———. 1954. Reproduction in the bobcat (*Lynx rufus*). Anat. Rec., 120: 816–817.

GRINNELL, JOSEPH, JOSEPH S. DIXON AND JEAN M. LINSDALE. 1937. Fur-bearing mammals of California: their natural history, systematic status, and relations to man. Univ. Calif. Press, Berkeley. 2 vols.

PALMER, RALPH S. 1954. The mammal guide. Doubleday and Company, Garden City, N. Y. 384 pp.

POLLACK, E. MICHAEL. 1950. Breeding habits of the bobcat in northeastern United States. J. Mamm., 31: 327–330.

ROBINSON, WELDON B. AND EUGENE F. GRAND. 1958. Comparative movements of bobcats and coyotes as disclosed by tagging. J. Wildl. Mgmt., 22: 117–122.

YOUNG, STANLEY P. 1958. The bobcat of North America. The Stackpole Co., Harrisburg, Pa. 193 pp.

U. S. Fish and Wildlife Service at Corvallis, Oregon, Denver, Colorado, and Salt Lake City, Utah. *Received 14 June 1960.*

FURTHER STUDIES ON LOCOMOTION OF THE CHEETAH

BY MILTON HILDEBRAND

ABSTRACT: A high-speed motion picture camera was used to record the gaits of a captive cheetah. A previous study (Hildebrand, J. Mamm., 40: 481–495, 1959) is corrected (in regard to estimated speed and rate of stride) and new data presented on motions of the body at the walk, trot and gallop. The slow gallop (± 33 mph) differs from the fast gallop (± 56 mph) in that stride is shorter (though scarcely slower), and also in the use of the spine, duration of the support periods, placement of leading feet and paths followed by the feet between footfalls.

Sharp flexion of wrist and ankle joints as their respective girdles pass over them is described and interpreted. The legs are extended relatively far forward (compared to horse) when they strike the ground. Frequent change of lead and sudden stops are described. The sequence of footfalls, phases of the stride and their duration are figured for the walk, trot, slow gallop and fast gallop. Motions of the scapula are described for a walking animal.

MATERIALS AND METHODS

At Ocala, Florida, John Hamlet has an animal show that includes a cheetah trained to run in a 65-yard-long enclosure. For rewards of meat the animal runs after a paper bag tied to a long cord that is reeled in with an adapted bicycle wheel and crank. The cheetah appears to regard the performance as a game: the observer feels that it could catch the bag at will; yet, although the cat may run beside the bag or even win the race, the bag is seldom touched till the end of the run. Usual maximum speeds are about 33 mph. As has been noted (*op. cit.*: 482), published claims of significantly greater speed for this cheetah are in error.

The animal was photographed by the author with a Trade 200 electric camera that takes 200 frames per second at exposures of 1/1000th of a second. The grass on the course was cleared out sufficiently so that the cheetah's feet could be seen when in contact with the ground. Chalk lines were placed across the track at exact, 5-yard intervals. Thus, since the camera speed is known, the animal's speed can be calculated directly from the film. Ten runs were photographed, and two sequences of walking and two of trotting.

Thanks are due Mr. Hamlet for his willing cooperation in this project. I am also indebted to Walt Disney Productions for furnishing, from the film "African Lion," an excellent close-up sequence of a walking cheetah.

The method of study was as described in the previous paper; clearer and more detailed images, however, permitted easier and more precise analysis.

CORRECTIONS

My first paper on the running cheetah was based on a film sequence obtained from Walt Disney Productions. Estimate of the animal's speed was based on an assumed body length of about 7 feet and a reported film speed of 48 frames per second. It was not until the article was in press that the photographer, Alfred Malotte, who had been abroad, corrected the studio's figure and informed me that the film speed was actually 64 frames per second. Estimate of maximum speed is changed from about 42 mph to a more respectable (for a cheetah) 56 mph, and duration of stride (or cycle of motion) becomes .28 second, or about 3½ strides per second. Further, I stated (*op. cit.*: 491) that the cheetah adds about 15 in. to each stride by a measuring-worm motion of the spine. This should have been 15 in. *two* times per stride (when the spine is being flexed and again when it is being extended). With the revised estimate of stride rate, the benefit to speed when the animal is running fast becomes about 6 mph.

