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LOCOMOTION IN HYAENIDAE

by

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ABSTRACT

Crocuta crocuta and *Hyaena hyaena* use a walking gait with lateral sequence and couplets. The duration of contact between the fore feet and the ground is always longer than that of the hind feet. *C. crocuta* varies the pace angle (slow walk) and the duty factor (fast walk) between the fore and hind limbs to compensate the effect of the relatively long fore limbs on the mode of locomotion. Fast symmetrical gaits were not observed. Both species use the transverse gallop for faster locomotion.

RÉSUMÉ

Crocuta crocuta et *Hyaena hyaena* montrent une démarche au pas avec séquence latérale et des couplets. La durée du contact avec le sol est toujours plus grande pour les pattes antérieures que pour celles postérieures. *C. crocuta* déplace l'angle d'amble (marche lente) et le facteur de tâche (marche rapide) entre les pattes antérieures et postérieures afin de compenser l'influence des pattes antérieures relativement longues sur le mode de locomotion. Des démarches symétriques, rapides, n'ont pas été observées. Pour un déplacement plus rapide, les deux espèces utilisent le galop transverse.

INTRODUCTION

Hyenas are said to be poor runners. This statement is largely based upon the somewhat awkward look of a galloping hyena. However with a maximum speed of over 60 km/h (Kruuk, 1972) in the spotted hyena, *Crocuta crocuta*, and up to 50 km/h (Halthenorth et al., 1979) in the striped hyena, *Hyaena hyaena*, both species can match the fastest among the Canidae.

In addition to previous studies on the body proportions and myology of hyenas (Spoor, 1985; Spoor & Badoux, 1986) this paper deals with their locomotion, especially in relation to their body proportions. Some information about the locomotion of hyenas is given by Hildebrand (1976), Dagg (1977) and Kingdon (1977), but the present paper has the locomotion of this family as the main subject.

MATERIAL AND METHODS

This study is based on the analysis of motion pictures supplemented with some naked-eye observations. *C. crocuta* was filmed at Artis Zoo (Amsterdam) and Amersfoort Zoo and *H. hyaena* at Burgers Zoo (Arnhem). A Beaulieu camera was used with 16 mm film (Kodak 7246) at a speed of 64 frames per second. The fragments selected for this study comprise at least two complete locomotion cycles (strides) performed at constant speed. They include for *C. crocuta* 15 fragments of walking (4 different adults) and 6 fragments of galloping (3 adults and 1 juvenile) and for *H. hyaena* 7 fragments of walking (2 adults). The gallop of *C. crocuta* was also analysed from a fragment of the film "The Year of the Wildebeest" (available from the "Stichting Film & Wetenschap", Utrecht).

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Observations on other species were made using films of the Institut für den Wissenschaftlichen Film, Göttingen and of the Zoological Laboratory of the University of Amsterdam.

The Analector projector (Oude Delft) was used for analysing the fragments. The method of analysis and the terminology follow that of Hildebrand (1976, 1977). Nine variables are needed to describe the cyclic events of a gait; the duration of one stride (the time that a reference foot strikes the ground a second time, one full locomotion cycle), the time that each of the four feet strikes the ground and the duration of the contact that each foot makes with the ground. Two general types of gaits can be recognized. Symmetrical gaits have the footfalls of a pair (fore or hind) evenly spaced in time (walks, trot and pace) and asymmetrical gaits have them unevenly spaced in time (gallops, bounds). By using ratios and assuming that the duration of contacts with the ground of the right and left feet of a pair is the same, the nine variables can be reduced to five for asymmetrical gaits and to two (sometimes three) for symmetrical gaits. The latter two comprise the gait formula. The duty factor is the percentage of the stride that each foot is on the ground (McGhee, 1968) and corresponds (for symmetrical gaits) with the first variable of Hildebrand's (1976, 1977) gait formula. The second variable of the gait formula is the percentage of the stride that the fore footfall follows the hind on the same side. The pace angle is the angle between the mechanical axis of the limb on the moment of maximum protraction and the moment of maximum retraction. The mechanical axis is the line that connects the tips of the toes and the estimated position of the shoulder joint (fore limb) or hip joint (hind limb). Only for some of the fragments the pace angle could be measured because this is only possible when the animal is filmed in an exact lateral aspect.

