Gaits and Their Development in the Infraorder Pecora

by

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THESIS

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I hereby declare that I am the sole author of this thesis.

I authorize the University of Waterloo to lend it to other institutions or individuals for the purpose of scholarly research.

Signature Anne Innis Dagg

Abstract

The gaits of twenty-eight species of the Infraorder Pecora are analyzed from motion picture sequences comprising over 45,000 frames. For each gait the percentage time spent on the various supporting legs during each stride and the order in which the combinations of supporting legs were used are tabulated. When possible the times for the strides are calculated.

The walk patterns of each of the four families studied are shown to be statistically distinctive. Within each family, those members that live where the vegetation is so dense that they must rely on hearing to warn them of danger use a more stable walk than those species that inhabit open grasslands. A stable walk is that in which diagonal legs are used in preference to lateral legs and three or four supporting legs are used rather than two. With a more stable walk, a species is able to pause quickly and to flee instantly if danger threatens. The data for these species suggest that the antelopes, giraffids and pronghorns evolved in an open environment while the cervids, including the caribou, evolved in a woodland habitat.

The variability in the walking strides of members of these species is assessed for the first time. The walk pattern varies with the nature of the terrain and with the speed at which the walk is executed. It also depends upon the age of an individual of a species and on the weight of its antlers or horns.

A trotting gait is shown to be the predominant one of the constantly moving caribou. This species has evolved anatomically in ways that ensure an effective trot. The preferred fast gait of several other species is

found to be a trot rather than a gallop, owing to their large size, their wooded environment, the swampy nature of the ground underfoot or their heavy antlers or horns.

The type of gallop of the Pecoran species is shown to be closely related to their environment and to their anatomy. Light Pecoran species use both flexed and extended suspensions in their fast gallops. The white-tail and the mule deer alone use the extended suspension primarily, since it is in this phase of their gallop that they leap over the bushes and logs that occur throughout their brush environment. Heavy Pecoran species do not use extended suspensions, nor generally do those animals with backs sloping downward posteriorly to relatively short hind legs.

A symmetrical bound is shown to be used by both cervids and antelopes either to navigate steep and rough slopes or to increase the field of vision.

The times taken for walking, trotting and galloping strides are shown to be longer in larger animals. The reason for this is discussed in terms of the leg considered as a pendulum.

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Part I. Introduction and Method

1. Introduction

Various workers have studied the locomotion of quadrupeds, describing how animals move their legs at different speeds and at different gaits (Muybridge, 1899 (1957); Magne de la Croix, 1928, 1929, 1930, 1931a and b, 1932, 1933, 1936; Bourdelle, 1934; Howell, 1944; Grogan, 1951; and Hildebrand, 1965 and 1966). Some have correlated the movements of a species with its muscular and skeletal systems (Eaton, 1944; Howell, 1944; Slijper, 1946; Smith and Savage, 1956; Gray, 1961 and Hildebrand, 1959, 1961 and 1965). Others have studied the mechanical forces involved in locomotion, by considering a quadruped as a segmented, flexible and overhung beam supported by four limbs which can operate as struts and as levers. They expressed the possible positions and forces of this beam and its appendages in physical terms (Gray, 1944, 1961; Rashevsky, 1948; Barclay, 1953).

No thorough work has been done in correlating an animal's locomotion with certain aspects of its environment. This study is limited to the infraorder Pecora.

The four families of this infraorder will be considered separately prior to the general conclusions. Each part will consist of -

a. a general discussion of previously known facts associated with the gaits found within the family - recorded speeds for each species, its jumping abilities, its habitat and its anatomical characteristics,

b. a presentation of the results of analyses of the gaits of each species and

c. a discussion of relationships that exist between gaits and environmental factors.

As a final conclusion it will be possible to show that locomotion is such a vital part of the life of these animals that they have evolved highly effective gaits. It seems evident that the evolution of locomotion has been affected not only by the type of terrain and the anatomy of a species but also by the availability of food, the climate and the species' gregariousness.

2. Classification and Brief Discussion of Gaits

There are three types of gaits. These are in order of increasing speed, and thus also in order of 1) decreasing stability, 2) generally decreasing number and extent of use of supporting legs, 3) increasing periods of suspension and 4) a more quickly attained state of exhaustion. They are walking, trotting and pacing, and galloping. These gaits intergrade more or less with each other as an animal changes speed, momentarily producing movements that have no name.

a. The Walk

The walk is the universally slow gait of quadrupeds, used when there is no reason to hurry. In walking, all the legs perform the same movements with the same timing, but each leg moves out of phase with the others. There is an equal time interval between each impact and each leg supports the body for about the same amount of time.

In a slow walk, three or four legs always support the weight of the body. When three legs act as supports, the centre of gravity of the animal falls within the triangle of these legs, so that the animal can pause without falling over. The lifted legs always follow each other in the same order - left front, right hind, right front and left hind. This sequence, which provides the best equilibrium, may be found in all the symmetrical gaits and in a slow gallop as well.

A walk can commence with either a front or a hind leg. Since two or three legs largely support the animal at any one time in a faster walk, this movement is less stable than the slower walk, but because it is faster the forward momentum compensates for reduced stability. When there are only two supporting legs, these are either diagonal (right fore and left hind or left fore and right hind) or lateral (both right legs or both left legs). In the ungulates the hind hoof is generally placed on or near the imprint of the forefoot of the same side (fig. 1).

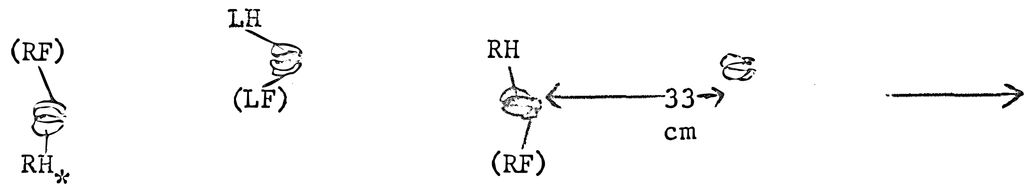
b. Trot and Pace

Trotting and pacing are also symmetrical gaits with regular beats. Each leg supports the body more or less to the same extent. In these gaits, however, pairs of legs move together - in the trot diagonal legs and in the pace lateral legs. Since the legs do not move in perfect unison, usually one, three or even four legs may support the animal momentarily between the use of diagonals or laterals. Most strides contain two or no periods of suspension since a stride is defined as one complete cycle of the feet, from a position of one particular foot until that foot is placed in the same position to start the next stride.

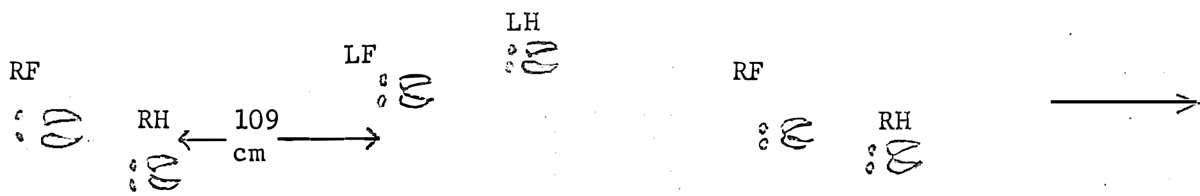
Figure 1

Tracks of various gaits, executed by cervids

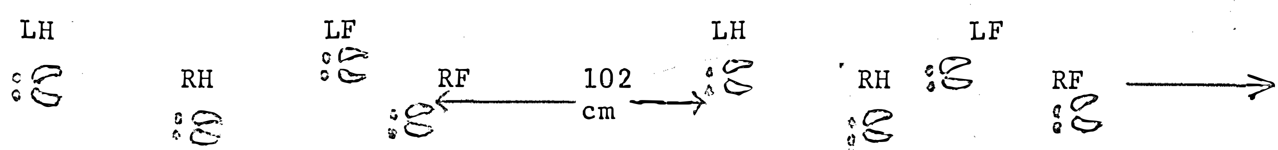
Walk. Young *Odocoileus virginianus*. after Murie, 1954.



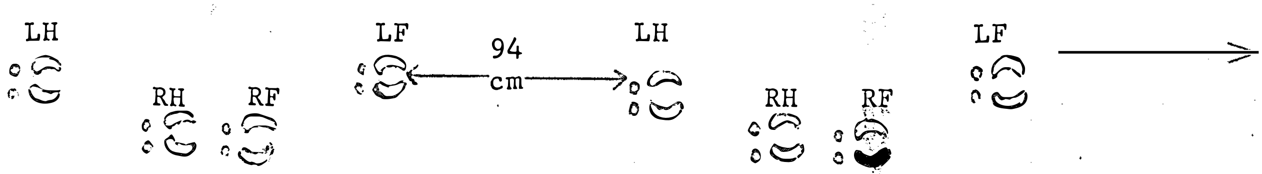
Trot. Adult female *Alces americana*. after Murie, 1954.



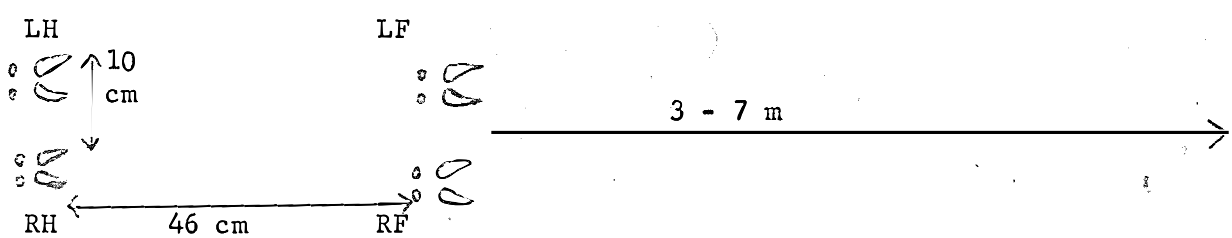
Transverse Gallop. Female *Cervus canadensis*. after Murie, 1954.



Rotatory Gallop. *Rangifer*, moving slowly. after Murie, 1954.



Bound. *Odocoileus hemionus*. after Linsdale and Tomich, 1953.



