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Abstract: The cheetah is the fastest of animals for a short dash and the horse has superlative endurance. These animals differ greatly in body size, so it is instructive to compare their ways of running. Analysis was made from slow-motion moving-picture sequences by tracing images of successive frames and arranging them in correct spatial relation to one another. The cheetah can sprint at 70 to 75 mph; the horse can attain 44 mph for 300 yds. The cheetah seldom runs more than 1/4mi., the horse can run at 20.5 mph for 20mi., and its rate of travel declines only slowly as distances increase over 30 mi. The endurance of the Mongolian wild ass is apparently superior to that of the horse. The horse uses the transverse gallop, usually covers 19 to 25 ft. per stride and complete about 21/4 strides per sec. At 35 mph. Its body is suspended once in each stride, during one-quarter of the stride interval. The leading front and trailing hind limbs support the body longer than their opposites. A change of lead usually occurs first for the front feet, but must be anticipated well before the trailing front foot strikes the ground. The forward motion of the front limbs as they pivot on the supporting feet raises the forequarters, but the resulting deceleration of the body is negligible. Its mass and inertia require that the horse minimize the motion of one part of the body relative to another and move its centre of mass in a nearly withers and croups, and the back is relatively rigid. The cheetah uses rotary gallop, covers as much ground per stride as the horse, and at 45 mph completes about 21/2 strides per sec. The body has two long periods of suspension (and probably a short one) in each stride, adding up to half of the stride. The trailing front foot is on the ground a little longer than the leading foot; the two hind feet have about equal periods of support. Changes of lead are smoothly accomplished, and can be initiated an instant before the trailing front foot strikes the ground. The front limbs do not raise the forequarters. Body size is about optimum for maximum speed: it is small enough so body form and motion can be adapted for speed with very little regard for efficiency, yet large enough to gain a long and rapid stride, as noted below. The feet are lifted high. There is pronounced up-and-down motion of shoulders and pelvis, and marked flexion and extension of the spine. Flexion and extension of the back contribute to speed by: (1) increasing the swing of the limbs, thus increasing the distance covered during suspended phases of the stride and increasing the duration of the supported phases; (2) advancing the limbs more rapidly, since two independent groups of muscles (spine muscles and intrinsic limb muscles) acting simultaneously can move the limbs faster than one group acting alone; (3) contributing to increased maximum forward extension of the limbs, which permits their greater backward acceleration before they strike the ground; (4) moving the body forward in measuring-worm fashion; and (5) reducing the relative forward velocity of the girdles when their respective limbs are propelling the body. Speed is the product of stride rate times length. Relative to shoulder height, the length of the cheetah's stride is about twice that of the horse. Factors contributing to its longer stride are: (1) two principal suspension periods per stride instead of one; (2) greater proportion of suspension in total stride; (3) greater swing of limbs, so they strike and leave the ground at more acute angles; and (4) flexion and extension of the spine synchronized with action of the limbs so as to produce progressions by a measuring-worm motion of the body. The rate of the cheetah's stride is faster than that of the horse because: (1) its smaller muscles have faster inherent rates of contraction; (2) its limbs are moved simultaneously by independent groups of muscles; (3) its feet move farther after starting their down strokes before striking the ground, thus developing greater backward acceleration; (4) the forelimbs have a negligible support role and probably actively draw the body forward; (5) the limbs are flexed more during their recovery strokes; and (6) the shoulders and pelvis move forward slower than other part of the body at the times that their respective limbs are propelling the body.

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MOTIONS OF THE RUNNING CHEETAH AND HORSE

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The horse is perhaps the most efficient running machine ever evolved; probably no other vertebrate has so many structural adaptations for rapid and untiring progress on the ground. The cheetah is conceded to be the fastest of all animals for a short dash, but lacks the endurance of the horse. This paper will analyze and contrast the running motions of these champions, and will reveal some of the secrets of the cheetah's superlative speed.

Several authors have noted cursorial adaptations of the cheetah (e.g., Pocock, 1927; Hopwood, 1947) but to my knowledge none has contrasted its mode of running with that of other cursorial quadrupeds. Morphological adaptations of the horse have been described by Howell (1944), Eaton (1944), Smith and Savage (1956) and many others. Those references emphasized structure; this paper stresses function. The classical study by Muybridge (1899) has remained the most important analysis of the motion of the horse. A paper by Grogan (1951) provides a concise review of the sequence of footfalls and combinations of supporting members.

MATERIALS AND METHODS

This study was inspired by the excellent film sequence of a running cheetah in the Walt Disney *True Life Adventure* picture "African Lion." I am grateful to Walt Disney Productions for furnishing film strips for analysis.

The photographer, Alfred Malotte, filmed the animal with a telephoto lens, so perspective changes slowly during the run. The chase presented is actually a combination of two dashes: a slower, shorter one, filmed at regular speed, and one taken in slow motion. Sequences of three and seven consecutive strides show the cheetah about side-on to the camera. With a Recordak Film Reader, 155 successive frames were traced. Registration points permitted these to be redrawn as a composite picture, with the images in proper spatial relationship to one another. The film outlines are not sharp, and low vegetation usually obscured the feet when they were on the ground, but there are enough nearly identical frames to establish a ground line and a reasonably accurate depiction of motions.

The analysis for the horse was made from photographs in Muybridge (1899:

171–179) and from the film "Horse Gaits," produced by the Horse Associa... of America, Inc. In the latter, action was filmed with an electric came... 128 frames per second; the sequence analyzed shows the horse "Citat... winning the mile-and-one-quarter American Derby in 1948. The metho... analysis was the same as with the cheetah.