RESULTS

Symmetrical gaits

Both *C. crocuta* and *H. hyaena* use gaits with lateral sequence (strike of the hind foot followed by that of the fore foot on the same side of the body) and lateral couplets (footfalls of the feet on the same side of the body related in time as a pair). Examples of these gaits are given in the gait graphs of fig. 1A, B. The estimated speed in the analyzed fragments ranges from 3 to 6 km/h and each stride takes 1.00-0.66 seconds.

The second variable of the gait formula of *C. crocuta* varies between 13 and 18 and for *H. hyaena* between 9 and 11. This difference between the two species illustrates the more pace-like walk of *H. hyaena*.

There is a notable difference in duration of contact between the fore and hind feet and the ground. The duty factor of the fore feet is between 104% and 120% of that of the hind feet in *C. crocuta* and between 106% and 115% in *H. hyaena*. Therefore, the first variable in the gait formulas in fig. 1 has been separately represented as a duty factor of the hind and of the fore feet. In fig. 2 the duty factor of the fore feet is plotted against that of the hind feet. A duty factor generally varies inversely with the speed of locomotion. Since the duty factor of the fore feet decreases proportionally slower than that of the hind feet, the difference between the duty factors increase with the increase of speed. In the observed range this relation may be linear.

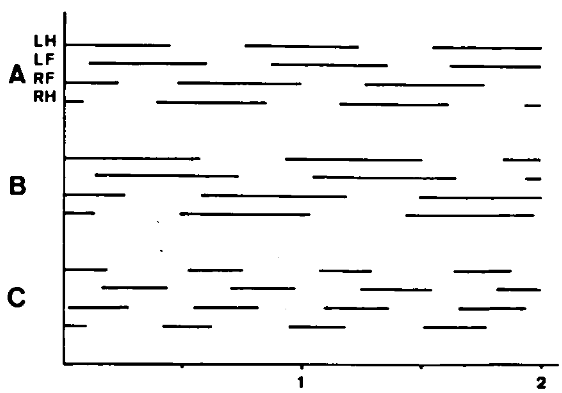

Fig. 1. Gait graphs of (A) walk of *Crocuta crocuta* (59/66,14), (B) walk of *Hyaena hyaena* (61/67,9), (C) transverse gallop of *Crocuta crocuta* (hind duty factor 42, fore duty factor 52, hind lead 49, fore lead 51, midtime-lag 33), starting at the strike of the left hind foot. L, R, H and F mean left, right, hind foot and fore foot. Time in seconds.

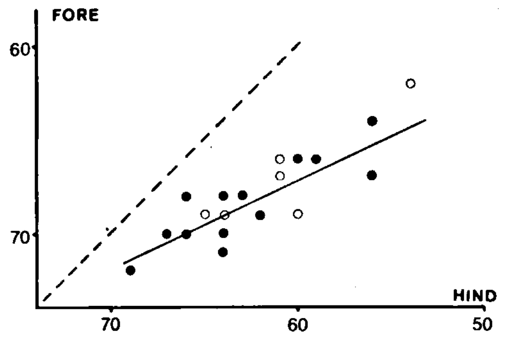

Fig. 2. The duty factor of the fore feet vs. the duty factor of the hind feet of *Crocuta crocuta* (●) and *Hyaena hyaena* (○). Uninterrupted line: regression line calculated for the data of *C. crocuta*. Broken line: X = Y.