*L - left; R - right; H - hind; F - front.

c. Regular Gallop

The regular gallop is an asymmetrical gait. The legs move out of phase, the beat is irregular and the different legs support the body for varying lengths of time. Only in very slow gallops is the footfall sequence the same as that of the walk. It may include no, one, two or even three periods of suspension per stride, in generally increasing order of speed. When no legs are touching the ground they may be tucked under the body in a flexed suspension following a push-off with the forelegs or they may be stretched fore and aft in an extended suspension following a push-off with the hind legs.

During the gallop the feet touch the ground in a rotary sequence (left hind, right hind, right fore, left fore or vice versa) or in a transverse sequence (left hind, right hind, left fore and right fore) (fig. 1). The lead foot is that which is the last to leave the ground before a period of suspension.

d. Bound

Although this fast gait is closely related to a regular gallop, it is difficult to catagorize it as such since the legs move symmetrically. In the suspension, following a push-off with the hind feet the legs are held close together under the animal. The animal is supported by four feet for a period during each stride. A long extended suspension in a regular gallop is often also referred to as a bound.

3. Osteological conditions of limbs in the infraorder Pecora

The legs of these cursorial ungulates have evolved from the primitive multipurpose form of early mammals into appendages specialized for fast locomotion over relatively open and flat surfaces. The bones in the legs are elongated and the animals stand on the very tip of the third and fourth digits. By becoming digitigrade the limb is in effect lengthened and the ankle bones are raised well off the ground, giving the leg increased resiliency. The ends of the two main digits and of the reduced dewclaws, if they are present, are protected by hooves composed of tough keratin.

The ulna and the radius, and especially the tibia and the fibula, are fused to varying degrees giving the legs greater strength, but reduced maneuverability. Similarly, the elongated metacarpals and metatarsals of the third and fourth digits are fused into single cannon bones. The range of movement for all leg joints is restricted to one plane parallel to the long axis of the body. The long legs of these ungulates have heavy thigh muscles for power and light leg muscles for quick action.

4. Analysis of Gaits

The only satisfactory way to study the gaits of animals is from motion picture films. Film sequences of animals walking or running were examined frame by frame in a viewer. Only footage of animals moving on level surfaces was used. For each frame, the feet which were flat on the ground and supporting an animal were noted. Sometimes, when the hooves were obscured by grass, it was impossible to tell if the hoof was flat or not; in such cases the leg was counted as a support if it was straight and not if it was bent prior to its swing forward or to its placement on the ground again. From these data the time each species was supported by a particular combination of legs could be calculated and the order in which the legs were set down could be established.

Seven hundred feet of film of moving animals were taken by the author over a three and a half year period with a Paillard-Bolex 8 mm camera set at a speed of 16 frames per second and also several thousand feet of African ungulates in 1956-57 with a 16 mm Paillard-Bolex camera, at the same speed. I also examined many other films taken by professional photographers or biologists. From these films, data were compiled from 45,183 pertinent frames. A list of the films studied is given in Appendix A.

In this type of research one should ideally photograph an animal at a specific camera speed moving over a known distance. With such information one can calculate the animal's speed. Unfortunately films taken under such ideal conditions are virtually non-existent; it is difficult enough to film an animal moving at a steady speed within camera range, and not toward or away from the camera, without specifying the exact measured path along which it must walk or run.

In sequences photographed by myself the time taken for one stride could be calculated from the camera speed. In sequences photographed by others the camera speed had too often not been recorded during the filming and it may be recalled inaccurately later. (For instance in one film which I examined in which all shots were reported as having been filmed at 24 frames per second, the strides of three sets of galloping horses in it lasted averages of 12, 26 and 50 frames. Obviously at least two parts of the film were taken at other speeds.)

In many cases the camera speed has not been noted at all. Walt Disney Productions wrote (1966) that, "The cameramen....do not retain this type of information, but merely record it on their daily records which are destroyed as soon as the picture is completed." This is unfortunate particularly in the galloping sequences as the pattern of the gallop may change with the speed at which the gait is executed.

Part II. Gaits of Cervidae

1. Factors Related to the Gaits of Cervidae

The gaits of cervids will be related to those characteristics of these animals that are associated with their modes of locomotion - recorded speeds, jumping abilities, habitats and anatomy.

a. Recorded Speeds

There is often controversy about the maximum speed at which a species is capable of moving, but in general most North American cervids can manage about 40 m.p.h. on flat open ground with possible slower movements of the caribou (Table 1). When they are in a hurry, moose, elk and caribou rarely gallop, preferring instead the slower but less tiring trot (Peterson, 1955; Green, 1933; Flerov, 1952 and Harper, 1955). The two species of *Odocoileus* always gallop when fleeing.

b. Jumping Abilities

Most cervids are good jumpers. The mule deer can jump over 6 m horizontally and 2.4 m vertically (Cahalane, 1947), feats that can be exceeded by the white-tailed deer (Breland, 1948). The moose can jump 2 m fences from a standing position (Peterson, 1955) and one female leaped over a 1.6 m fence in full flight without apparent effort (Findley, 1951). The elk can jump over 2.4 m vertically (Howell, 1944).

c. Habitats Frequented.

Odocoileus virginianus lives in "edge conditions" where the vegetation ranges from open grassy areas to dense thickets. When escaping from danger, these deer often have to bound over logs, boulders and bushes, among or behind which predators like wolves, dogs, bobcats

Table 1

Recorded Speeds of Cervidae

Species	Speed	Reference	Comment
Fast Walk			
Odocoileus virginianus	6 m.p.h.	Hayes, 1960.	
Rangifer t. groenlandicus	5-6 m.p.h.	Symington, 1965.	For 30 miles a day
Trot[1]			
Rangifer tarandus	13.3 m.p.h.	Seton, 1953.	For 1.5 miles
Cervus canadensis	6-8 m.p.h.	Green, 1933.	
Cervus canadensis	17 m.p.h.	Seton, 1953.	
Alces americana	6 m.p.h.	Peterson, 1955.	Undisturbed female for one mile
Alces americana	15 m.p.h.	Colby, 1966.	For several miles
Alces americana	15-21 m.p.h.	Walker, 1964.	
Gallo			
Odocoileus virginianus	18 m.p.h.	Sell, 1964.	Max. for 55 wild deer in their natural habitat.
Odocoileus virginianus[2]	40 m.p.h.	Bronson, 1942.	Sprint on flat ground
Odocoileus virginianus	30 m.p.h.	Bronson, 1942.	For 3-4 miles
Odocoileus hemionus	38 m.p.h.	McLean, 1940.	Sprint, large male
Odocoileus hemionus	40 m.p.h.	Bronson, 1942.	Sprint
Rangifer t. groenlandicus	32 m.p.h.	Lane, 1954.	
Rangifer t. groenlandicus	25 m.p.h.	Cockrum, 1962.	
Cervus canadensis[3]	45 m.p.h.	Cottam & Williams, 1943.	
Cervus elaphus	42 m.p.h.	Grzimek, 1966.	
Alces americana	40 m.p.h.	Grzimek, 1966.	
Alces americana	35 m.p.h.	Cottam & Williams, 1943.	For ¼ mile

1 - A champion trotting horse with sulky can trot 31 m.p.h.

2 - A speed of 49 m.p.h. has been cited for this species but Howell (1944) doubts the accuracy of this figure.

3 - Murie (1951) feels the top speed of the elk is 29 m.p.h.

and man can hide. The home range of one individual is generally only about one square mile (Severinghaus & Cheatum, 1956). It is safer on its home range than elsewhere since there it is familiar with its runways; deer are often injured by sticks or branches if they are forced to leave their trails while rushing from danger (Rue, 1962). Although this species is generally restricted to a small home range, Skinner (1926) reports that it migrated up to ten miles seasonally in Yellowstone National Park.

Odocoileus hemionus is not a "brush" deer like the white-tail but more of an "open-country" animal that generally prefers the broken, high, mountainous regions of western North America. Where the ranges of these two species overlap, white-tailed deer inhabit the denser river valleys, while mule deer live in the hills (Ormond, 1958; Skinner, 1929). To escape danger, mule deer must often dash up steep slopes. Mule deer migrate more than white-tailed deer; marked individuals have ranged two hundred miles or more (Keller, 1966).

Both races of caribou (Rangifer tarandus)[1] live in large herds in the north where snow is present for over half the year. These animals are continually on the move because the density of lichen-growth, their staple food, is not capable in any one area of supporting their large numbers for very long. They travel long distances daily in search of food and R. t. groenlandicus migrates as much as 100 miles

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[1] The classification follows that of Banfield (1961).

per day (Seton, 1953), and up to 1600 miles yearly to the taiga in the south each winter and back to the barren grounds for the summer (Symington, 1965). Woodland caribou (R.t. caribou) inhabit the boreal forest and the taiga throughout the year.

The moose, Alces americana, is also found in the boreal forests of North America, where windfalls and swampy ground pervade the landscape in the summer and snow up to two meters in depth accumulates in the winter. Moose do migrate, but not over long distances. Edwards and Ritcey (1956) report seasonal migrations of forty miles in the Rocky Mountains. In general, except during the rut, moose are quite sedentary, ranging in areas of perhaps six square miles for most of the year (Keller, 1966).