FINDINGS

Speed.—Figure 1 shows speed records of the horse and, for comparison, ... man, for distances up to 900 yards, expressed as rate of travel and lapsed ti... Approximate speed of the cheetah is also indicated.

The maximum measured speed for man is 22.28 mph, over 220 yds. The plotted curve shows that he could average 22.6 mph for 155 yds.

The horse has run ¼ mi. at 43.27 mph; it could probably average 44 mph for 300 yds.

The speed of the cheetah is legendary, yet scantily documented. Auth... quote each other and the estimates of lay observers. However, there is both direct and indirect evidence of great speed. Because many artiodactyls will run parallel to a moving vehicle, accurate data are available on the speed of some of them. Einarsen (1948) reported that the pronghorn normally can run at 50 mph, and under favorable conditions can attain 60 mph. On a California desert a pet cheetah overtook a young buck pronghorn (Mam... 1949). Craighead (1942) stated that the cheetah often runs down its qu... within 150 yds., and that it is not unusual for a cheetah to overtake an antelo... that has had a head start of 100 yds. or more.

At Ocala, Florida, John Hamlet includes a cheetah in an animal show ... turing species employed in hunting. The cheetah is trained to run in a ... enclosure. A popular article (Severin, 1957) reported the results of a sp... test stating that "from a deep crouch Okala spurted to the end of the 80 ... course in 2¼ seconds, for an average speed of about 71 miles an hour." Unfo... tunately, this record must be disregarded because the enclosure is, in fa... about 65 yards long, the method of timing was inexact, and there is an ... metical error.

It is a general consensus that this remarkable cat can run at least 70 mph.

The speed of the cheetah in the film strips analyzed in this paper could ... computed if the film speeds and the animal's body length were exactly kno... but these can only be approximated. The studio reported film speeds of ab... 24 and 48 frames per second; efforts to check these figures with the photograp... were unsuccessful. The animal shown is a male. Male cheetahs average ab... 7 ft. in length (records taken from Hollister, 1918; Shortridge, 1934; Bry... 1936; Roberts, 1951); the largest of record measured 7 ft. 9 in. Separate ... culations based on assumed animal lengths of 6½ and 7¾ ft., and (for the ... motion sequence) on film speeds of 46 and 50 frames per second give a ... of possible speeds between 37½ and 49 mph. Since the animal had to ...

its footing among scattered shrubs that were 6 to 24 in. high, these less-than-optimum speeds seem expectable.

Endurance.—Records of animal endurance that are accurate and comparable are difficult to secure. Figure 2 presents some relatively reliable data. The human distance records were taken from various editions of *The World Almanac*. Records for the horse are from the same source and from Howell (1944), who also cited a record (dating from 1853) of 100 mi. at 11.2 mph. If accurate, this is truly remarkable: on the basis of curves plotted from other records one would expect no more than a 9–10 mph rate for this great distance.

Andrews (1933) reported following another perissodactyl, the Mongolian wild ass (*Equus hemionus*), over open country with an automobile. One particular animal ran 16 mi. at an average speed of 30 mph "as well as could be estimated"; the next 4 mi. were covered at about 20 mph. It ran 29 mi. before it stopped from exhaustion. Since it repeatedly changed direction and speed, these figures must be taken as approximate, but it is unlikely that any other

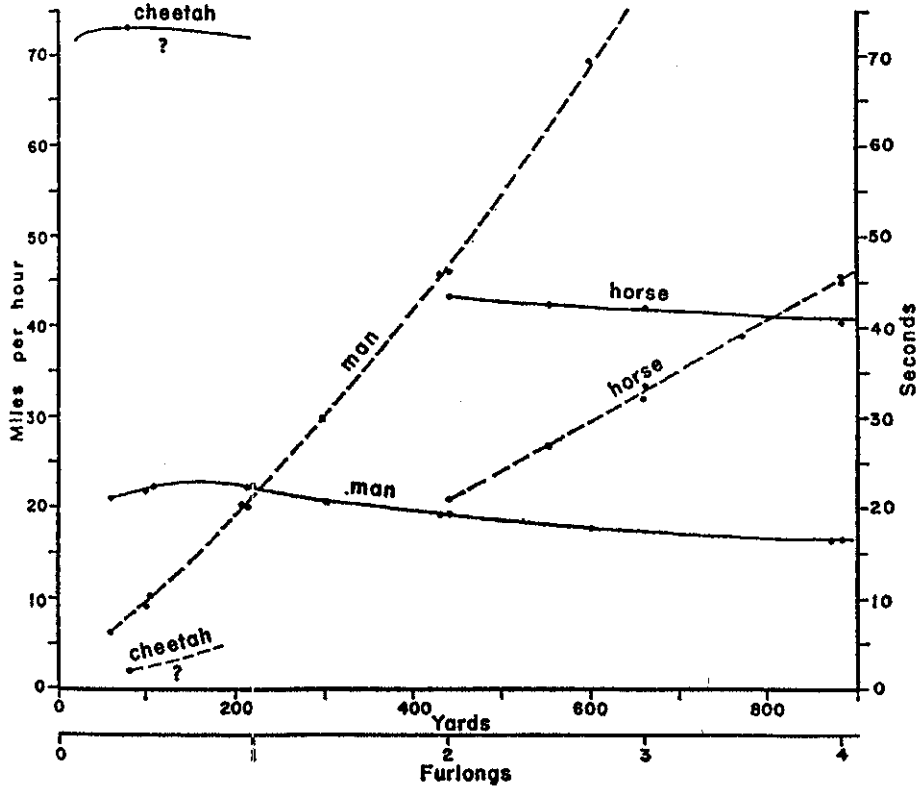

FIG. 1.—Speed records of the cheetah (approximate), horse and man, expressed as rate of travel (solid lines and left ordinate scale) and lapsed time (dashed lines and right ordinate scale). Source for man and horse: several editions of *The World Almanac*.

animal could equal this feat over distances greater than 3 mi. (The pronghorn is faster for short distances, according to Einarsen, 1948.)

