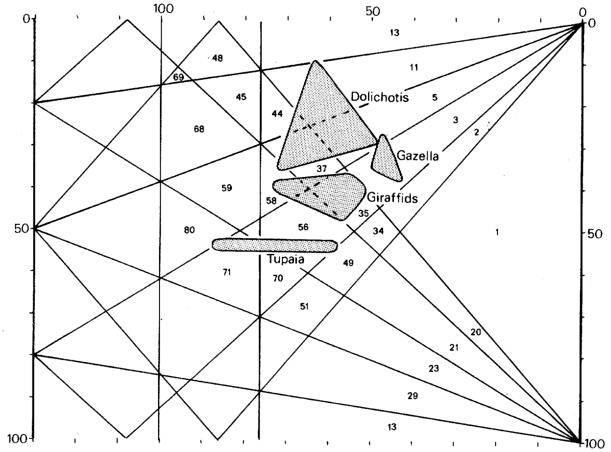
use either *bound* or *hop* for the gaits more exactly defined above as half bounds and bounds.

If the specialist wishes to describe a particular performance (or a calculated average performance), then a gait diagram is best. If words and numbers are used, the variables described should be selected in such a way that all other variables can be derived from them; that is, the gait diagram can be reconstituted. (One published table lists 11 variables for certain gallops, but I was unable to derive the gait diagrams, and hence could not utilize the data.) The gait descriptions at the right in Fig. 1 serve the purpose (though other choices could be made).

(The two or three percentage figures describing symmetrical gaits are written in sequence to form a gait formula, Hildebrand, 1966, 1976. Similarly, the five percentage figures at right in Fig. 1, plus a symbol for lead sequence, could be written in a standard order to make a gait formula for asymmetrical gaits. The data could also be condensed to five numbers only, without directly showing lead sequence. In this paper I do not find such a shorthand to serve clarity.)



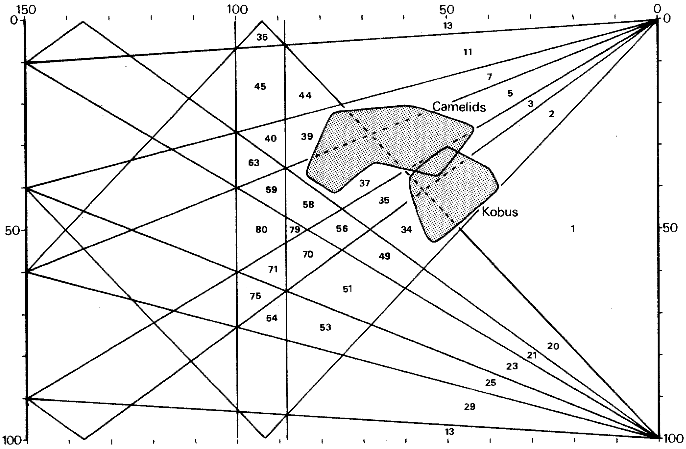
F. contact = 100% of h. contact. H. lead = 50% of h. contact. F. lead = 50% of f. contact.



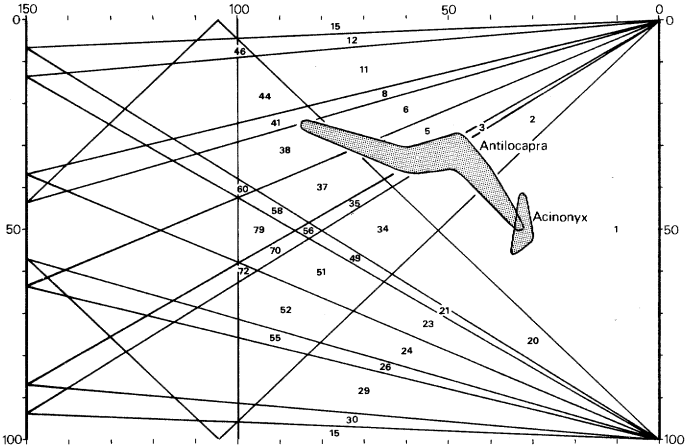
F. contact = 100% of h. contact. H. lead = 30% of h. contact. F. lead = 70% of f. contact.