Cervus canadensis once ranged over vast areas of the continent in both mountains and plains and in a variety of habitats. Today it survives in relatively open areas where it can walk and run without being impeded much by the habitat. The elk that live in mountainous country undergo altitudinal migrations, but these cannot be compared with the long treks of the barren ground caribou.

d. Anatomical Characteristics

i. Feet

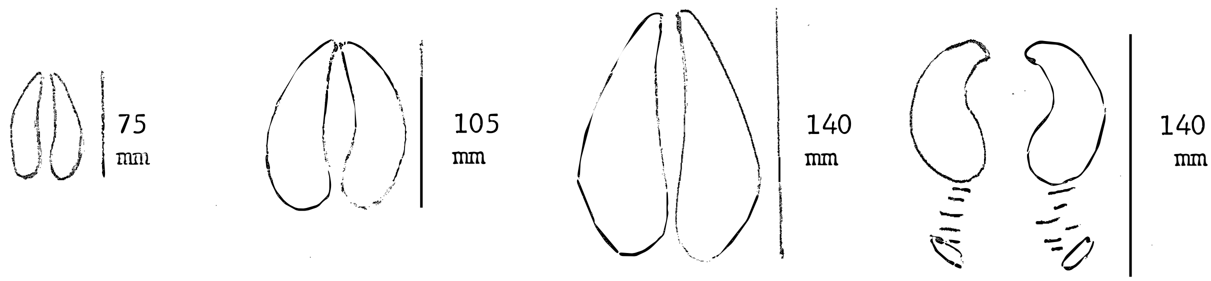
The hooves of members of the genera of Odocoileus, Alces and Cervus are similar in shape while those of Rangifer are quite different (fig. 2). The sharply edged hooves of the former cervids are ideal for providing a firm grip on all types of ground; the centres of their toes are slightly retracted so that the external edges can grip the

Figure 2

Hoof Prints of North American Cervids. after Colby, 1966

Standing

Odocoileus* | Cervus | Alces | Rangifer t. groenlandicus



Running

Odocoileus | Cervus | Alces | Rangifer t. groenlandicus

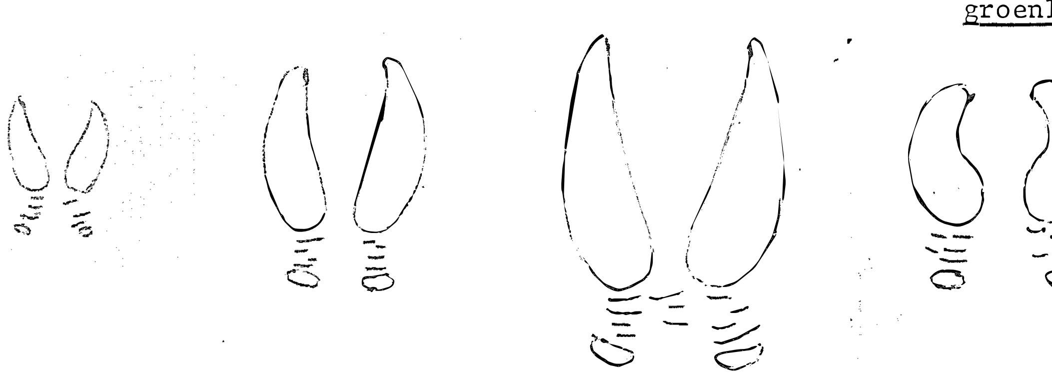
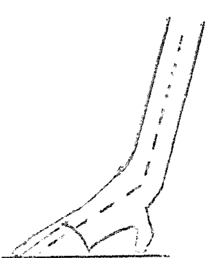


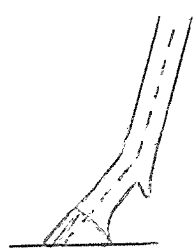
Figure 3

Forefeet of Rangifer and Odocoileus illustrating the larger bend in the former. after Bartlett, (pers. comm., 1966) and Putnam, 1947.

Rangifer



Odocoileus



*The tracks of O. virginianus and O. hemionus are indistinguishable (Seton, 1953).

surface of even smooth rocks. When these animals run, the hooves hit the ground solidly and the foot bones bend so that the toes spread apart and the dewclaws leave an imprint. The spreading hooves and vestigial toes increase the area of contact with the ground.

The hooves of Rangifer are broader, with a circumference that approaches a round shape. The toes are fairly widely separated even in standing animals. The dewclaws are long and the foot bones bend at such an angle that these vestigial toes appear in constant contact with the ground on the forefoot and within 2.5 cm of the ground on the hind foot (Bartlett, pers. comm., 1966). These differences in the feet of Rangifer and Odocoileus are illustrated in figure 3.

The average pressure on one forehoof of a standing animal as computed by the author is listed in Table 2 for each of the four species of cervids. The data show that the average pressure on the foot is much less for the caribou than for the other cervids. The much larger area of the caribou's foot in relation to its weight allows this animal to walk and run in regions of swamp or snow where the other cervids would quickly become mired.

ii. Size and Body Conformation

The shoulder heights of cervids listed in Table 3 are taken from Burt (1952), Flerov (1952) and the author's estimate of the size of the individuals filmed.

Table 2

Pressure on one Forehoof of Five Cervids[1]

Species	Mass of female in kgs	Ref.	Forehoof area length x width in mm	Ref.	Pressure in 10^3 newtons/ square m on a forehoof	Comments
Odocoileus	70	Seton, 1953	75x50	Seton, 1953	46	
Alces americana	385	Seton, 1953	140x102	Seton, 1953	66[2]	
Cervus canadensis	293	Green, 1933	105x80	Green, 1933	86	
R.t. caribou	85	Seton, 1953				
without support of dewclaws			102x133	Seton, 1925	15	
with support of dewclaws			178x133	Seton, 1925	9	
R.t. groenlandicus	81	Banfield, 1961				Pressure values for the caribou will lie between the two figures given.
without support of dewclaws			76x121	Seton, 1925	22[2])	
with support of dewclaws			140x121	Seton, 1925	12)	

[1]The values in Table 2 are given for females, since in general their range of weights is less extreme than that of the males and, except for the caribou, they do not grow antlers seasonally. Even so, the values are only approximate, for, as well as variation in body weight, the hooves vary in size depending not only whether they are fore or hind and belong to a male or a female, but on the condition of the terrain, both in winter and in summer, on the season itself and on individual variation.

[2]Seton (1953) gives values of 55×10^3 newtons/m^2 for the moose and of 14×10^3 newtons/m^2 for the reindeer. Pruitt (1959) suggests this latter figure may be high by a factor of two. Considering the variations possible in both body mass and hoof area, these values are in reasonable agreement with those in Table 2.

Table 3

Shoulder Heights of Cervids

Dama dama	0.9m
Cervus nippon (races nippon and taiouanus)	0.9m
Odocoileus virginianus	1.0m
Odocoileus hemionus	1.0m
Rangifer t. groenlandicus	1.1m
Rangifer t. caribou	1.4m
Elaphurus davidianus	1.4m
Cervus elaphus	1.4m
Cervus canadensis	1.5m
Alces americana	2.1m

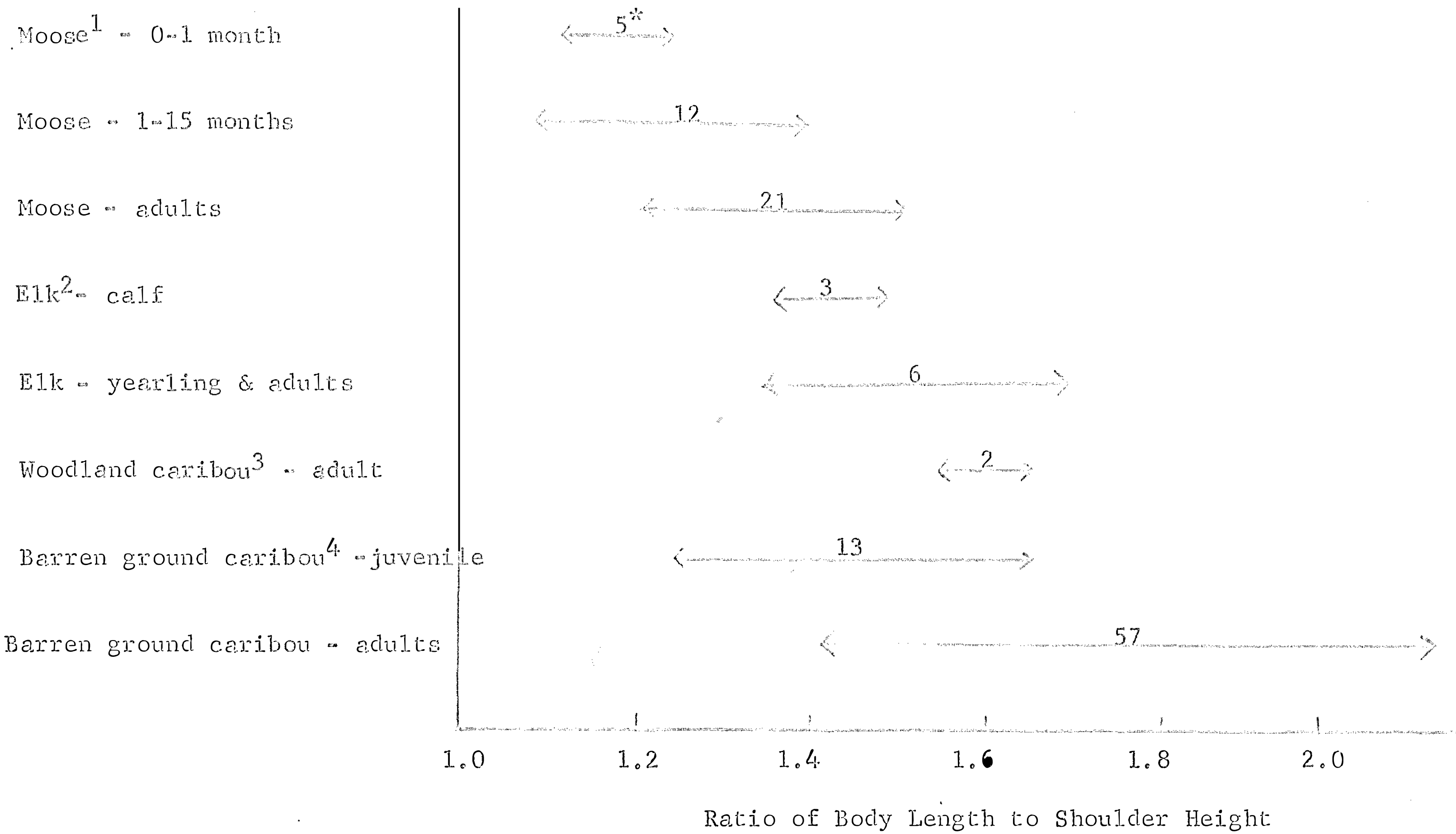
Flerov (1952) reports that the backs of most of these species are horizontal and flat, with the exception of the fallow deer (Dama dama) which has its rump higher than its withers and the moose (Alces americana) which has its withers somewhat higher than its rump.

iii. Proportion of Body Length to Shoulder Height

The ratios of measurements for body length and shoulder height for many individuals recorded in the literature are presented in fig. 4. Moose tend to have long legs in proportion to their body, while barren-ground caribou tend to have short legs, findings confirming generalizations of Flerov, (1952). The values for Cervus canadensis are intermediate. The young of each species tend to have relatively longer legs than the adults. Long legs enable the young to keep up with travelling adults at an early age and to reach their mother's teats at birth.