In sharp contrast to the equids noted, the cheetah seldom runs more than ¼ mi. Pocock (1927) claimed that 600 yds. is the maximum distance for a chase at speed, and Bryden (1936) stated that two mongrel dogs brought one to bay in 2½ mi. Prey species are almost invariably overtaken by the cheetah and usually knocked to the ground. However, if they can scramble to their feet and run again, the cheetah often abandons further pursuit.

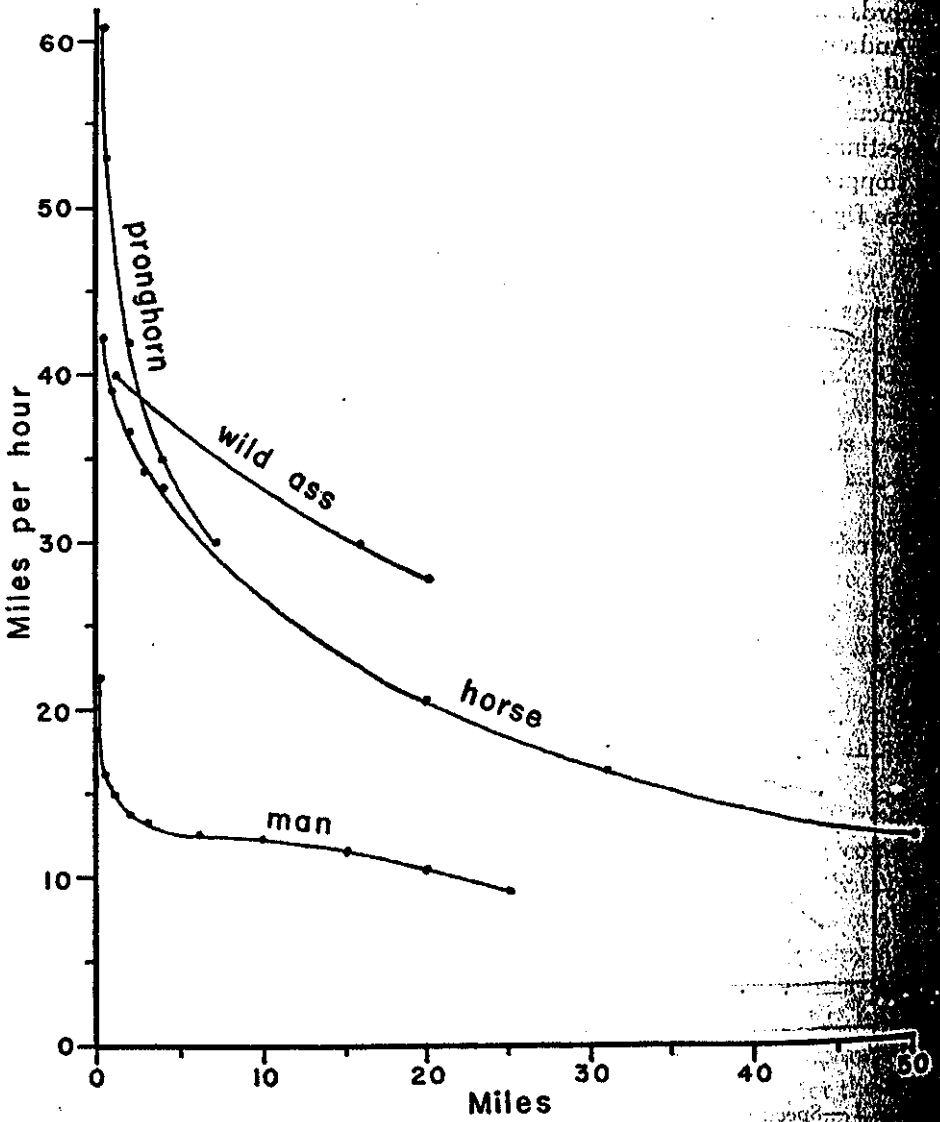

FIG. 2.—Endurance records of the pronghorn, Mongolian wild ass, race horse and man expressed as average rate of travel for different distances. Sources cited in text.

The longer of the dashes on the film analyzed in this paper was about 325 yds.

Sequence of footfalls.—The leading front or hind foot is second of the pair to touch and leave the ground in each stride or cycle of movement. An unqualified reference to lead applies to the front feet: an animal is said to be running with a left lead if the left forefoot is placed in front of its opposite. I will call the other member of each pair the trailing limb.

In the extreme flexed position the galloping horse passes one hind foot forward of one forefoot (Fig. 4*e*). Since the legs have little lateral motion and nearly equal straddle, the animal can avoid interference only by a sequence in which the leading forefoot is followed with the hind foot on the other side of the body. Thus the front and back legs must use the same lead. This sequence of footfalls, diagrammed in Fig. 3, is termed the transverse gallop.

In the extreme flexed position the cheetah passes both hind feet forward of both forefeet (Fig. 5*h*). To avoid interference it must therefore straddle the forelimbs with the hind limbs. It would seem that the lead of the fore- and hind limbs could be independent, but in practice the leading forefoot is followed by the hind foot on the same side—a sequence of footfalls called the rotary (or lateral) gallop. If the legs on one side of the body were extended as those on the other side were gathered together, and if the spine were flexed to right and left, then the rotary sequence of footfalls would increase the reach of the limbs slightly (about 2 inches per stride for a 7° swing of shoulders and pelvis with a straddle of 8 inches), but this is not the case. Perhaps the rotary sequence provides subtle benefits to balance or muscle function.