If the swing of each limb is interpreted as that of a pendulum and the proximal end of all limbs are supposed to exhibit an equal linear velocity, there is a direct relation between the ratio of the lengths of the fore and hind limbs, that of the pace angles and that of the duty factors of the fore and hind feet. Since this ratio of the duty factors varies and the limb lengths are constant, the ratio of the pace angles is expected to vary too. In table I the ratios of the pace angles of fore and hind feet of 6 fragments are given together with the corresponding ratios of the duty factors. With an increasing difference between the duty factors of fore and hind feet (increased speed), the pace angle of the fore feet becomes relatively larger. Unfortunately, no pace angles could be measured of gaits with the largest observed differences in duty factors. No clear relation could be found between the speed and the second variable of the gait formula.

TABLE I

Ratios of duty factors and pace angles of the fore and hind limb of *Crocuta crocuta* and *Hyaena hyaena*.

	C. crocuta					*H. hyaena*
duty factor fore/hind feet × 100	103	104	108	110	111	110
pace angle fore/hind feet × 100	79	86	88	95	93	91

Running symmetrical gaits (duty factors smaller than 50) were not observed. When *C. crocuta* and *H. hyaena* increase their speed the walk abruptly changes into a slow gallop.

Asymmetrical gaits

C. crocuta and *H. hyaena* use the transverse gallop (the foot of a pair that strikes the ground first is the same for the fore and hind feet, fig. 1C) for faster types of locomotion and a half-bound (the hind footfalls are simultaneous) to initiate this gallop from a position of rest. In the analyzed fragments (all of *C. crocuta*) the estimated speed is 9-15 km/h (each stride takes 0.53-0.42 seconds) for the adults and 6 km/h (each stride takes 0.44 seconds) for the juvenile.

The duty factor of the fore feet is between 102% and 124% of that of the hind feet, but no relation between this ratio and the speed can be shown. The fore lead (time interval between the footfalls of the fore feet as percentage of the period of contact with the ground of each fore foot) is less than the hind lead in the three fragments with the largest speed, the reversed situation is found in the fragments with slower gallop. In the two fragments with the highest speed, the gallop has a gathered suspension of 5-6% of the stride. The gallop of the juvenile is characterized by relatively larger duty factors and smaller leads.

DISCUSSION

The type of symmetrical gaits of the two studied hyenas does not differ from those observed in other large carnivores (e.g. Hildebrand, 1968, 1976). The lateral sequence is most stable for walking (Gray, 1944) and the lateral couplets are often used by long-legged mammals to avoid interference between the fore and hind limbs (Hildebrand, 1968). The difference of the second variable of the gait formula between *C. crocuta* and *H. hyaena* can possibly be explained by the relatively longer limbs of the latter (Spoor, 1985).

Differences in the relative limb lengths between Hyaenidae, Canidae and Felidae are expressed in the ratios of the pace angles and duty factors. Hyaenidae have relatively long fore limbs, Felidae short ones and those of Canidae are intermediate in length (Spoor, 1985). Comparing the ratios of the pace angles and duty factors of *Canis lupus* and *Panthera leo* with those of *C. crocuta* (table II) it appears that for ratios of the duty factors close to 100 the different ratios of fore and hind limb length correspond with those of the pace angles. With the increase of speed the ratio of the pace angles of *C. crocuta* increases to values observed for *C. lupus* and *P. leo* and the effect of the long fore limb is mainly expressed in the relatively larger duty factor of the fore feet. Roughly speaking it seems that to "compensate" the effect of the relatively long fore limbs, *C. crocuta* mainly profits from the pace angle during slow walking and from the duty factor during faster walking.

TABLE II

The speed (gait formula), limb length and the ratios of duty factors and pace angles of *Crocuta crocuta* compared to those of *Canis lupus* and *Panthera leo*.