Figure

Ratios of Body Length to Shoulder Height for Three Cervids



References
1 - Peterson, 1955
2 - Blood and Lovaas, 1966
3 - Simkin, pers. corr. 1966
4 - Kelsall, 1957 and Harper, 1955

* - Number of ratios used

iv. Sexual Differences

The males of all these cervid species not only are heavier than the females, but the distribution of their mass can be different when their antlers are full grown (Table 4).

The females of Odocoileus and of Alces lift their feet higher than the males: in less than 10 cm of snow, especially in the fall when he has a heavier neck and shoulders to carry his antlers, a buck leaves drag marks where his front hooves were not lifted high enough as they were swung forward. The female leaves no such marks under these conditions (Koller, 1948). Bull moose in the rutting season are more likely to leave drag marks on the snow than are other moose, although all moose lift their legs high while walking so that the snow must be rather deep before any drag marks are evident (Formozov, 1946; Flerov, 1952).

Table 4

Sexual Differences in Some Cervids

Species	Largest weight given for species by Burt, 1952. - in kgs	Relative weight of female	Reference	Weight of antlers - in kgs	Reference
Odocoileus virginianus	125	over 25% less	DeVos, pers.comm.	0.7	Holman, pers. comm.
Odocoileus hemionus	91	similar	-	0.7	Linsdale & Tomich, 1953
R. t. groenlandicus	170	25% less	Banfield, 1961	c4.5 to 6.8	Kelsall, 1966 pers. corr.
		10% less	Hall & Kelson, 1959		
R. t. caribou	182	25% less	Seton, 1953		
		10% less	Hall & Kelson, 1959		
Cervus canadensis	409	30% less	Burt, 1952	13 to [illegible]	Green, 1933 Blood & Lovaas, 1966
Alces americana	591	10-15% less	Seton, 1953	to 36	Seton, 1953

2. Observations on Odocoileus virginianus

Eleven white-tailed deer penned in a large paddock in Waterloo Park, Ontario (subspecies borealis) were studied extensively at various times of the year. I was able to take ample photographs of the gaits of bucks, does and fawns.

a. The Walk

i. Source of data - all filmed by the author.

Adult male with mature antlers - 15 sequences.* of 54 strides of 1233 frames. His shoulder height was 1.8m.

Yearling male with spike antlers - 3 sequences of 13 strides of 236 frames. His shoulder height was 0.95 m.

Several adult females - 38 sequences of 145 strides of 2857 frames. Their shoulder heights were about 0.95 m.

Several fawns 3-6 months old - 18 sequences of 50 strides of 967 frames.

Fawn 3 weeks old - 5 sequences of 9 strides of 155 frames.

ii. Description and Film Analysis

As it moves from bush to bush, while browsing, or walks from one area to another, Odocoileus must be constantly on the alert for danger, relying as much on its hearing and sense of smell as on its sight. It must be ready to stop moving at an instant to try to identify strange noises and to dash off if the noises indicate real danger; it must place each hoof down as quietly as possible to prevent attention

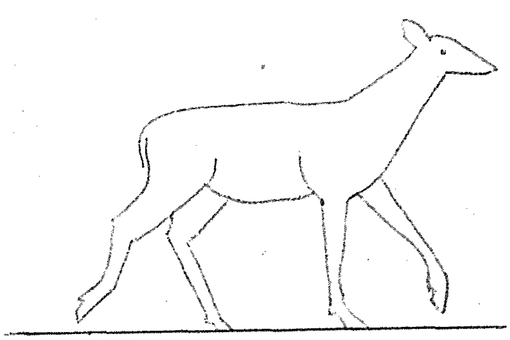
*A sequence is a length of film taken at one time of from one half to ten strides of an animal.

being drawn to itself and to prevent the masking of other sounds. An apprehensive white-tail that senses danger looks as if it is walking on eggs. Its strides are mincing. Each hoof points downward as it slowly approaches the earth; as it reaches the ground it pushes aside twigs that might snap or leaves that might rustle, instead of stepping on them. As the hoof is neatly lifted again the litter settles back into place leaving little or no trace of the animal's passage.

As the deer walks, its hind foot fits nearly into the imprint left by the forefoot on the same side, ensuring firm footing and a minimum of noise. It does so just after the forefoot is raised, so that an observer wonders if the hind foot might not sometimes strike the forefoot. A deer is therefore only briefly supported by lateral legs, but it is supported by diagonal legs for relatively long periods (fig. 5). It can balance this way while listening for danger. The slender legs are lifted high during the walk, even when no branches or grass need be avoided, so that the general impression of the gait is one of precision and daintiness.

Figure 5

Odocoileus using Diagonal Supports in a Walk



The results of the analysis are shown in Table 5 where the average percentage times spent on each of the combinations of legs are given. The walk patterns are similar for the three adult groups (χ^2 test, p= $>$ .02) so that these are averaged together. The data for the fawns are highly significantly different from those of the adults (χ^2 test, p= $<$ .01). The extensive use of the diagonal legs mentioned earlier is obvious from the data.

The variability[1] in the pattern of an individual walking on smooth earth can be assessed by examining the differences in the strides of one individual. For three photographed sequences of the animal's walk executed at identical speeds, each of which is the average of at least three strides, the time spent on a combination of supporting legs varies by as much as six percent. This underlines the importance of accumulating as many data as possible on which to base a species' pattern of walk.

The causes of such variability are numerous - slightly uneven terrain, the animal's mood, stiffness in an animal, a sound which may make an individual pause for a fraction of an instant or the bite of an insect which may disrupt the animal's movements. As well, variations in "reading" the supporting legs in each photographic frame are inevitable since, although the animal may be walking smoothly, its movements are only recorded at fixed intervals. These variations will average out over a large number of frames.

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[1]This same sort of variability is of course present in all subsequent data and will not be discussed again.

Table 5[1]

Time Spent on Combinations of Supporting Legs of Walking White-tailed Deer in Waterloo Park, Ontario

Kind of Deer	Two Legs		Three Legs		Four legs down	Total	Number of strides averaged
	Lateral legs	Diagonal legs	One hind leg off	One front leg off			
Adult male							
Frames observed	69	189	497	478	0	1233	54
Percentage of stride	6	15	40	39	0	100	
Yearling male							
Frames observed	20	50	82	84	0	236	13
Percentage of stride	8	21	35	36	0	100	
Does							
Frames observed	135	531	1070	1113	7	2856	145
Percentage of stride	5	19	37	39	0	100	
Fawns 3-6 mos.							
Frames observed	11	181	394	366	15	967	50
Percentage of stride	1	19	41	38	1	100	
Fawn 3 wks.							
Frames observed	1	31	57	65	1	155	9
Percentage of stride	1	20	36	42	1	100	
Percentage average of all adults	5	18	38	39	0	100	212

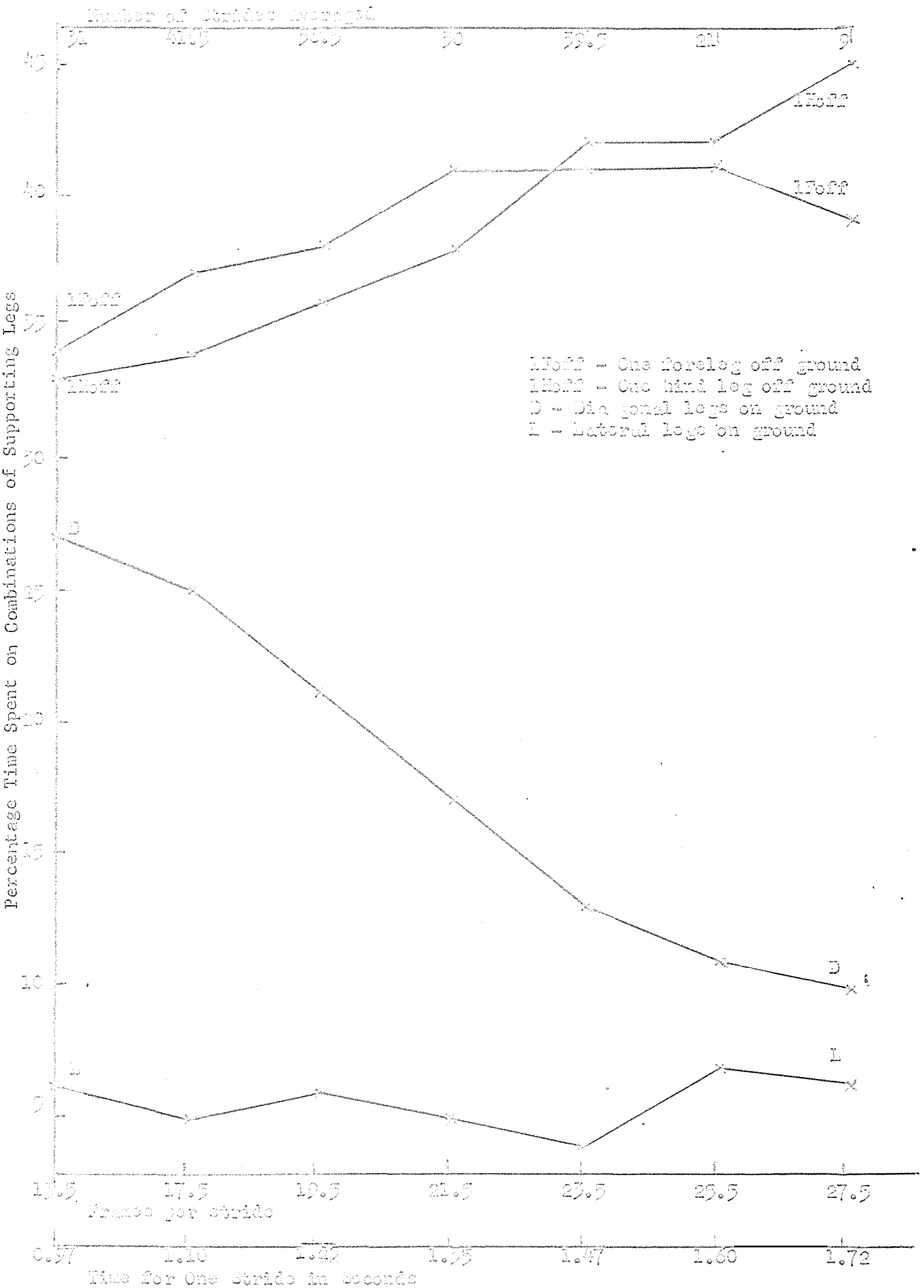
[1]Hildebrand (1965, 1966) has evolved an ingenious formula to describe the walk of any quadruped that gives the two main features of this gait; the percentage of the stride that each foot is on the ground and the percentage of the stride that the front footfall follows the hind footfall on the same side of the animal. With these data the walks of diverse quadrupeds can be illustrated on a graph in an illuminating manner. This formula assumes that the contact periods of the forefeet are the same as those of the hind feet. They are usually similar and if they are not a more complicated diagram may be compiled to portray the differences. However, in this study of a limited number of relatively closely related species, where large numbers of photographic sequences instead of one or two are analyzed, the walks can be compared in greater detail when the relative amounts of time spent on each combination of supporting legs are calculated. The gait formula for the average walk pattern of each species is given in Appendix B.