FIG. 14.—Overlay to Fig. 6 showing the ranges of available plots for the genera indicated, and the distribution of footfall formulas under the stated conditions. The numbers are keyed to the respective formulas in Figs. 20 and 21 (and to the equivalent rotary gallops).

It is desirable for mammalogists to have another terminology for gaits that could be applied following observation of the moving animal (or, better, of slow motion pictures) without constructing gait diagrams. The system of terms should be accurate, but in recognition of the wide range of variation from cycle to cycle, and of the impossibility of exact analysis by eye, the system should not be precise. I suggest that the subjective terms presented in Figs. 2 (rate of travel), 9 (lead sequence), 4 (length of hind and fore leads), and 7 (kind and duration of suspension) can be combined to serve the purpose. Thus, the gait of Fig. 1A is a fast transverse gallop having a medium hind and long fore lead, and a short gathered suspension. The gait of Fig. 1B is a very fast rotary gallop having a short hind and very long fore lead, and short gathered and extended suspensions. At Fig. 1C is a medium half bound having a medium fore lead and no suspensions. At D is a very fast bound with a very long extended suspension. At E is a very fast pronk with a very long suspension. The relative duration of fore and hind contacts is omitted from this terminology because it is so variable and difficult to observe by eye.



F. contact = 100% of h. contact. H. lead = 50% of h. contact. F. lead = 70% of f. contact.



F. contact = 80% of h. contact. H. lead = 50% of h. contact. F. lead = 70% of f. contact.

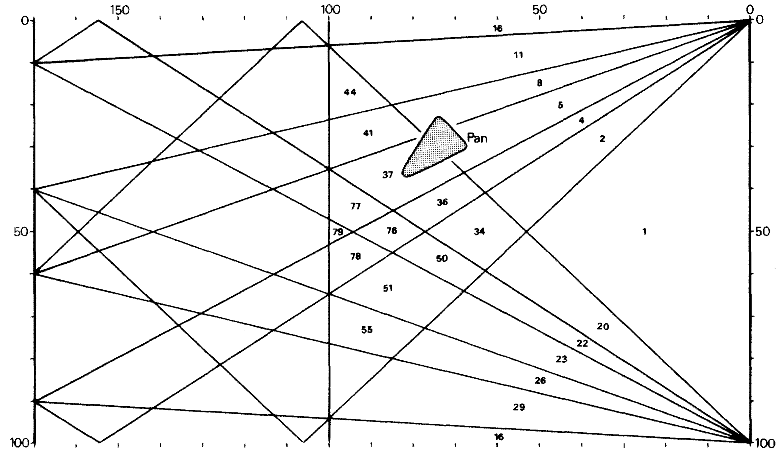
FIG. 15.—Overlay to Fig. 6 showing the ranges of available plots for the genera indicated, and the distribution of footfall formulas under the stated conditions. The numbers are keyed to the respective formulas in Figs. 20 and 21 (and to the equivalent rotary gallops).

One other way of distinguishing among asymmetrical gaits, with or without the assignment of terms, has been by footfall formula.