The domestic cat commonly places the hind feet nearly opposite one another when running (a gait termed the half bound) but, curiously, it may on occasion follow the horse rather than the cheetah, using the transverse gallop (Muybridge, 1899).

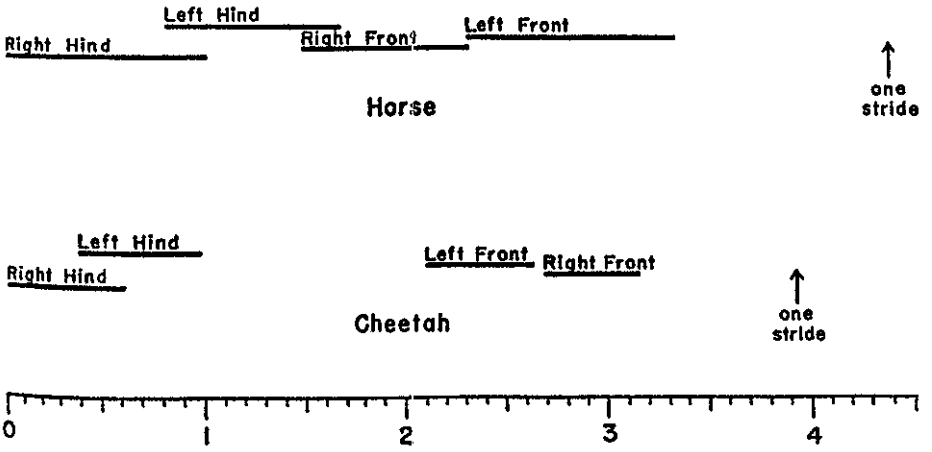

FIG. 3.—Sequence of footfalls and phases of one representative stride, shown in relation to time in tenths of seconds. The period that each foot is on the ground is shown by the length of its respective line.

Phases of the stride and their duration.—The galloping animal has all feet off the ground one or more times in each stride, and during periods of support the legs are used in different combinations. Each suspended period and each combination of supporting members is called a phase. There is much individual variation in the phases of gaits. Indeed, Howell (1944: 222) reported 16 different phase formulas for galloping horses. However, a usual phase formula can be selected for analysis. The nature and duration of the phases of such a formula of the galloping horse and cheetah are shown in Fig. 3.

The horse has all feet off the ground once in each stride—in the flexed position (see Fig. 4*e*). Howell (1944: 240) depicted a light horse that had a second, brief suspended phase, just before the trailing forefoot struck the ground, but this is unusual.

The cheetah is suspended when flexed, and again when extended. I believe there is sometimes a third, though fleeting, instant of suspension—between falls of the front feet (Fig. 3 and positions *d*, *f* and *h*, Fig. 5). Muybridge (1899: 157) anticipated this circumstance when he wrote, "It is probable that future research will discover—with the horse and some other animals—during extreme speed, an unsupported transit from one anterior foot to the other."

Analysis of Fig. 3 shows that the galloping horse characteristically has one suspended and seven supported phases (the supported transit from one fore foot to the other being almost instantaneous when galloping at good speed). The cheetah has three suspended and five supported phases.

The duration of each phase varies not only with speed but also with the

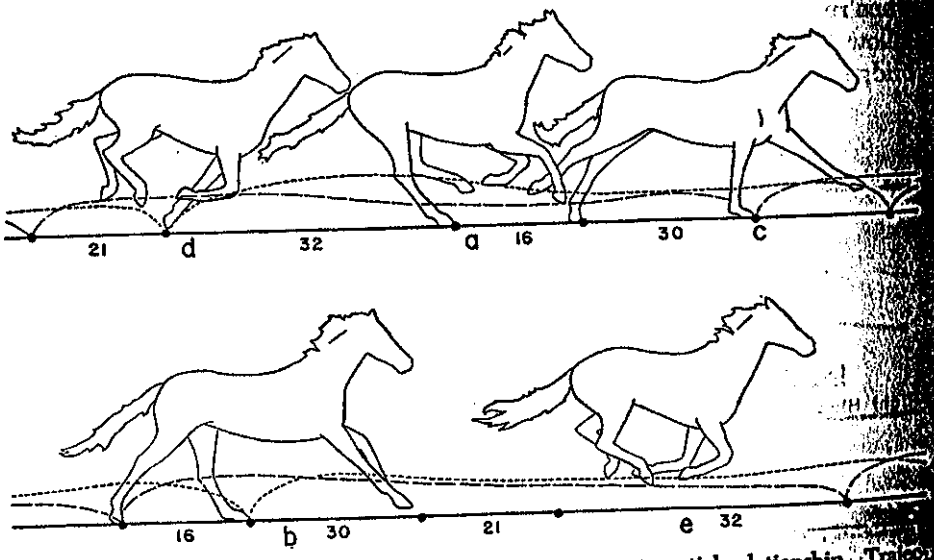

FIG. 4.—Five positions of a galloping horse shown in correct spatial relationship. Trajectories followed by the front feet are indicated above, those by the hind feet below, long dashes for right feet and short dashes for left feet. Positions of footfalls are shown by spots on the ground line. Figures below ground line give for each interval its percentage of total stride distance.

individual and for the same individual at different times. The following statements are as representative as the material available permits, but are only approximations of any particular performance.

When galloping at 35 mph the horse completes one stride in about .44 second, or 2¼ strides per sec.; at about 45 mph the cheetah completes one stride in about .39 second, or 2½ strides per sec. The horse is supported during ¾ of its stride and the cheetah during only half of its stride. Each animal is supported by two legs for 11 to 12 per cent of its total support period.