The data are used to test the effect of speed on the walk pattern. The percentage time spent on each of the supporting leg combinations is plotted, using the various sequences in which the animals walk at different speeds. This was first done separately for bucks, does and three-to-six month fawns to test the possible effect of age and sex on the relation between the speed and the walking gait. These three graphs were very similar, and also comparable to the comprehensive graph (fig. 6) for all adult deer, grouping the data for males and females where the number of strides for any one speed was two or more. Thus the effect of speed on the walking gait is independent of the age or sex of the animals.

From figure 6 it may be seen that at increased speed deer use two supporting legs more, and three supporting legs less, as one would expect. The use of lateral legs does not change with speed, since the hind foot steps into the spot that the forefoot is leaving. However the use of the diagonal legs increases greatly with speed, from 10% to over 25% of the time of the stride. The walk pattern at the fastest speed is highly significantly different than that at the slowest speed (χ^2 test, p= $<$.01). No change in the pattern of the walk at different speeds has been recorded in the literature before. This emphasizes again the need for as many data as possible on which to formulate the walk pattern of a species.

From the preceding paragraph it is evident that the walk pattern is not definitive but depends to some extent on the speed at which the strides are executed. If most of the strides are executed at a moderate pace and few are executed at very fast or very slow speeds, the walk

Figure 6 Walking Patterns of White-tailed Deer at Varying Speeds



pattern will be relatively stable; for example the large use of diagonal legs at fast speeds will tend to balance out the limited use of diagonals at slow speeds. The number of strides executed at each speed is given on figure 6. From these values, collected from strides photographed at random, it is seen that the deer use a variety of speeds and none significantly more than another.

The times taken for one walking stride are similar for the bucks and does. The average for these adults is 1.34 seconds (range = 0.94 to 2.06 second, N sequences = 56). That for 3-6 month fawns is 1.23 seconds (range 0.94 to 1.44 seconds, N sequences = 18). That for the 3-week fawn is 1.13 seconds (range 0.81 to 1.56 seconds, N sequences = 5).

b. The Trot

i. Source of Data

One sequence of 4 strides of 40 frames of a four-month old fawn filmed by the author at Waterloo Park.

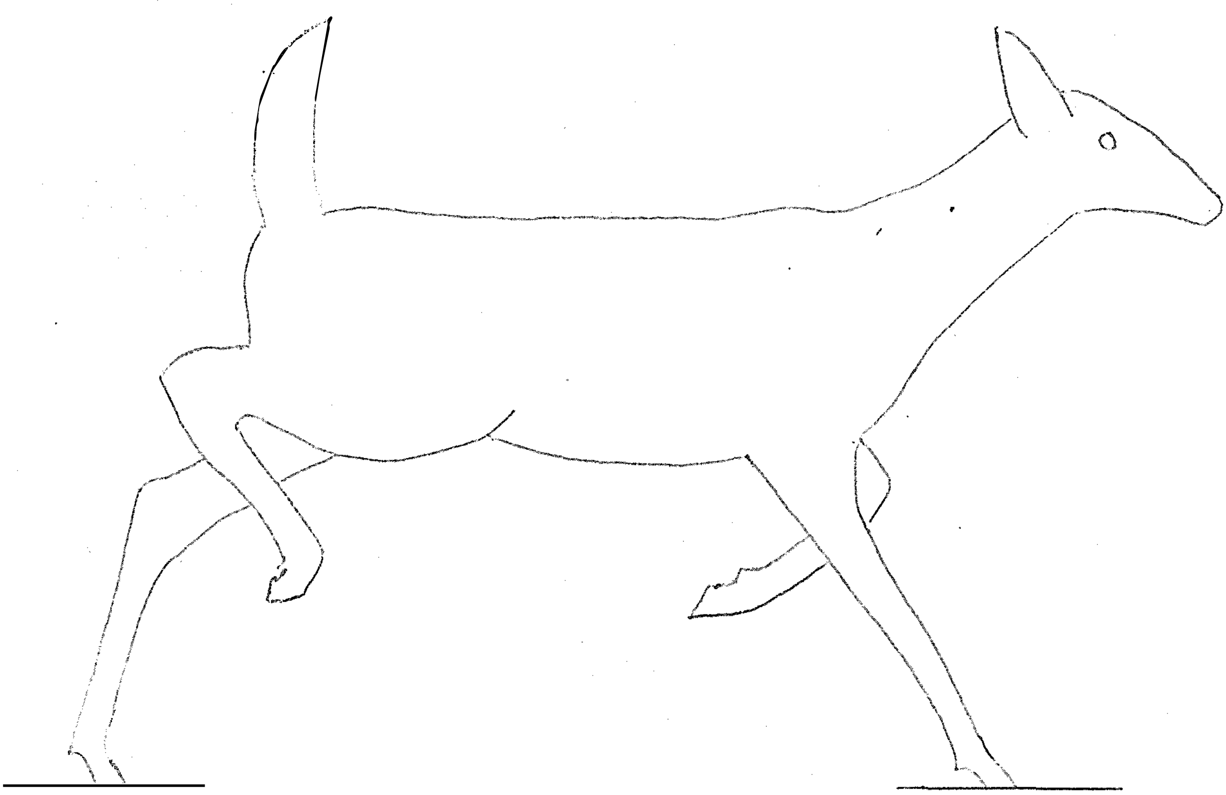
One sequence of 3 strides of 48 frames from "The Deer Family of North America."

ii. Description and Film Analysis

Considering the prominence in the use of the diagonal legs in the walk of the white-tailed deer, it is not surprising that these animals trot rather than pace. They resort to this gait infrequently, usually walking if relaxed or galloping if alarmed. Many running deer carry their tails up so that other individuals can more easily keep track of this "flag". The head and ears are also held erect, since the animal continues to be alert for danger (fig. 7). The hind foot is placed in front of the imprint left by the forefoot - the farther forward the faster the gait. The hind legs swing forward outside the front legs. This overlapping is especially noticeable in the bouyant trot of the long-legged fawns.

Figure 7

A White-Tailed Doe Trotting - after Rue, 1962.



The trotting strides of the fawn range from 0.56 to 0.69 seconds. During an average stride the fawn spends 77% of the time on diagonal legs, 3% with only one hind leg off the ground, 5% with only one foreleg off the ground and 15% with all four legs on the ground.

c. The Gallop

i. Source of Data

Eight sequences of 29 strides of 725 frames of antlerless deer galloping in fairly open fields covered with several inches of drifting snow. The films were taken from an airplane by the Michigan Department of Conservation.

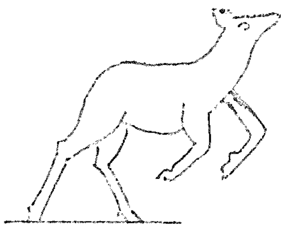
ii. Description and Film Analysis

If possible, a white-tailed deer will skulk away from danger so as not to draw attention to its presence; if not, an individual will gallop off, usually with its tail up, flashing white. Generally it does not have to run far before it loses its pursuers in the undergrowth. The deer sometimes has all its feet off the ground after pushing off with a forefoot in a flexed suspension as does a galloping horse (figure 8), but it nearly always has a period of extended suspension following the push-off with a hind leg as a horse does not. The extended suspension is illustrated in figure 9. Only relatively light quadrupeds can sustain such a suspension during each gallop-stride. It is during this part of its gallop that a deer can clear an eight foot fence, glance behind it or leap across a twenty-five foot stream (Severinghaus & Cheatum, 1956). The height of these bounds is greatly decreased if the deer is running full out on flat ground where there are no obstacles in its way.

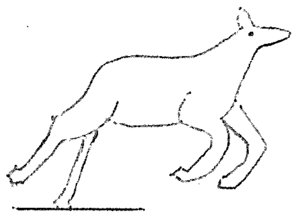
The results are listed in Table 6. The descriptions of the different terms used in the first column of the table are illustrated in figure 8. The importance of the extended suspension can be seen from the values

Figure 8

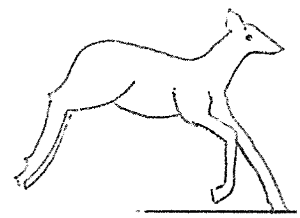
The Gallop of a White-Tailed Deer - successive photographs taken at 16 f.p.s. (Stride lasted 0.5 seconds).