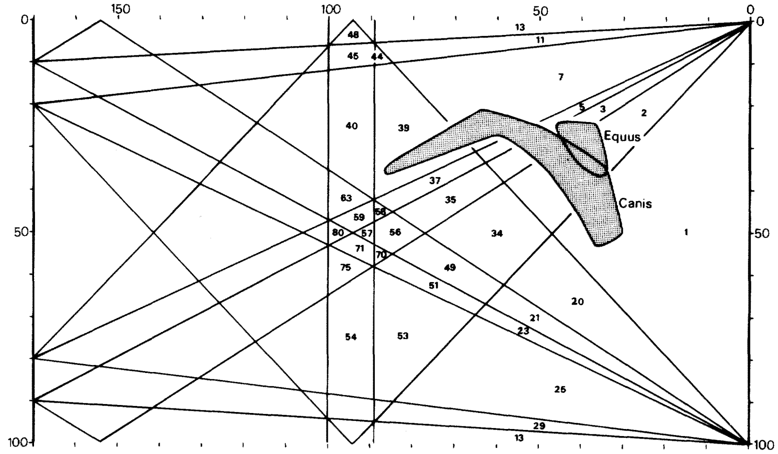
FOOTFALL FORMULAS

A footfall formula is a stylized notation that shows the sequence of combinations of supporting feet as an animal progresses (Fig. 19). All formulas are here standardized to begin with the footfall of the left hind foot. The formula is less informative than the gait diagram (Fig. 5) because the relative durations of the successive combinations of support are not shown. Nevertheless, the formula has great utility. Being compact, many gaits are easily recorded and compared; it serves for exploring the diversity of gaits.

Footfall formulas change with each gait variable. As noted above, different numbers and combinations of variables may be selected for study (six are shown at the right in Fig. 1), yet the minimum number for a complete description is five, so at least five



F. contact = 100% of h. contact. H. lead = 70% of h. contact. F. lead = 50% of f. contact.



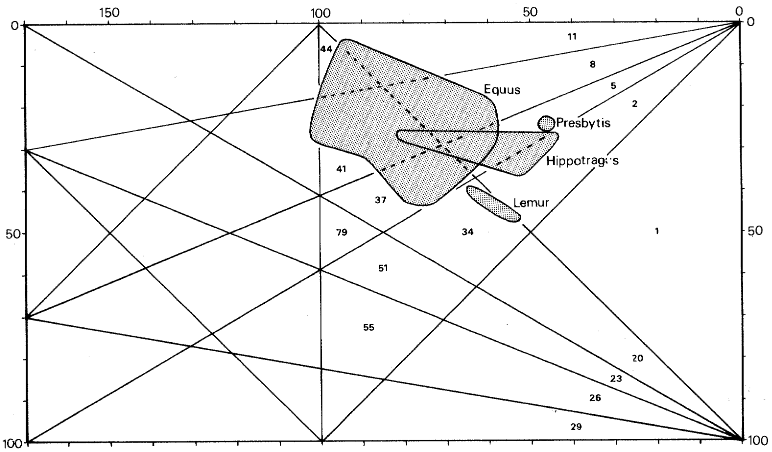
F. contact = 100% of h. contact. H. lead = 70% of h. contact. F. lead = 90% of f. contact.

FIG. 16.—Overlay to Fig. 6 showing the ranges of available plots for the genera indicated, and the distribution of footfall formulas under the stated conditions. The numbers are keyed to the respective formulas in Figs. 20 and 21 (and to the equivalent rotary gallops).

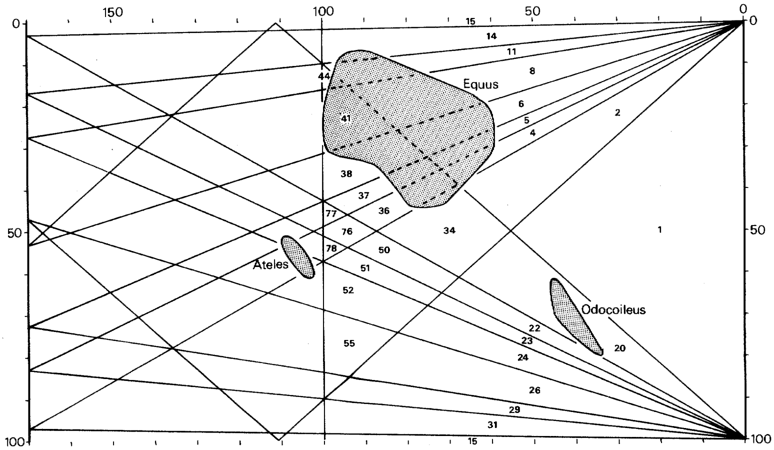
must be used in the study of footfall formulas. Three continuous variables can be correlated by a three-dimensional graph, but trial showed that any combination of three gait variables produces a very irregular terrain. Multivariate analysis is in this instance questionably valid, and would introduce an undesirable degree of abstraction.