The trailing hind foot of the horse is on the ground about 85 per cent as long as the leading hind foot, whereas the two hind feet of the cheetah are on the ground about the same amount. The disparity betwen the animals is greater for the forefeet: the trailing forefoot of the horse is on the ground 80 per cent as long as the leading foot, whereas with the cheetah the foot that has the shorter contact is the leading foot (about 95 per cent as long as that of the trailing foot).

Change of lead.—These differences in duration of support and the asymmetry in resulting stresses require a change in lead from time to time to postpone fatigue. Further, a galloping animal can turn more sharply by leading with the inside forefoot.

Unless rider or terrain demand frequent turning, a horse changes its lead most often to compensate for the relatively great discrepancy in the duration of support provided by leading and trailing legs. Actual lead reversal is usually accomplished first by the forelimbs, but the motion of the hind limbs must be coordinated to avoid the interference that would otherwise result. Probably the spacing of the footfalls must also be altered, and it is likely that average speed will be reduced slightly if the lead is changed frequently.

The cheetah's leading and trailing legs share the exertion of running more evenly, but sharp and frequent changes of direction are usually dictated by the evasive quarry. The cheetah in the film strip changed lead three times in a sequence of 33 strides, and nine times in a sequence of 34 strides. Only once was the same lead used consecutively more than seven times, and five times it was changed after three or fewer strides.

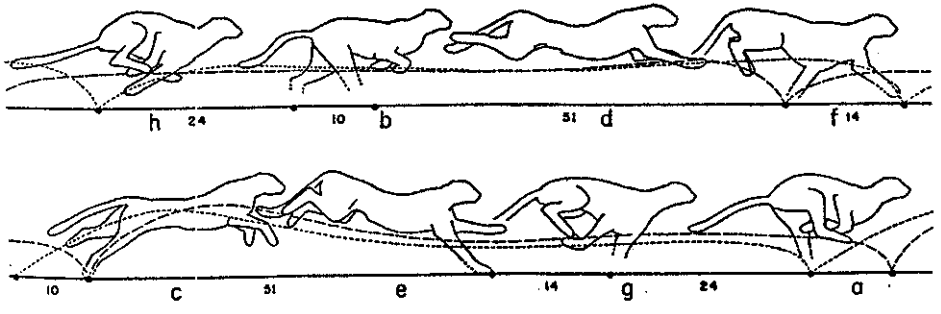

FIG. 5.—Eight positions of a galloping cheetah, shown in correct spatial relationship. Symbols and figures as for Fig. 4.

Several factors contribute to the facility with which the cheetah changes lead, and it is unlikely that speed is sacrificed. In contrast to the horse, there is a time in the stride of the cheetah (just following position *d*, Fig. 5) when the two front and two hind feet are opposite one another in both the horizontal and vertical planes. At this instant the lead can be changed as quickly and smoothly as not, and since this position immediately precedes the placement of the first (trailing) forefoot, the animal need not long anticipate the change of lead required by a turn, and cannot easily be thrown off balance by the dodging of its prey.

Length of stride.—The spacing of footfalls, and hence total length of stride, varies considerably with speed and individual performance. The data presented here are indicative of usual distances. They are based on five strides of three horses and on ten strides of a cheetah.

The strides of the galloping horse recorded by Muybridge (1899) varied from nearly 19 ft. to nearly 23 ft., and averaged 22.8 ft. Exceptional horses are reputed to cover 25 ft. at a stride (Howell, 1944: 241). Assuming the cheetah of the film strip to be 7 ft. long, the shortest of the seven strides traced was 21 ft., the longest 26 ft., and the average 23 ft.

Thus the cheetah covers at least as much ground per stride as does the horse in spite of the great disparity in body sizes: the stride of the cheetah is 8½ to 11½ times its shoulder height (with supporting forelegs vertical), compared with 4½ to 5 for the horse; or 5¼ to 6¼ times its chest-rump length (in position of maximum extension), compared with 3½ to 4 for the horse. The cursorial skill of the cheetah results in large measure from its ability to achieve so long a stride. The number and duration of the suspended phases of its gait contribute; other factors are considered further in following sections of this paper.

In Figs. 4 and 5 the footfalls are marked by dark spots on the ground lines. The per cent of total stride involved in each interval is indicated by the numbers below the ground lines. The most evident difference between the two animals in spacing of footfalls is the greater percentage of stride (51 against 30) that the cheetah achieves between the strike of the leading hind foot and that of the trailing forefoot. At this time it is bounding forward with all feet off the ground; at a corresponding time the horse is supported (compare Figs. 4*b*, and 5*d*). If we arbitrarily eliminate the difference by reducing this particular interval of the cheetah's stride to 30 per cent of total stride (as with the horse) and adjust the remaining three percentages accordingly (making the sum of the intervals again 100 per cent), the horse still has a slightly longer reach between the two hind feet and covers less ground in its suspended transit from leading front foot to trailing hind foot.

Support role of the forelegs.—It has been said that the front legs of a galloping horse do nothing that a wheel would not do better. To be strictly true, the wheel would need to be versatile at banking and at shifting track to maintain the balance of its load, yet support is certainly the principal function of the

equid forelimbs. The hind quarters are closest to the ground when the hind feet are on the ground (see croup-to-ground curve, Fig. 7), but the withers, in contrast, start to rise when the first (trailing) front foot strikes the ground and continue to rise until the leading front foot is lifted. The cushioning of body impact by the digital ligaments (Camp and Smith, 1942) and the muscles that suspend the thorax between the shoulder blades does not prevent the forequarters from rising as they pass over the stiff front legs which are pivoting on the supporting feet. The variation in withers-to-ground height is only 1½ to 2 inches, about one-third of the variation in croup-to-ground height.