NEW FINDINGS

Nature of stride in relation to speed.—From the Disney film it was evident that the animal in Florida was by no means extending itself. This circumstance is at first disappointing, but it permits a contrast between the ways that the cheetah runs at different speeds.

For each of nine runs, speed was determined over the 5-yard interval most favorable to accurate observation (when the animal was side-on to the camera). The slowest speed was 27.7 mph, the fastest 37.5 mph, and the average 33.0 mph. Nine determinations of rate of stride indicate that one cycle of motion was completed variously in .34 to .29 second, averaging .31 second. Within these limits there is little correlation between rate of travel and rate of stride. Five determinations of length of stride range from 12 to 16½ ft, averaging 14.3 ft. (The corresponding speeds average 30.5 mph.)

My previous study (as corrected) established that at about 56 mph the cheetah completes one stride in about .28 second and averages roughly 23 ft per stride.

We may conclude that length and rate of stride vary even at a single rate of travel, but that, as the cheetah accelerates from about 33 to about 56 mph, its stride rate increases only slightly, whereas its stride length increases considerably.

Galloping carnivores increase their speed by alternately flexing and extending the spine. When its body was flexed, the chest-rump length of the fast-running Disney cheetah was only 67 per cent of the extended chest-rump length. As expected, eight determinations for the Florida cheetah show that the activity of the spine was less extreme at the lesser speeds: chest-rump length of the flexed body averaged 73 per cent of the length of the extended body.

Four other differences between the way the animal runs at 33 and at 56 mph relate to the placement of the feet and the duration of the various phases of the stride (a phase is a particular combination of supporting members or an unsupported period). These differences are illustrated in Fig. 4. (1) The Disney cheetah was supported by one or more feet during about 54 per cent of stride duration; the support period of the Florida animal was variable but always greater than 54 per cent of the stride, averaging 68 per cent in six records. (2) The trailing front foot (first of the pair to strike the ground in each stride) of the Disney cheetah appeared to be lifted again about the moment that the leading foot struck the ground—indeed, although the exact instant when the feet touched the ground was difficult to determine, I suggested tentatively that there was a fleeting instant between the support periods of the two front feet. The Florida cheetah, on the other hand, did not reach out so far in placing the leading front foot: the two feet were on the ground simultaneously for 19 per cent (average of five records) of the total interval between the strike of the trailing foot and the lifting of the leading foot. (3) Similarly, both hind feet of the Disney cheetah were on the ground simultaneously for only about 23 per cent of the interval between the strike of the trailing foot and the lifting of the leading foot, whereas the Florida cheetah increased this figure to 39 per cent (average of six records) when running at 30 to 35 mph. When traveling more slowly than 15 mph it commonly placed the hind feet at nearly the same instant, in the fashion of the half-bound of domestic cats. (4) The leading feet (front and hind) of the Florida cheetah

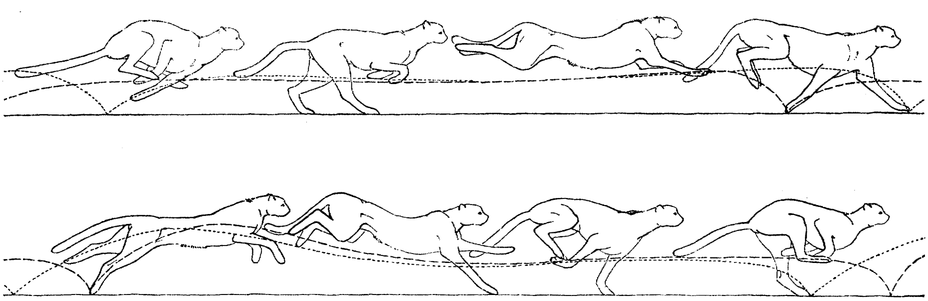

FIG. 1.—Eight positions of a cheetah galloping 50 to 60 mph. Trajectories followed by the front feet are indicated above, those by the hind feet below, long dashes for right feet and short dashes for left feet.