The solution adopted here is to show the distribution of footfall formulas on the basic gait graph, that is, Fig. 6 (where the continuous variables are support by one or both hind feet, and midtime lag), for representative combinations of the remaining three variables. This procedure is direct, relatively simple, and provides for comparison of footfall formulas with the data presented on the same graph (Figs. 7 to 9) for suspensions, lead sequence, and body size.

Because the three variables treated in this procedure as discontinuous can, in fact, have a spectrum of values, it would, in theory, require an infinite number of figures to represent all combinations. In practice, however, a manageable number of graphs



F. contact = 100% of h. contact. H. lead = 70% of h. contact. F. lead = 70% of f. contact.



F. contact = 80 % of h. contact. H. lead = 70% of h. contact. F. lead = 70% of f. contact.

FIG. 17.—Overlay to Fig. 6 showing the ranges of available plots for the genera indicated, and the distribution of footfall formulas under the stated conditions. The numbers are keyed to the respective formulas in Figs. 20 and 21 (and to the equivalent rotary gallops).

adequately represents all situations. This is because (1) animals do not, in practice, combine the variables in all possible ways; (2) the range of variation among different corresponding locomotor performances being great, it is desirable to generalize when describing the locomotion of a kind of animal, or even of an individual animal; (3) if one wishes to learn the footfall formula for a particular performance, it is usually convenient and preferable to work directly with a gait diagram, not with an overlay to a gait graph. The latter are needed to learn how many footfall formulas there are, which are most used, and how they are related.

The distribution of footfall formulas associated with 18 combinations of the three discontinuous variables are shown in Figs. 10 to 17. The combinations are selected to be representative of usual (not extreme) cycles of a maximum number of mammals. Numbers on these figures are keyed to the 104 gait formulas shown in Figs. 20 and 21, where the notation is as explained by Fig. 19.

All formulas for gallops depict the transverse lead sequence, For each transverse gallop, an equivalent rotary gallop is derived by reversing the positions of the forefeet

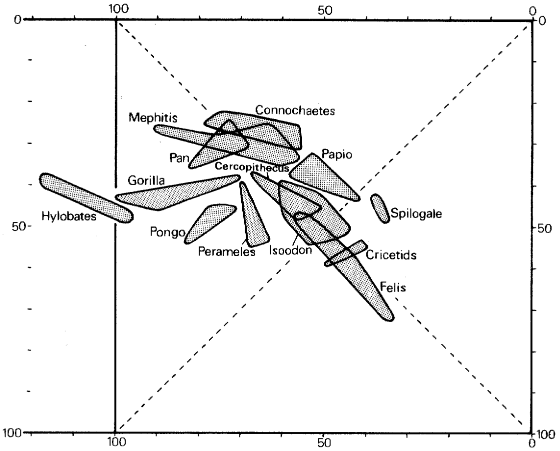


FIG. 18.—Overlay to Fig. 6 showing the ranges of available plots for the genera indicated.

only; the patterns of the distribution of rotary gallops on the graphs are identical to those of transverse gallops.

Footfall formulas are here identified only for areas of the graphs. All such formulas have eight phases unless the two feet of a pair strike the ground simultaneously (bounds and half bounds, see Fig. 10). Each line and each intersect of lines represents another formula. These relate to gaits that are transitional between the gaits of the adjacent areas; there are as many of them as there are combinations of differently numbered adjacent areas. Transitional formulas have from two to seven phases. The formulas represented by all parts of any one of the long lines radiating from the right hand corners of a graph have the same number of phases, and formulas represented by intersects along that line have a lesser number of phases (not the same at each intersect).