It is not possible to determine the deceleration of forward motion that results from the lift given the body by the front legs, but, making some reasonable assumptions, we can learn its order of magnitude. If a 1150-lb. horse galloping 40 mph lifts half of its weight 2 inches as the stiff forelegs pivot forward over the supporting feet, the resulting deceleration will be .034 mph. Conclusion: in regard to speed, a wheel would do nothing for a horse that its front legs don't do just about as well.

Figure 7 shows that the shoulders of the cheetah are falling when the trailing forefoot strikes, continue to fall all the time the front feet are on the ground, and start to rise again only as the first hind foot strikes the ground. Evidently the front legs provide little support and no deceleration, yet, before concluding that the cheetah could run without wheel *or* forelegs, we must consider other functions of its front legs.

Role of the back.—Like other carnivores the cheetah sharply flexes and extends the spine when running. For reasons considered in the next section, the heavy-bodied horse must hold its back nearly rigid, although there is some motion at the sacrum. The amounts of flexion and extension for the two animals, approximated from photographs, are shown in Fig. 6.

The angle that the pelvis makes with the scapula changes about 60° in the unning horse, and about 130° in the running cheetah. The rotation of the capula on the spine is about the same (roughly 20°) in each animal, so the 70° lifference between them is attributable to the spine. In both animals the motion f the spine in the vertical plane is greater at the pelvis than at the shoulder.

Of what advantage is a supple spine to a cursorial animal?

One would expect flexion and extension of the spine to increase the swing f the limbs, thus increasing the distances covered during the suspension hases of the stride and extending the duration of the support phases. If this i true, the angles between ground line and limbs as they strike and leave he ground should be more acute for the cheetah than for the horse. The istant of impact of the feet is difficult to determine from the somewhat lurred images of the available moving-picture frames, so I cannot offer quanti- itive data, but it appears that these angles are indeed more acute for the heetah.

Swing of the limbs is accomplished for the horse almost exclusively by muscles iserted on the limbs, while muscles of the back also contribute for the

cheetah. This is of significance. If two muscles move one bone on another, the force of rotation is equal to the sum of the individual forces whereas the velocity is limited to that of one muscle acting alone (assuming comparable and adequate leverages and intrinsic rates of contraction). However, if a muscle moves one bone on a second while another muscle moves the second bone in the same direction on a third bone, then there is summation of both force and velocity. Thus, on the recovery stroke, the swing of a limb can be hastened by flexing several of its joints. (Shortening the limb also decreases the load on the muscles.) But when a limb is supporting the body, only a limited amount of motion is possible between the limb joints. Therefore, by swinging its limbs with two independent sets of muscles (of the limbs and of the back) the cheetah increases the speed of its stride.

Although the forward extension of the limbs when the feet strike the ground is only a little greater for the cheetah than for the horse, the more supple spine of the former contributes to substantially greater maximum forward extension before the feet start their backward acceleration preliminary to striking the ground (Fig. 6). Further, comparing the trajectories traced by the feet, as shown in Figs. 4 and 5, it is clear that, in the position of maximum forward extension, the limbs of the cheetah are held higher than are those of the horse. Indeed, they are not only higher relative to body size, but actually higher by about one-third for the front feet and trailing hind foot. It follows that the feet of the cheetah travel farther in moving to the ground. It may be inferred that they have greater backward acceleration when they strike the

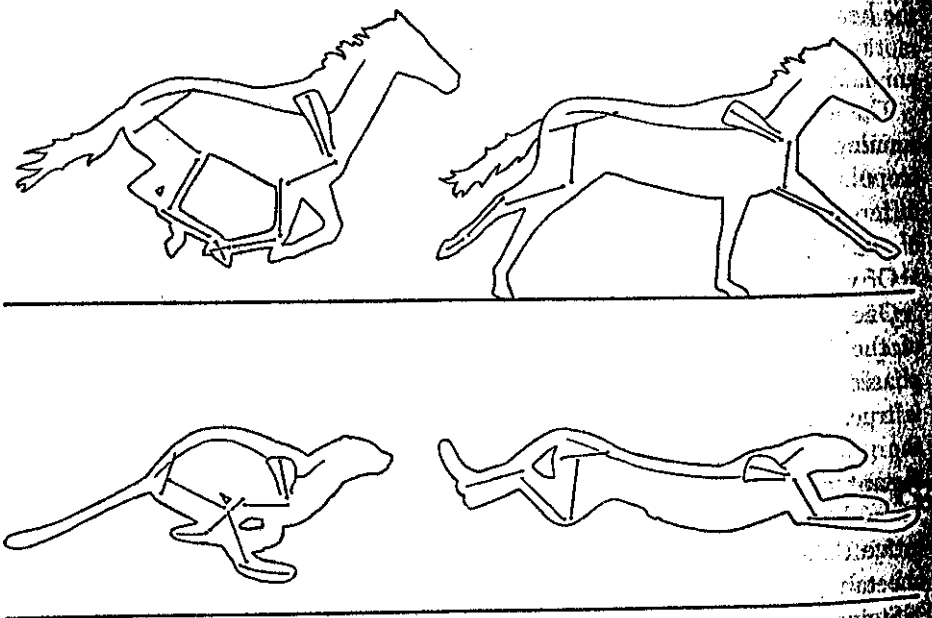

FIG. 6.—The galloping horse and cheetah, shown in positions of maximum flexion and extension of the spine and maximum rotation of the scapula on the spine.

ground and that they probably develop enough traction to prevent any deceleration from factors discussed below and in the next section.