supported the animal about as long as their opposites—in any particular stride either a leading or trailing foot might have the longer contact with the ground. This observation is somewhat at variance with my previous conclusions on the Disney cheetah. Whether the discrepancy is due to the difference in speed or to inadequate data I cannot say, but quite possibly the latter is partly responsible: the more one studies the gaits of animals the more one is impressed by the range of variation.

The trajectories, or paths, followed by the feet in relation to the ground are shown for the fast-running cheetah in Fig. 1. The slower-moving cheetah displayed similar trajectories, but without lifting the feet so high. In particular, there is much less follow-through of the hind feet, and the front feet do not reach nearly so high before returning to the ground.

The Florida cheetah has an exceedingly variable body posture at the speeds studied. In approaching the bait closely it may run in a low crouch with legs partly flexed and motions of the spine in the vertical plane restricted. Other runs are made with shoulders and pelvis alternately bouncing up and down in the extreme. The cat runs easily while looking back over one shoulder, and on occasion runs slowly sidewise by alternately bouncing the fore- and hindquarters to one side. The observer is impressed by the animal's agility, flexibility, coordination, and lithe flowing motions.

I had hoped to record acceleration rates for fast starts—such records are almost completely wanting for cursorial animals. This cheetah, however, to start its run, turns into the track from a position to one side and does not get under way with a sudden burst of speed.

Other motions of legs and feet.—The wrist and ankle joints of the running cheetah, as their respective girdles pivot over them, are sharply flexed. When the forearm is vertical it forms an angle of about 110° with the axis of the

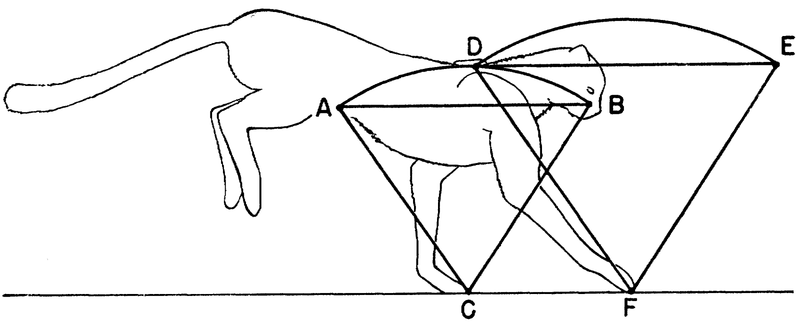

FIG. 2.—Relation of motions of the scapula and wrist joint to the path followed by the spine at the shoulder. *DC,* functional length of leg when in flexed, or shortened, position; *DF,* functional length of leg when in the extended, or lengthened, position. Arc *AB* = path of spine, and chord *AB* = advance of body if leg were held rigid in the flexed position while supporting the body. Arc *DE* = path of spine, and chord *DE* = advance of body if leg were held rigid in the extended position. Chord *DE* also = both actual path of spine and actual advance of body as the leg is alternately extended, flexed and extended again while the shoulder moves forward.

front foot, and when the pelvis passes over the heel, the shank forms an angle of 85 to 90° with the axis of the hind foot. Figure 1 is a revision of a figure in my earlier paper (*op. cit.*: 487) to show the feet positions more completely and accurately. Marked flexion of these joints is of considerable importance in two ways: (1) A forward thrust is achieved by the extension of each foot just before it is lifted from the ground. This adds both power and velocity to the stride. (2) Flexion of these joints shortens the limbs just as their respective girdles pivot over them, thus permitting the girdles to move forward without rising and falling in arcs centered at the feet, as would be the case if all joints of the leg were held rigid while the feet pivoted on the ground. This is a factor of particular importance when the limbs strike and leave the ground at relatively acute angles to the ground line (see next paragraph), because then, if the limbs were not shortened, the girdles would follow larger arcs and twice in each stride would rise and fall markedly (Fig. 2).