Footfall formulas are here identified only for areas of the graphs that lie within the smoothed limits of the available plots (as per Fig. 6). It is seen that many areas of the left hand and lower left parts of the graphs represent footfall formulas of only passing interest for their position in the total scheme. Further, if the range of variation of the three variables here treated as discontinuous were extended even to known extreme values, numerous additional formulas would be introduced. Clearly, one cannot say just how many footfall formulas there are for actual asymmetrical gaits, but there are many. Even without those of transitional and improbable gaits, there are more, by an

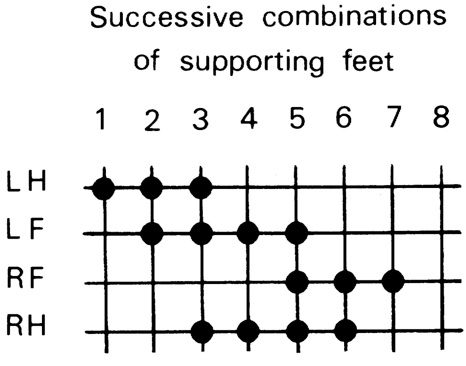


FIG. 19.—Notation of a footfall formula. The initials, L, R, F, and H stand for left, right, fore, and hind feet.

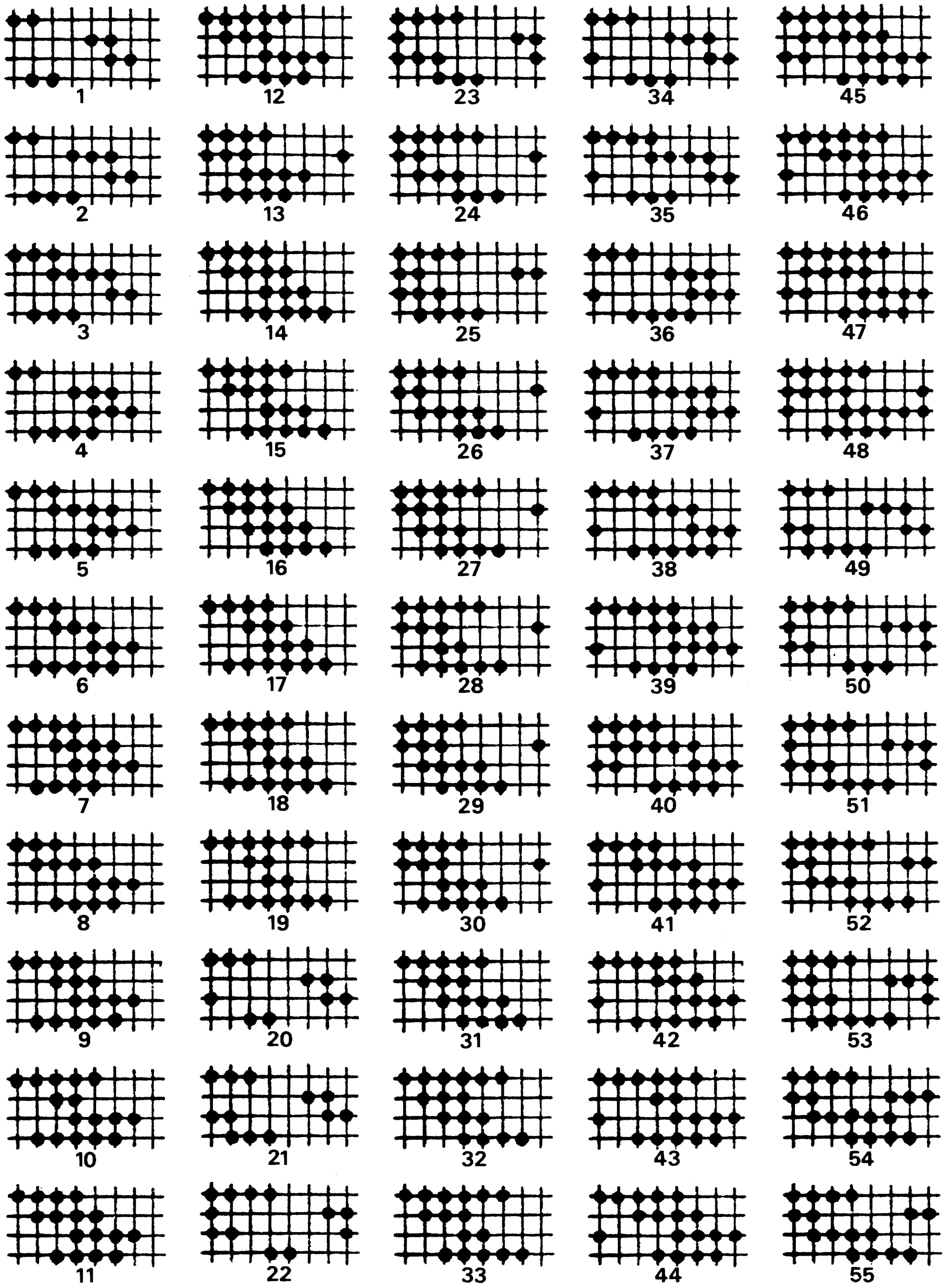


FIG. 20.—Footfall formulas of asymmetrical gaits. The numbers are keyed to Figs. 11 to 17. The notation is explained by Fig. 19. For each transverse gallop shown, an equivalent rotary gallop is derived by reversing the positions of the forefeet only.

order of magnitude, than have heretofore been described. The horse alone may be expected to use about 21 nontransitional formulas.

Figs. 10 to 17 show the footfall formulas that are within the ranges of available data for 41 genera when the respective values of the three discontinuous variables are