In the flexed position the chest-buttock length of the horse is 80–90 per cent of its length in the extended position (87 in my analysis; 81 in an instance reported by Howell, 1944: 240). The flexed length of the cheetah is only about 67 per cent of its extended length. The actual shortening of the body accomplished by flexion is about 16 in. for the cheetah and 9 in. for the horse. In Fig. 7, changes in chest-buttock length are synchronized with duration of contact of each foot with the ground. For the cheetah, flexion from the position of maximum body length (high points on upper curve) is initiated when the body is unsupported. This helps impart backward acceleration to the front foot that is about to strike the ground. However, any considerable body flexion at this time would tip the shoulders forward and reduce the reach of the leading front leg, so sharp flexion is postponed to the instant the leading foot strikes. Flexion is then rapid, and is nearly completed while that foot is on the ground; only a little more body shortening is accomplished as the leading front foot follows through. Thus the fore- and hindquarters are not significantly drawn toward one another by flexion of the spine: the hindquarters alone move toward the forequarters as the latter are fixed by the forelegs (with reference to the ground, their deceleration is prevented).

In similar manner, extension of the body starts as the trailing hind foot initiates its down stroke. Again this action must help give that foot acceleration to the rear. Some extension also accompanies the unsupported follow-through of the hind legs, but most of the body extension occurs when the hind feet are on the ground. Since backward motion (deceleration) of the hindquarters is thus prevented by the hind legs, nearly all of the increase in body length resulting from extension is added to the length of the stride.

We see that the body of the cheetah moves forward like that of the measuring worm. The added distance is nearly 15 in. per stride, giving an increment in speed of 2 to 2¼ mph at a rate of about 40 mph. What the increment might be at greater speeds will depend on the relative roles played by increased length of stride and increased rate of stride as the animal moves faster. It seems probable that at 60 mph the animal adds in this manner at least 3 mph to its rate of travel.

A limber spine contributes to speed in still another way. As the cheetah's trailing foreleg strikes the ground, its forequarters and hindquarters are moving with equal velocity. But while the front feet are on the ground, the body is flexed on the forelimbs so that, at the instant the leading foot leaves the ground, the hindquarters have greater forward velocity than the forequarters. (The energy necessary to bring this about is here considered to be exerted by muscles of the back and forelimbs, against the ground as traction.) The difference between the velocity of the shoulders and of the center of mass of the entire body is nearly 3½ ft. per sec. when the animal is running at 45 mph. (The figure was derived by estimating the positions of the respective points on tracings

of the animal plotted from successive moving-picture frames and then measuring their relative motion in a known time interval.) In other words, when the forelimbs are on the ground, the portion of the body to which they are joined is moving forward nearly 2½ mph. slower than the body as a whole. Similarly, when the hind feet are on the ground the pelvis is also moving slower than the body as a whole. It is reasonable to surmise that speed is benefited by this circumstance, for it reduces the backward velocity (though not the force) required of the legs in order to propel the body forward.

Body size, speed and endurance.—The speed at which an animal can run is a function of length and duration of stride. Each of these factors is related to body size.

If it were possible to disregard mass, then animals of like form would run at the same speed regardless of body size, because length of stride varies in direct proportion to linear measure whereas intrinsic rate of muscle contraction, and hence rate of stride, varies inversely with linear measure (Hill, 1950).

It is true that the red fox can run as fast as a horse although it is one-tenth as long, but mass cannot be neglected: the horse weighs 100 times as much as the fox, and with like form could scarcely run at all. The force of contraction of a muscle is proportional to the cross-sectional area of its fibers, therefore varying as the square of linear measure. The mass of the body varies as the cube of linear measure, so largeness places the muscles at a disadvantage even when the body is at rest. In motion the disadvantage is greater (Hill, *op. cit.*) because as body size increases the power the muscles can deliver does not quite keep up with the demands placed on them to control the kinetic energy developed in oscillating parts of the body.

To avoid impossible stresses, a large animal must therefore modify the form and function of its body to reduce the load placed on its muscles and supportive tissues. Since momentum is the product of mass and velocity, this can be done by minimizing the motion of one part of the body relative to another, by causing its center of mass to move in as nearly a rectilinear fashion as possible, and by reducing the mass of such structures as must change their velocities. These principles, and related structural adaptations, are noted in publications cited above and in the introduction to this paper.

To run at all, the horse must have a degree of efficiency that assures both speed and endurance. The fox has both speed and endurance for a different reason: its mass is so small that inertia does not increase sufficiently with speed to cause distress. What of the cheetah?

At 125 lbs. the cheetah is only about one-ninth as heavy as the horse, but it is about 14 times as heavy as the fox. *Miohippus*, some litopterns, and many artiodactyls are (or were) of comparable size, but have cursorial mechanisms that conserve energy more effectively than does that of the cheetah. Why is not this cat either smaller or more like the horse in the form of its body and the way that it runs?

The answer is that the cheetah does not need to be efficient; it needs to be

fast, and its size is about optimum for maximum speed. Its muscles can stand the strain long enough for the animal to run the necessary 400 to 600 yds., so greater efficiency is not needed. However, if its body were heavier, then even for such short distances it could not employ every mechanism for gaining speed while disregarding those that improve efficiency. Its speed, then, imposes an upper limit on its body size. There are probably several reasons why the cheetah is not smaller: its size gives it wide vision, independence of irregularities in the terrain, and enough weight to bring down its prey.

SUMMARY

The cheetah is the fastest of animals for a short dash, and the horse has superlative endurance. These animals differ greatly in body size, so it is instructive to compare their ways of running.

Analysis was made from slow-motion moving-picture sequences by tracing images of successive frames and arranging them in correct spatial relation to one another.