I have suggested that one way the cheetah achieves a stride that is longer, relative to body size, than that of the horse is by reaching out farther, front and back, as the feet strike and leave the ground. This point can now be detailed further. When each is running at 30 to 35 mph, the angle made by the leg (front or hind) with the ground line at the moment the foot is lifted from the ground is nearly the same for the two animals, though probably slightly greater for the horse; the corresponding angle when the feet (again front or hind) strike the ground, however, is more acute for the cheetah by about 12°.

I have postulated that the front feet of the hard-running cheetah have enough backward force when they are on the ground to develop a traction that prevents any deceleration of the body as the spine is flexed on itself. Efforts to verify this point for the Florida cheetah are somewhat inconclusive: in some instances the front feet had no forward motion in relation to the ground immediately before striking the ground, and in other instances they retained slight forward motion.

The paths followed by the feet in relation to fixed points at the shoulder and the hip are contrasted in Fig. 3. The drawing is based on the Disney animal except that the Florida film has been used to verify the positions of the feet when near, or in contact with, the ground—not an ideal analysis, but

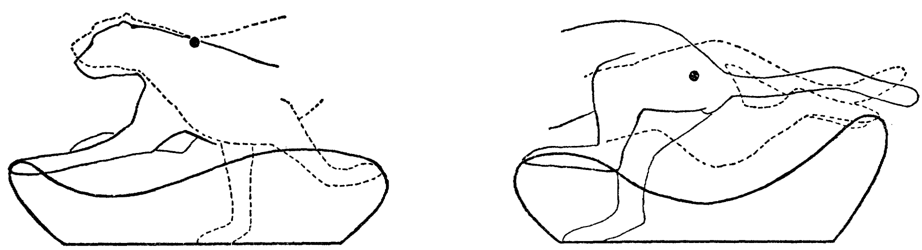

FIG. 3.—Paths followed by the feet of the cheetah in relation to approximate limb pivots at shoulder and hip.

probably within the limits of variation. The cheetah lifts its feet higher, reaches the feet out farther to the front and rear, and maintains relatively longer contact of the feet with the ground than does the horse.

Change of lead.—It was learned from the Disney film that the running cheetah changes lead frequently and easily. I surmised that lead was changed because of irregularities of terrain or changes in the direction of travel, but the Florida film demonstrates that the cheetah frequently changes lead even when running on a straight and unobstructed track. Each run required only six to eight strides (excluding turns at the start and end of the course), yet lead was changed, on the average, once in each run.

Stopping and turning.—When running straight ahead, the cheetah requires but a single stride to stop from an estimated speed of at least 20 mph. The two front feet first come down at about the same instant and then the two hind feet. All four feet are placed far to the front and the toes are spread.