	Crocuta crocuta	*Canis lupus*	*Panthera leo*	*Crocuta crocuta*
gait formula	(66/68,18)	(71,15)	(68,21)	(62/69,15)
duty factor fore/hind feet × 100	103	103	101	111
pace angle fore/hind feet × 100	79	90	94	93
relative length of fore limb	long	inter-mediate	short	long

The position of the centre of gravity probably has also influence on the duty factors. In hyenas it is situated more cranial than in other large carnivores due to the heavy musculature of the fore limb, the long neck and the powerful jaws (Spoor & Badoux, 1986). In this situation it is plausible that the relatively greater duty factors of the fore feet increase the stability because the triangle of support formed by two fore feet and one hind foot is maintained for a longer period of the stride. Superficial analysis of the gaits of mammals with heavy fore quarters like *Bison bison* however, indicates that the relation between the position of the centre of gravity and the ratio of duty factors of fore and hind feet is far more complex.

Both Kingdon (1977) and Dagg (1977) mention the absence of fast symmetrical gaits in Hyaenidae. Both the trot and the pace require a fore and a hind limb to operate as a propulsive unit. Therefore the body proportions of hyenas, showing a large difference between the length of fore and hind limb probably prohibit this group of gaits.

The use of the transverse gallop is the most stable asymmetrical gait which does not require a period of suspension (Hildebrand, 1980). This is especially important for hyenas since they use a slow gallop (little dynamical stability) where other large carnivores use the trot or pace.

Comparison of the silhouettes of Felidae, Canidae and Hyaenidae shows that the awkward look of galloping hyenas, to which has been referred in the introduction, is due to the lack of bending movements of the spine in combination with the long neck. During the whole stride of the gallop hyenas keep their back and long neck almost in a straight line (fig. 3).

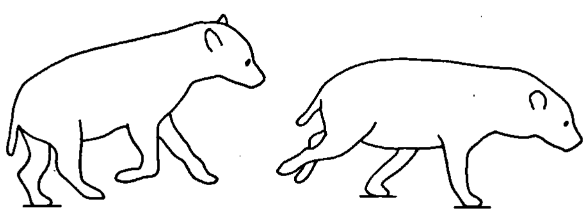

Fig. 3. Silhouettes of a galloping spotted hyena (*Crocuta crocuta*) with a half stride (0.23 sec.) in between.

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REFERENCES

DAGG, A. I., 1977. Running, walking and jumping: 1-148 (Wykeham Publs., London).

GRAY, J., 1944. Studies in the mechanics of the tetrapod skeleton. J. exp. Biol., **20**: 88-116.

HALTHENORTH, Th., H. DILLER & C. SMEENK, 1979. Elseviers gids van de Afrikaanse zoogdieren: 1-374 (Elsevier, Amsterdam).

HILDEBRAND, M., 1968. Symmetrical gaits of dogs in relation to body build. J. Morphol., **124**: 320-330.

——, 1976. Analysis of tetrapod gait: general considerations and symmetrical gaits. In: R. M. HERMAN, S. GRILLNER, P. S. G. STEIN & D. G. STUART, Neural control of locomotion: 203-236 (Plenum Press, New York).

——, 1977. Analysis of asymmetrical gaits. J. Mamm., **58**: 131-156.

——, 1980. The adaptive significance of tetrapod gait selection. Am. Zool., **20**: 255-267.

KINGDON, J., 1977. East African mammals, **3**: 1-436 (Academic Press, London).

KRUUK, H., 1972. The spotted hyena: 1-335 (Univ. of Chicago Press, Chicago).

MCGHEE, R. B., 1968. Some finite aspects of legged locomotion. Math. Biosci., **2**: 67-84.

SPOOR, C. F., 1985. Body proportions in Hyaenidae. Anat. Anz., **160**: 215-220.

SPOOR, C. F. & D. M. BADOUX, 1986. Descriptive and functional myology of the neck and forelimb of the striped hyena (Hyaena hyaena L. 1758). Anat. Anz., **161**: 375-387.

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