The cheetah can sprint at 70 to 75 mph; the horse can attain 44 mph for 300 yds. The cheetah seldom runs more than ¼ mi., the horse can run at 20.5 mph for 20 mi., and its rate

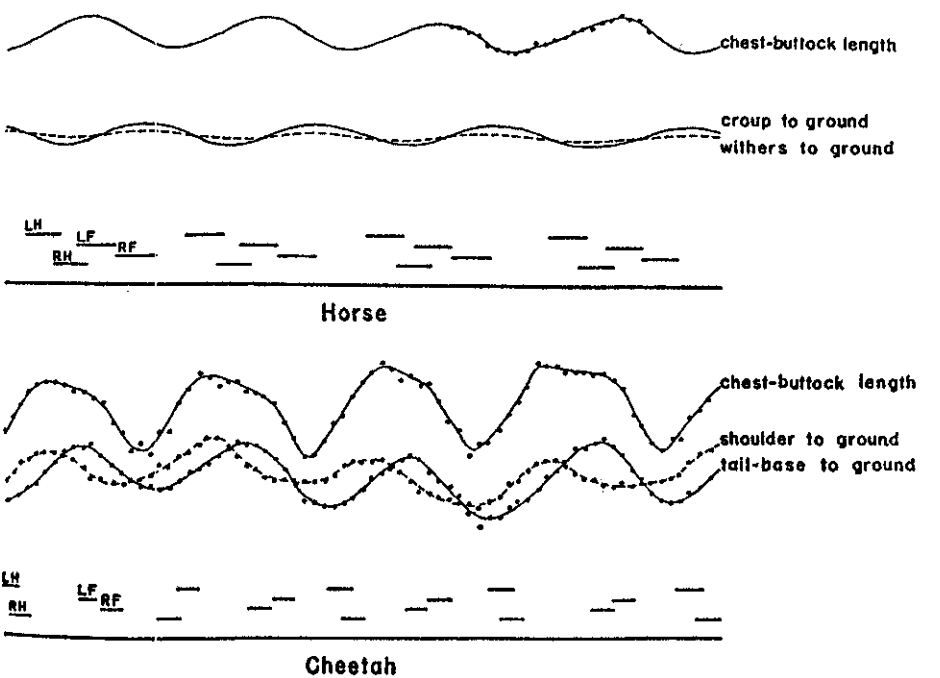

FIG. 7.—Relation of body movement to action of the feet during a little more than four strides. Motion is from left to right. Lower broken lines show, in the manner of Fig. 3, the periods of contact of the feet with the ground; letters *R*, *L*, *H* and *F* mean right, left, hind and front, respectively. Upper curves indicate, by distance above the base lines, variation in chest–buttock length. Middle curves depict height of shoulders (withers) and tail base (or croup) above the ground. All distances above the base line are in proportion to maximum chest–buttock length, which is equated for the two animals.

of travel declines only slowly as distances increase over 30 mi. The endurance of the Mongolian wild ass is apparently superior to that of the horse.

The horse uses the transverse gallop, usually covers 19 to 25 ft. per stride and completes about 2¼ strides per sec. at 35 mph. Its body is suspended once in each stride, during one-quarter of the stride interval. The leading front and trailing hind limbs support the body longer than their opposites. A change of lead usually occurs first for the front feet, but must be anticipated well before the trailing front foot strikes the ground. The forward motion of the front limbs as they pivot on the supporting feet raises the forequarters, but the resulting deceleration of the body is negligible. Its mass and inertia require that the horse minimize the motion of one part of the body relative to another and move its center of mass in a nearly rectilinear fashion: the feet are not lifted high, there is little up-and-down motion of withers and croup, and the back is relatively rigid.

The cheetah uses the rotary gallop, covers as much ground per stride as the horse, and at 45 mph completes about 2½ strides per sec. The body has two long periods of suspension (and probably a short one) in each stride, adding up to half of the stride. The trailing front foot is on the ground a little longer than the leading foot; the two hind feet have about equal periods of support. Changes of lead are smoothly accompilshed, and can be initiated an instant before the trailing front foot strikes the ground. The front limbs do not raise the forequarters. Body size is about optimum for maximum speed: it is small enough so body form and motion can be adapted for speed with little regard for efficiency, yet large enough to gain a long and rapid stride, as noted below. The feet are lifted high. There is pronounced up-and-down motion of shoulders and pelvis, and marked flexion and extension of the spine.

Flexion and extension of the back contribute to speed by: (1) increasing the swing of the limbs, thus increasing the distance covered during suspended phases of the stride and increasing the duration of the supported phases; (2) advancing the limbs more rapidly, since two independent groups of muscles (spine muscles and intrinsic limb muscles) acting simultaneously can move the limbs faster than one group acting alone; (3) contributing to increased maximum forward extension of the limbs, which permits their greater backward acceleration before they strike the ground; (4) moving the body forward in measuring-worm fashion; and (5) reducing the relative forward velocity of the girdles when their respective limbs are propelling the body.

Speed is the product of stride rate times length. Relative to shoulder height, the length of the cheetah's stride is about twice that of the horse. Factors contributing to its longer stride are: (1) two principal suspension periods per stride instead of one; (2) greater proportion of suspension in total stride; (3) greater swing of limbs, so they strike and leave the ground at more acute angles; and (4) flexion and extension of the spine synchronized with action of the limbs so as to produce progression by a measuring-worm motion of the body.

The rate of the cheetah's stride is faster than that of the horse because: (1) its smaller muscles have faster inherent rates of contraction; (2) its limbs are moved simultaneously by independent groups of muscles; (3) its feet move farther after starting their down strokes before striking the ground, thus developing greater backward acceleration; (4) the forelimbs have a negligible support role and probably actively draw the body forward; (5) the limbs are flexed more during their recovery strokes; and (6) the shoulders and pelvis move forward slower than other parts of the body at the times that their respective limbs are propelling the body.

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