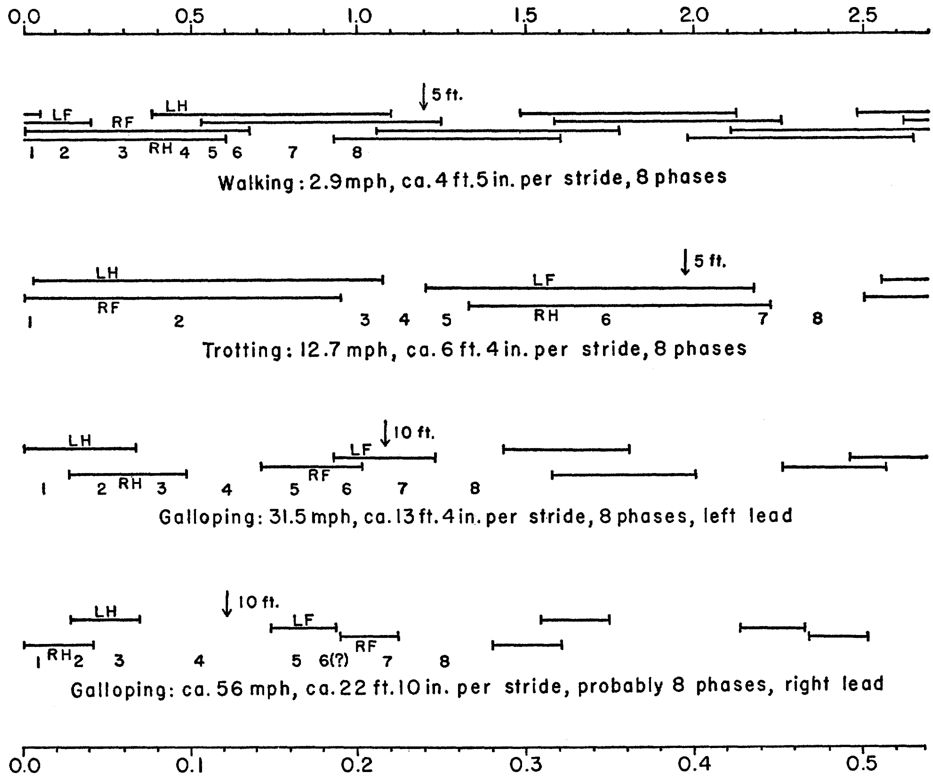

FIG. 4.—Sequence of footfalls and phases of representative strides of the cheetah shown in relation to time in seconds. Letters *R*, *L*, *H* and *F*, respectively, mean right, left, hind and front feet. The period that each foot is on the ground is shown by the length of its respective line. Upper time scale is for walking gait; lower time scale is for other gaits. Time intervals required to cover specified distances are indicated. Phases of the strides are numbered.

In Florida the sandy soil sprays widely, and repeated stops create a trough that must be filled from time to time.

This cheetah also enjoys finishing a run with a remarkably sharp turn around a tree that stands beside the end of the course. On these runs the animal's body leans into the turn to such an extent that its dorso-ventral axis forms an angle of only about 29° with the ground (average of four records).

I looked in vain for a correlation between lashings of the long tail and maneuvering of the body. The tail was often raised just before a turn, yet did not consistently perform any particular motion during sharp turns.

Walking and trotting.—Figure 4 shows, for representative strides at the walk and trot (and gallop as already noted), the sequence of footfalls, phases of the strides and duration of the phases. The data are accurate for the strides represented; variation is considerable, however, when consecutive strides are compared. For any particular stride, at either gait, either the front or hind feet may have slightly the longer contact with the ground. Each gait has eight phases. The trot is erect, symmetrical and springy; the body is supported by one or two feet at a time, or is unsupported. In the walk the body may be supported by two, three or four feet.

A close-up film record made it possible to study in some detail the motions of the shoulder of the walking animal. One could identify the positions of the vertebral border of the scapula, the greater tuberosity of the humerus and parts of the long head of the triceps, acromiodeltoid and supra-spinatus