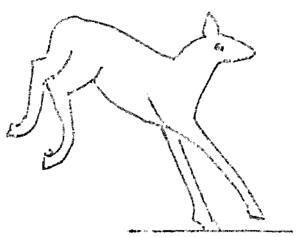
1. Both hind legs support deer



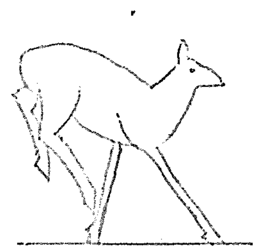
2. Lead hind leg supports deer



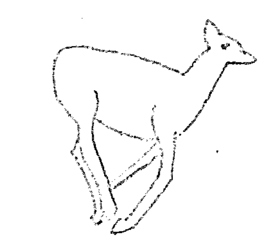
3. First foreleg down



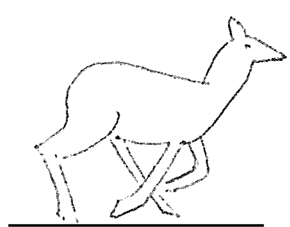
4. First foreleg down



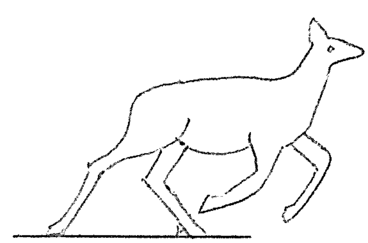
5. Both forelegs down



6. Flexed suspension



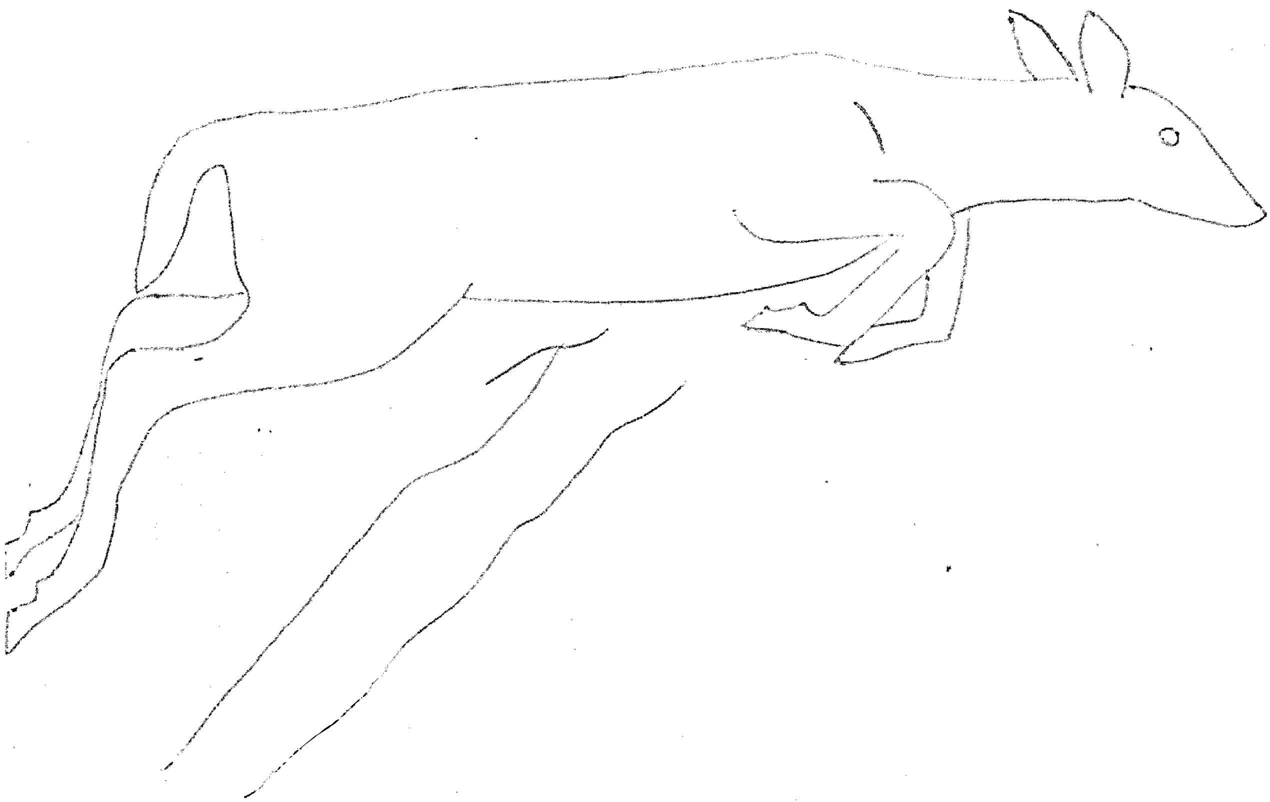
7. First hind leg down



8. Both hind legs down

Figure 9

A White-Tailed Doe in Extended Suspension during the Gallop - after Rue, 1962.



Note: The forelegs are well forward preparatory to landing and close to the head to decrease air resistance. The head is stretched forward which in turn brings the centre of gravity of the animal forward. This helps increase the length of this bound.

in the final column of Table 6. Up to 55% of the time of a stride is spent in a period of extended suspension. The four changes of leads present in these strides occur only during this suspension; since both front and hind legs are virtually parallel it is as easy to land on one foreleg as on the other.

Table 6

Analysis of 29 galloping strides of white-tailed deer. 64 f.p.s.

Combinations of supporting legs not in the order in which they occur.	Average time per stride in seconds.	Range of times - in secs.	Average percentage time of stride.
One foreleg on ground	.051	.016-.141	14
Both forelegs on ground	.059	.016-.125	16
Lead foreleg on ground	.017	0-.047	5
Flexed suspension	.034	0-.125	9
One hind leg on ground	.009	0-.047	2
Both hind legs on ground	.095	0-.141	25
Lead hind leg on ground	.016	0-.047	4
Extended suspension	.080	0-.281	21
Fore and Hind legs - two	.008	0-.031	2
Fore and Hind legs - three	.008	0-.031	2
Total	.377	.30-.51	100

There is no correlation between the gallop pattern and the speed of a stride, nor is more time spent on the push-off hind leg before the long suspensions than before the short ones. More time is spent on the forelegs than on the hind legs, with the non-lead foreleg supporting the deer for longer than any other leg. Three legs support the deer rarely - only when there is no flexed suspension - indicating that the animals are galloping quickly. The foot impacts follow each other in a rotary sequence.

3. Observations on Odocoileus hemionus

a. The Walk

i. Source of Data

Seven sequences of 18 strides of 349 frames filmed by the author at Assiniboine Park Zoo, Winnipeg.

Six sequences of 11 strides of 329 frames filmed by V. Geist.

Three sequences of 17 strides of 253 frames from "The Vanishing Prairie"

ii. Description and Film Analysis

The walk of this species appears similar to that of the white-tailed deer. A mule deer that is apprehensive of danger uses a stiff-legged walk. This movement probably signals its fears to nearby deer, and the short steps are suitable in case, suddenly spotting a predator, it wants to escape in a rush.

The analysis of the walking patterns of these deer are given in Table 7. The walk patterns of the male and females are similar (χ^2 test, $p > .30$) so these patterns are averaged together. The data for the newborn fawn in Table 7 are taken from one sequence of only one animal, but it is interesting to note that a deer only a day or two old is able to support itself for half the stride on two diagonal legs.

The pattern of the walk was calculated at different speeds with the limited data available. The resultant graph shows that, as for the white-tailed deer, the mule deer spends more time on three legs and less on diagonal legs as it walks more slowly. The use of lateral legs is independent of the speed. The walk pattern at the fastest speed is highly significantly different than that at the slowest speed

Table 7

Time Spent on Combinations of Supporting Legs of Walking Mule Deer.

Kind of deer	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs down	Total	Number of strides averaged
Adult males with full antlers							
Frames observed	27	84	178	187	1	477	20
Percentage of stride	6	18	37	39	0	100	
Adult females							
Frames observed	21	86	127	150	0	384	12
Percentage of stride	5	23	33	39	0	100	
Newborn fawn							
Frames observed	4	34	14	18	0	70	3
Percentage of stride	6	48	20	26	0	100	
Percentage average of all adults	6	20	35	39	0		32

(χ^2 test, p= $<$.01).

The times for one walking stride are similar for the does and buck. They average 1.31 seconds, with a range of 0.75 to 1.83 seconds (N sequences = 13).

b. The Trot

i. Source of Data

Three sequences of 13 strides of 121 frames of adult mule deer filmed by the author at Assiniboine Park Zoo, Winnipeg.

ii. Description and Film Analysis

The mule deer possesses a springy trot similar to that of the white-tailed deer. The mule deer fawn trots in the same manner as the white-tailed fawn, with the hind legs moving well forward and outside of the forelegs.

These adult mule deer are supported an average of 86% of each stride on diagonal legs, 6% with one foreleg off, 1% with four legs on the ground, 2% with only one hind leg on and 2% with only one foreleg on the ground. Three percent of an average stride is spent in a period of suspension, despite Linsdale and Tomich's (1953) contention that trotting mule deer never have all feet off the ground at once.

These trotting strides range from 0.44 seconds to 0.63 seconds. (average 0.56, N sequences = 13).

c. Gallop

i. Source of Data

Five sequences of 10 strides of 67 frames of a mule deer at Assiniboine Park Zoo filmed by the author.

One sequence of a baby fawn filmed by the author at the same zoo.

ii. Description and Film Analysis

The results of the analysis of galloping strides are given in Table 8. The sequence of footfalls is rotary. These galloping strides, which were fairly slow, include periods of extended suspensions but not of flexed suspensions.

Both Muybridge (1899) and Hildebrand (1959) anticipated the possibility of a suspension between the impacts of the front feet, something which would only be possible in a light quadruped traveling quickly. This has been observed in a sequence of a galloping fawn (not included in Table 8). There are two periods of suspension, none following a push-off with a hind foot, but one following that of one forefoot and one following that of the other.

Table 8

Analysis of Five Galloping Strides of Mule Deer. 16 f.p.s.

Combinations of supporting legs not in the order in which they occur	Average time per stride - in seconds	Range of times - in seconds	Average percentage time of stride	
One foreleg on ground	.06	0-.13	15)	
Both forelegs on ground	.04	0-.06	11)	35%
Lead foreleg on ground	.04	0-.13	9)	
Flexed suspension	0	0	0	
One hind leg on ground	.01	0-.06	2)	
Both hind legs on ground	.06	0-.13	15)	28%
Lead hind leg on ground	.04	0-.13	11)	
Extended suspension	.06	0-.13	15	
Fore and hind legs - two	.03	0-.06	7	
Fore and hind legs - three	.05	0-.19	13	
Fore and hind legs - four	.01	0-.06	2	
	.40	.31-.50	100	

d. Bound

i. Source of Data

Two sequences of 5 strides of 59 frames of a female mule deer bounding down and then up the sides of a steep valley. From "The Vanishing Prairie."

ii. Description and Film Analysis

This gait is a very useful one as it enables an animal to navigate in steep and broken country with ease. In such areas there may not be enough flat open space for the feet to land and push off as in a regular gallop, but there is room for a deer's four feet to descend in a bunch more or less perpendicularly to the ground. The hooves land nearly simultaneously, often the front legs touching the ground slightly before the hind legs. The spreading toes and the dewclaws absorb the initial impact. Then the hocks bend and the animal springs upward again, forefeet first, with the forelegs and the hind legs each stiff and close to each other. The mule deer can cover seven meters between impacts and jump up to two and a half meters vertically, - a useful feature in dense cover that allows the deer to glance back to see its pursuer as well as to clear most obstacles (Cahalane, 1947).