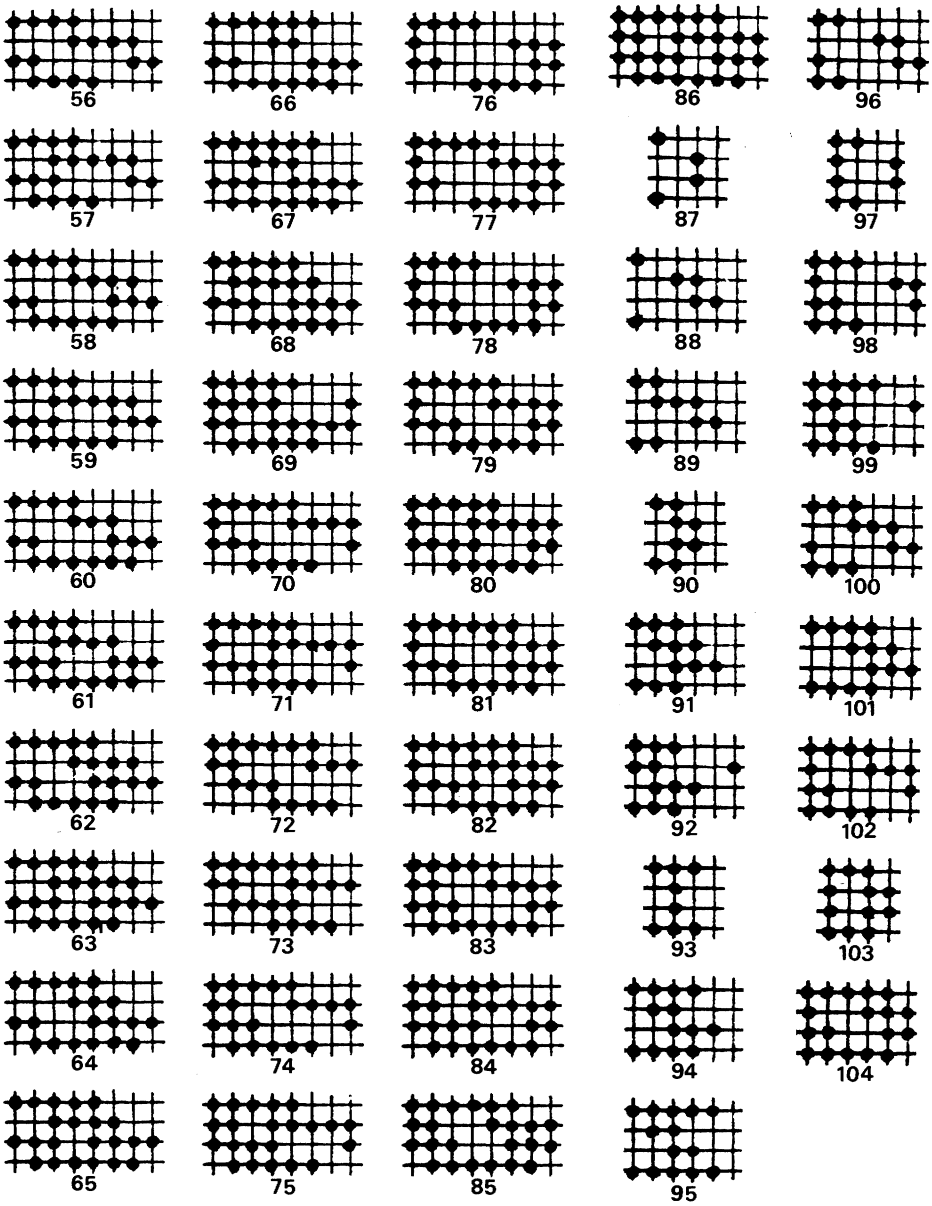


FIG. 21.—Footfall formulas of asymmetrical gaits. The numbers are keyed to Figs. 10 to 17. The notation is explained by Fig. 19. For each transverse gallop shown, an equivalent rotary gallop is derived by reversing the positions of the forefeet only.

typical. Fig. 18 shows the distributions of an additional 14 genera on the gait graph, but without identification of footfall formulas. All shaded areas would be enlarged and made more regular by more plots.

Excluding bounds and half bounds, Muybridge (1899) named and figured the formula here numbered 1, in rotary sequence, and formulas 2 and 8, in transverse sequence. Howell (1944) did not name asymmetrical gaits by footfall formula, but figured formulas 1, 2, 5, 8, and 41 in transverse sequence, and formulas 5 and 21 in rotary sequence. Gambaryan (1974) names and figures gallops as follows: 1 equals light gallop; 2 equals heavy gallop; 5 equals slow gallop (these all in both sequences); 20 equals ricochetal jump; 49 equals slow ricochetal jump.

PHYLOGENY

Few persons have written about the phylogeny of asymmetrical gaits. Magna de la Croix, a pioneer student of locomotion, had notions about kinesthetic feedback, and the correspondence of limb and pendulum cycles, which must be abandoned, yet he was perceptive. His phylogeny (1920, modified in 1932) derives a slow transverse gallop having a gathered suspension from the trot, or from lateral sequence walks. From this evolved faster gallops having both of the lead sequences and both suspensions. Next came gallops with both lead sequences and only an extended suspension. Finally, there evolved bounding gaits and the bipedal ricochet. It is unlikely that gathered gallops preceded other asymmetrical gaits, yet Magna de la Croix did arrange the gaits in the same sequence seen in moving from upper left to lower right on Fig. 9.

Gambaryan (1974) postulates that asymmetrical gaits originated with small, forest-dwelling mammals that abandoned the ancestral, symmetrical advancement of the feet to benefit posture while foraging with the forelimbs. The initial gait was a very slow or slow gallop, with no suspensions (my terms). Soon added, for the sake of clearing obstacles, was a slow, medium, or fast gallop with an extended suspension (see gaits 49 and 20, respectively, on Figs. 11 to 16). Surviving mammals using these gaits are said to be some marsupials and insectivores, and some rodents of each suborder. These animals tend to rely mostly on the hind limbs and to move with relatively inflexible backs.