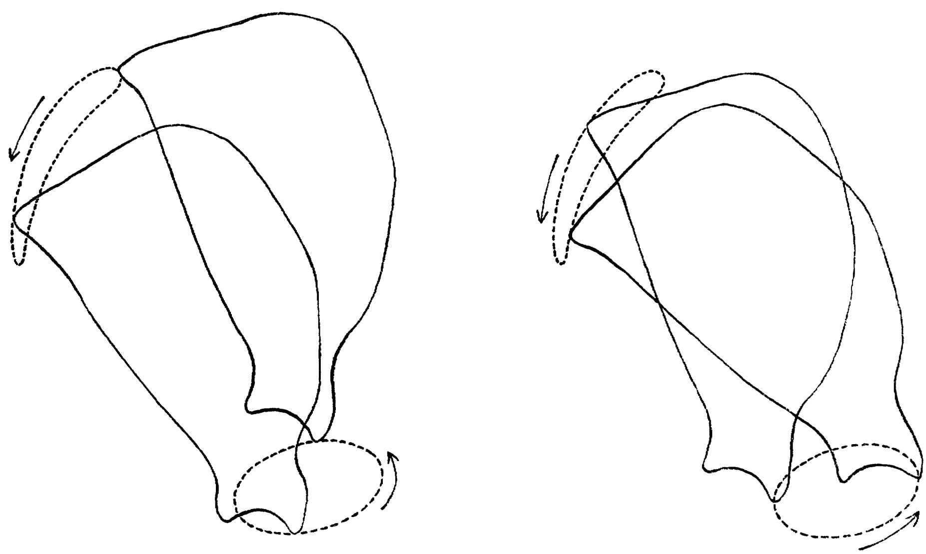

FIG. 5.—Motions of the scapula of the walking cheetah shown in relation to a fixed thorax. LEFT FIGURE: weighted (upper) and unweighted positions. RIGHT FIGURE: positions when leg is extended forward and backward. Paths traced by the coracoid process and posterior angle of vertebral border are indicated. The magnitudes of the motions are given in text.

muscles. Guided by these features, a clear plastic silhouette of the scapula, cut to exact scale, was positioned in turn over successive images projected on tracing paper, and outlines of the scapula were drawn. Certain markings on the pelt at the base of the neck and on the side of the thorax were selected as reference points so that successive drawings of the scapula could subsequently be superimposed to reveal the motions of that bone with reference to a fixed thorax. These motions are shown in Fig. 5.

One is impressed by the extent of the motions: the coracoid process describes an oval that is about 2¼ in. long by 1¼ in. high; the posterior angle of the vertebral border describes a crescent that is about 3⅛ in. long and ⅝ in. in maximum width. Each end of the right scapula makes its circuit in a counter-clockwise direction.

Clearly, the horizontal travel of the glenoid cavity is incorporated into the length of the stride. Since each shoulder blade contributes once in each full cycle motion, each stride is lengthened by about 4½ in.

The scapula rotates in the vertical plane through about 26°. (The thorax of the walking animal rotates little in this plane, therefore the motion must be attributed to rotation of the scapula on the thorax.) The magnitude of this rotation somewhat exceeds my estimate (based on less favorable material) of the equivalent motion of the running cheetah (*op. cit.*: 489), which, therefore, was probably too conservative.

It was noted that, to prevent marked up-and-down motions of the spine, long-striding animals must shorten their limbs materially as the respective girdles pass over them. Further, it was shown that carnivores accomplish this shortening largely by flexing the wrist and ankle joints. (Ungulates flex the fetlock joints.) This method of shortening is sufficient for the hind limb of the cheetah, but not for the forelimb, which has a shorter foot. It is seen from Fig. 5 that the glenoid cavity is carried about ¾ in. higher when the limb is under the body (midway in the weighted part of the cycle) than when the limb is extended to the front or rear. This additional shortening of the leg permits the thorax to glide smoothly forward without rising up over the supporting leg.

The vertical travel of the vertebral border of the scapula is even greater—about 3 in. at the posterior angle—than the vertical travel of the glenoid cavity. When in the elevated position the vertebral border of the scapula is well above the neural spines and passes slightly across the midline of the body to a position directly above the same border of the depressed scapula of the other side. One can scarcely force one's fingers down between the two shoulder blades, and then only if the hand is slanted down under the higher bone of the weighted side. As the walking animal is viewed from behind, the rise and fall of the shoulder blades is striking, as is the way in which their upper margins alternately cross over the sagittal plane.

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