This gait is also useful in enabling the mule deer to dodge and twist around rocks and logs; since all the hooves land grouped together it is easy for the animal to change direction between one stride and the next. Sometimes a startled individual gives short leaps, landing with a thump each stride as if warning other deer of danger by the noise (Linsdale & Tomich, 1953).

The data on the bounding strides (Table 9) show that over half the time is spent in the air (with considerable variation among strides) and that one-fifth of the time is spent in pushing off with the two hind legs. (Most descriptions of the take-off state that all four feet leave the ground together). Usually the suspension of a quadruped following a push-off with the hind feet is accomplished with the fore and hind legs spread fore and aft in the air; here following such a push-off the legs remain close together.

Table 9

Analysis of Four Strides of One Bounding Mule Deer, taken at an unrecorded camera speed.

Combinations of supporting legs in the order in which they occur	Average number of frames per stride	Range of frames per stride	Average percentage of time of stride
Suspension	7.0	3 - 13	55%
Four legs	3.5	3 - 4	27%
Two hind legs	2.3	1 - 4	18%

4. Observations on Rangifer tarandus groenlandicus

a. The Walk

i. Source of Data

Nineteen sequences of 41 strides of 1214 frames from "The Behaviour of the Barren-Ground Caribou."

Fourteen sequences of 55 strides of 1502 frames from "Caribou Mystery."

Ten sequences of 21 strides of 454 frames from "The Deer Family of North America."

Eight sequences of 14 strides of 324 frames from "On the Edge of the Barrens."

Four sequences of 8 strides of 276 frames from "The Caribou Hunters."

One sequence of 1 stride of 18 frames filmed by L. Linnard.

These films were taken on the barren grounds of Canada where the terrain is often rougher than that found in zoos. The films were mostly taken at camera speeds reported as 24 f.p.s. Moving picture cameras tend to slow down in the cold temperatures of the north however, so that the speed is uncertain below 25°F (N.F.B., pers. comm., 1966). It may fall as low as 20 f.p.s., unknown to the photographer (Geist, pers. comm., 1966). For this reason it has not been possible to analyze the pattern of the walks at different speeds.

ii. Description and Film Analysis

No especial characteristic distinguished the walk of this species from that of Odocoileus. The walk patterns for the barren-ground caribou are given in Table 10. Those of the fawns and of the yearlings are very similar (χ^2 test, p=> 0.95). These patterns grouped together are very similar to the walk pattern of adults with small or no antlers (χ^2 test, p=>.50). The walk pattern of caribou with antlers between 30 and 60 cms in length and that of caribou with antlers over 60 cms are very similar (χ^2 test, p= .80). The data for these two antlered groups are grouped together. This grouping is highly significantly different from that of caribou with antlers less than 30 cms long or with no antlers at all (χ^2 test, p=<.01). The decreased use of two supporting legs in those caribou with large antlers is therefore correlated with the presence of these antlers.

In all the caribou the time spent with only one foreleg off the ground is at least 4% greater than that with only one hind leg off. Since both front and hind legs move forward the same distance during a stride, the foreleg must move more slowly or be lifted higher.

The average time of a walking stride of fawns and yearlings is 1.08 seconds (range 0.88 to 1.38, N sequences = 9). That of all the adults is 1.25 seconds (range 1.00 to 1.83, N sequences = 25).

Table 10

Time Spent on Combinations of Supporting Legs of Walking Barren-Ground Caribou on Tundra Areas.

Kind of Caribou	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs down	Total	Number of strides averaged
Adult - antlers over 60 cms							
Frames observed	49	192	321	370	0	932	30
Percentage of stride	5	21	34	40	0	100	
Adult - antlers 30-60 cms							
Frames observed	84	294	467	541	2	1388	50
Percentage of stride	6	21	34	39	0	100	
Adult - antlers under 30 cms							
Frames observed	79	207	233	264	0	783	33
Percentage of stride	10	26	30	34	0	100	
Yearlings							
Frames observed	28	79	103	119	1	330	13
Percentage of stride	9	24	31	36	0	100	
Fawns							
Frames observed	30	87	102	126	1	346	14
Percentage of stride	9	25	30	36	0	100	
Percentage average of all adults	7	22	33	38	0		113

b. The Trot

i. Source of Data

Eleven sequences of 48 strides of 666 frames from "Caribou Mystery."

Four sequences of 8 strides of 129 frames from "The Behaviour of the Barren-Ground Caribou."

Three sequences of 13 strides of 175 frames from "The Deer Family of North America."

Two sequences of 2 strides of 25 frames from "On the Edge of the Barrens."

ii. Description and Film Analysis

Caribou have a long striding trot that enables them to cover long distances without tiring. The legs are lifted high as they are swung forward and the nose is held forward so that the antlers sweep backwards over the shoulders. The hind legs usually over-reach the forelegs on the outside, touching the ground slightly ahead of the place the forelegs left a fraction of a second earlier.

The use of supporting legs varies considerably in different sequences but for an average stride of antlered adults (N = 43) diagonals support the caribou 83% of the time of a stride, three legs with one hind leg off 1%, three legs with one fore off 5%, all four legs on 1% and one hind leg alone 3%. The animal is suspended 7% of the stride and for up to 0.12 seconds.

In one group of caribou trotting the strides of a six month old fawn (N strides = 31) took 80% as much time as those of the adults (N = 43). As the height of these young was less than 80% that of the adults, their gait was even springier than that of the adults.

The range of times for a trotting stride of adults is 0.54 to 0.83 seconds (average 0.69, N sequences = 50) and for yearlings from 0.50 to 0.75 seconds (average 0.61, N sequences = 6).

c. The Gallop

i. Source of Data

Four sequences of 20 strides of 224 frames from "Caribou Mystery."

One sequence of 1 stride of 10 frames from "The Behaviour of the Barren-Ground Caribou."

One sequence of 2 strides of 24 frames from "On the Edge of the Barrens."

ii. Description and Film Analysis

A caribou looks ungainly when it gallops because of the large hooves on its slender legs. It does not bound into the air while galloping as a white-tailed deer often does, unless it must to navigate in deep snow.

The analysis of the gallop strides is given in Table 11. The pattern of the young and adult caribou are grouped together, since these are similar. In these strides the flexed suspension is used more than the extended suspension. The adult strides include three transverse and seven rotational series of impacts; those of calves have three transverse and one rotational strides. Changes in stride are to be expected when the caribou are galloping over uneven tundra.

Table 11

Analysis of 21 Strides of Galloping Barren Ground Caribou. 24 f.p.s.

Combinations of supporting legs not in the order in which they occur	Average time for a stride - in secs.	Range of times - in seconds	Average percentage of time of stride	
One foreleg on ground	.004	0-.042	1)	
Both forelegs on ground	.058	0-.167	12)	32%
Lead foreleg on ground	.087	0-.208	19)	
Flexed suspension	.004	0-.125	9	
One hind leg on ground	.003	0-.083	5)	
Both hind legs on ground	.089	0-.250	19)	26%
Lead hind leg on ground	.007	0-.083	2)	
Extended suspension	.004	0-.083	1	
Fore and hind leg(s) on ground				
Two legs	.035	0-.083	6)	
Three legs	.113	0-.167	24)	32%
Four legs	.007	0-.042	2)	

Gallop strides of adults last from 0.42 to 0.63 seconds (N strides = 15) and of young from 0.38 to 0.50 seconds (N = 7).

d. Excitation Jump

i. Source of Data

Two sequences from "The Behaviour of the Barren-Ground Caribou."

Two sequences from "Caribou Mystery."

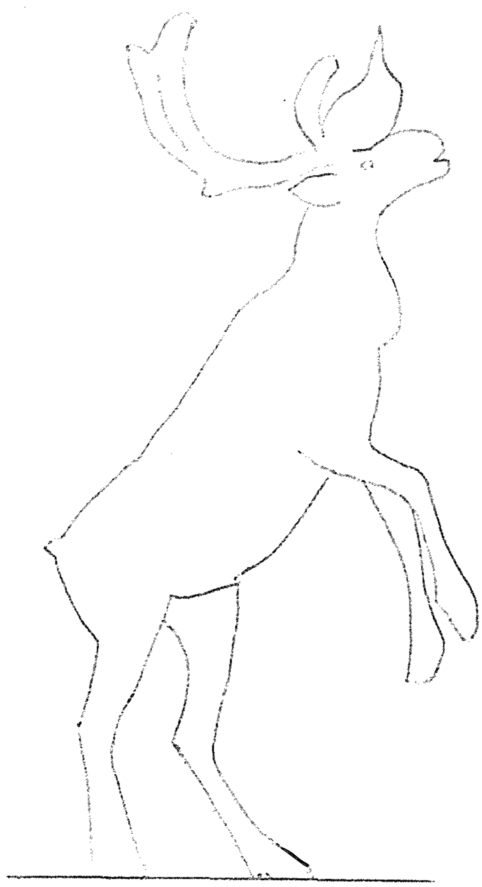
ii. Description and Film Analysis

In three of the sequences, all taken in summer, three adults stood facing the camera, two of them bulls with very large antlers. In each case the animal turned away and within several yards gave a leap into the air, pushing off with both hind feet more or less simultaneously. Although each seemed about to give a true bound into the air as he took off, (fig. 10) his trunk and head remained facing upward and forward in the air while his hind legs swung under him in preparation for the landing. The hind legs hit the ground together, following which the forequarters swung down and forward. In each case the gallop changed to a trot within several yards. During their jumps the three adults remained in the air 0.21, 0.21 and 0.29 seconds. Within one-fifth of a second one of the animal's forelegs was on the ground following the initial contact of the hind feet.

When rising onto its hind hooves the toes spread apart because of the weight of the animal and fluid from the interdigital glands between the hooves falls onto the ground (Dugmore, 1913). A scent then remains to alarm other caribou at the spot long after the original animal has trotted away. The interdigital glands of the caribou are more highly developed in the hind than in the forehooves while those

Figure 10

Stance of the Barren Ground Caribou Immediately Prior to the Excitation Jump. - after Pruitt, 1960.



in the white-tailed deer, in which such behaviour as the excitation jump has not been recorded[1], are more or less atrophied (Quay, 1955, 1959). The histology of the glands of male and female caribou are similar, although a buck usually performs the jump (Pruitt, 1960).

[1]Rarely a white-tailed deer when startled may give one tremendous leap into the air as if to get its bearings from an elevation before it rushes off. This has been called a spy-hop (Seton, 1953).