From these origins, Gambaryan's phylogeny radiates three principal locomotor groups. In the first, which includes ungulates and some rodents, advancement of the hind legs was delayed enough to give the forelegs a more important role, and the spine became even more rigid. A second locomotor group includes carnivores and sciurids. Here both fore and hind limbs are powerful and the spine is flexible. Lagomorphs characterize the last group in which the hind limbs are dominant, yet the spine is flexible. Gambaryan superimposes another classification of locomotion on the above general phylogeny–quadrupedal mammals are cursorial , saltatorial-cursorial, saltatorial, mediportal, or graviportal or they have "stilt" or "batteringram" gaits.

Most of his scheme is plausible or probable, yet I concur with the criticism by Cartwell (1975) of Gambaryan's views on the origins of asymmetrical gaits. Small *Crocodylus* gallops with both lead sequences, bounds, and half bounds (Zug, 1974), and there is growing evidence that various extinct reptiles were more cursorial than formerly thought. Overlooked is the fact that the hop of anurans is a kind of bound, and an asymmetrical gait as here defined. Also, though not yet investigated, it is probable that lizards that make rapid successive jumps from rock to rock are, in fact, galloping on a discontinuous substrate. I believe that asymmetrical gaits evolved among small animals at least once in the Amphibia, several times in the Reptilia, and probably also in certain Mammalia.

It is probable that the initial selective advantage of asymmetrical gaits for at least most of these progenitors was rapid escape. (Gans and Parsons, 1966, propose this interpretation for anurans.) If so, powerful thrusts from the hind legs (bounds, half bounds, and gallops with a short hind lead) and capacity to clear obstacles (extended suspension) would have been primitive.

Ancestral asymmetrical gaits performed without suspensions were probably those that fall at, or a little below, the apex of the left hand triangle in Fig. 8 (which includes, but need not be limited to, the footfall formula of Gambaryan's ancestral slow ricochetal jump). These would be the fastest asymmetrical gaits having no suspensions. The very slow asymmetrical gaits may have evolved from faster gaits, rather than the reverse. These views are summarized in Fig. 8.

Further, I believe that bounds, half bounds, and gallops in both lead sequences are all very old and may have evolved almost simultaneously. The frog probably does not "know" when it leaps the exact sequence of the impending footfalls, the result depending on terrain and balance. The small animal that makes a controlled escape over uneven terrain can better maneuver and maintain balance if it has gait versatility. Most small mammals have such versatility–many, I believe, to a much greater degree than has as yet been reported. It is animals of large size (rhinoceros), highly modified conformation (kangaroo), or both (giraffe) that sacrifice locomotor versatility.

The interface between symmetrical and asymmetrical gaits can probably occur any place over the occupied portion of the basic gait graph for symmetrical gaits (Hildebrand, 1976, Fig. 17). It has been most often observed at diagonal sequence, diagonal couplets walks (some primates) and the trot (individual horses), but these particular performances have nothing to do with escape, and also for other reasons are not examples of the origin of asymmetrical gaits. Symmetrical and asymmetrical gaits remain distinct modalities, even though some performances are at the interface. Gaits at the interface look too jolting, crooked, or irregular to be symmetrical, yet do not have the characteristics, or appearance, of asymmetrical gaits (dotted areas of Fig. 4).

When fore and hind contact intervals and leads are both equal, then, in my scheme for displaying asymmetrical gaits, there is for every value of the contact interval, some value for the lead (expressed as percent of the contact) that makes it 50 percent of the cycle—and the gait is symmetrical. Thus, if the contact interval is 60 percent of the stride interval, and the lead is 83 percent of the contact, then the lead is also 50 percent of the stride, and the gait is a moderate to fast walk. This is a transition at which the leading and trailing feet reverse, right for left. This observation shows that symmetrical gaits are a special instance of the more general relationships presented here, and further illustrates the breadth of the interface between symmetrical and asymmetrical gaits.

A deficiency of written accounts of animal locomotion, and of graphs, is that it is difficult to translate these into a mind's eye view of the living behavior. I hope to prepare films of both symmetrical and asymmetrical gaits that can be made available for study and teaching.

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