5. Observations on Rangifer tarandus caribou

a. The Walk

i. Source of Data

Eight sequences of 17 strides of 811 frames from "Survival Perilous."

One sequence of 8 strides of 300 frames from W. Carrick.

All of these sequences were taken in summer, of adults with small or no antlers. In seven of them the caribou were walking in several inches of water or in mud.

ii. Description and Film Analysis

The walk resembles that of the barren ground caribou. When the woodland caribou must thread its way over logs and around rocks it moves carefully, balancing on diagonal legs or on three legs while lifting the other legs high.

The pattern of the walk of the woodland caribou is given in Table 12. The table shows an extensive use of diagonal supporting legs which is to be expected in animals walking in watery or muddy terrain.

Table 12

Time Spent on Combinations of Supporting Legs of Woodland Caribou Walking in Rough Terrain

Woodland Caribou	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs down	Total	Number of strides averaged
Adults with small or no antlers							
Frames observed	66	247	285	213	0	811	17
Percentage of stride	8	31	35	26	0	100	

In a sequence not included in Table 12 in which an adult is walking in particularly difficult circumstances - in shallow water among numerous logs - the diagonal legs support the animal only 3% of the time and the lateral legs only half that much (N strides = 8); three legs to support it 93% of the time and four legs 2% of the time, so that its walk is very stable but also very slow.

b. The Trot

No sequences of trotting woodland caribou were available. This is not surprising as few of these animals live in zoos and it is difficult to photograph wild individuals in the denseness of the boreal forests.

c. The Gallop

i. Source of Data

Two sequences of 5 strides of 63 frames from "Survival Perilous."

ii. Description and Film Analysis

In both sequences the strides resemble bounds, with the caribou navigating over logs and through either grass or water.

The gallop strides of a young adult bounding among logs reflects the caribou's nimbleness. For half of a stride the animal was supported only by its forefeet and for the other half only by its hind feet. It was never supported by front and hind legs at one time.

The two strides of a newborn fawn showed much more caution, although they lasted the same amount of time. The fawn was supported by both front and hind legs 50% of the time and by front legs only and hind legs only each 25% of the stride. There were no periods of suspension in any of these galloping strides.

6. Observations on Alces americana

a. The Walk

i. Source of Data

Fifteen sequences of 34 strides of 1720 frames filmed by V. Geist.

Four sequences of 7 strides of 174 frames filmed by the author at Assiniboine Park Zoo, Winnipeg.

Three sequences of 4 strides of 130 frames from "Expedition Moose."

Two sequences of 1 stride of 91 frames from "The Deer Family of North America."

ii. Description and Film Analysis

The walk of the moose is generally slow and stately. In deep water or snow they draw their legs straight upward out of the substrate before beginning to swing them forward.

The footage includes pictures of moose walking on various terrains, some on flat ground, some in shallow water or snow and some in deep water or snow. The walk patterns are given in Table 13. The pattern for moose walking on flat ground is highly significantly different from those for moose walking in shallow or deep snow or water (χ^2 test, p = $<$.01). The patterns for moose walking in shallow as against deep water or snow are similar (χ^2 test, p = $>$.02).

Table 13

Time Spent on Combinations of Supporting Legs for Moose Walking on Varied Terrain.

Adult moose, with or without antlers	Lateral legs	Diagonal legs	One hind leg off	One fore-leg off	Four legs on	Total	No. of strides aver-aged
On flat ground							
Frames observed	78	101	336	293	9	817	20
Percentage of stride	10	12	41	36	1	100	
In snow or water to 30 cms deep							
Frames observed	37	182	189	209	0	617	13
Percentage of stride	6	29	31	34	0	100	
In snow or water over 30 cms deep							
Frames observed	44	249	194	193	1	681	13
Percentage of stride	7	37	28	28	0	100	

The walk pattern on flat ground for those moose with large antlers is compared with that of those with small or no antlers in Table 14. They are highly significantly different (χ^2 test, p = $<$.01), the moose with large antlers using diagonal supporting legs for much shorter periods of time.

Table 14

Time Spent on Combinations of Supporting Legs for Moose with Large Antlers and with Small or no Antlers.

Moose	Lateral legs	Diagonal legs	One hind leg off	One fore-leg off	Four legs on	Total	No. of strides averaged
Small or no antlers							
Frames observed	17	41	73	59	0	190	6
Percentage of stride	9	22	38	31	0	100	
Large antlers							
Frames observed	39	32	162	148	7	388	9
Percentage of stride	10	8	42	38	2	100	

When the patterns are calculated for adult moose on flat ground walking at various speeds, it is found that three legs are used more and diagonal legs less at slower speeds. This is shown in figure 11. The walk pattern at the fastest speed is highly significantly different than that at the slowest speed (χ^2 test, $p = < .01$).

The average time for one walking stride for moose on flat ground is 1.80 seconds (range 1.38 to 2.50, N sequences = 7). The average time is 2.40 seconds (range 1.75 to 3.58, N = 6) for moose walking in snow or water 15 to 30 cms deep and 2.34 seconds (range 1.79 to 3.29, N = 6) for moose walking in snow or water over 50 cms deep. The times are similar for the moose walking in shallow and deep snow or water (Student's t test, $p = > 0.1$). They are very significantly different for moose walking in either depth of water or snow as opposed to moose walking on flat ground (Student's t test, $p = < .001$). Using the limited data for moose walking on flat ground the average time for a stride is found to be slower for a male (1.85 second, N = 3) than a female (1.54 second, N = 2) but not significantly so.

a. The Trot

i. Source of Data

Ten sequences of 35 strides of 830 frames filmed by V. Geist

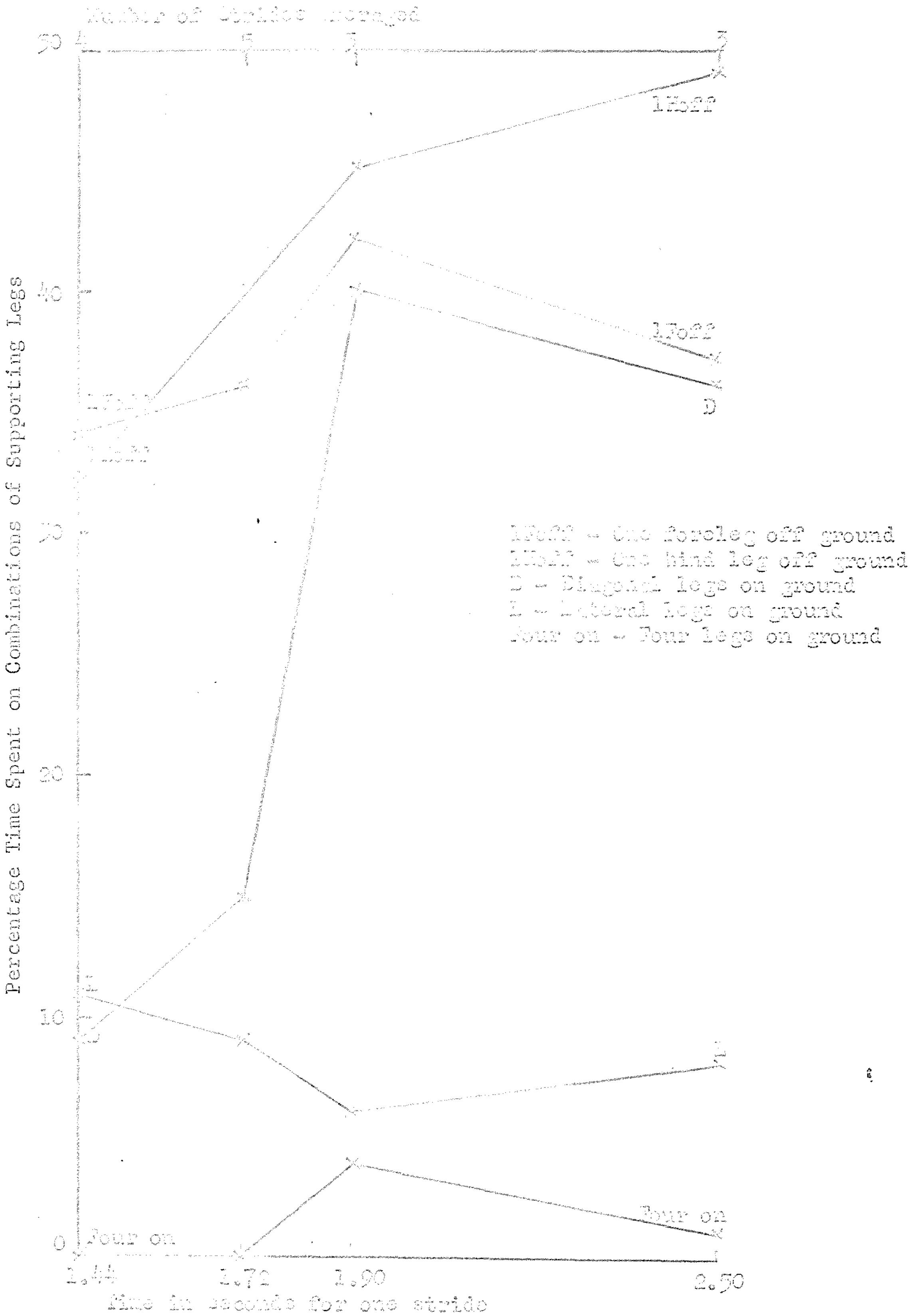
Two sequences of 6 strides of 218 frames from "The Deer Family of North America."

One sequence from "Expedition Moose"

ii. Description and Film Analysis

The trot of the moose is a springy gait. In one sequence in "Expedition Moose" in which a moose trotted out of the water the gait seemed to have periods of suspension although it was impossible to be

Figure 11 Walking Patterns of Moose at Varying Speeds



sure because of the splashing water. The nose is held forward and the legs stretch well out before each step.

In the 13 strides in which the supporting feet of the moose can be clearly identified, the animals are supported by diagonal legs an average of 80% of the time of the stride, by three legs with one hind leg off 6%, by three legs with one foreleg off 13%, and by four legs 1%. None has a period of suspension.

The trotting strides of adults last from 0.79 to 1.38 seconds (average 1.02 seconds, N = 31); those of calves last 0.71 to 1.13 seconds (average 0.89 seconds, N = 5).

c. The Gallop

i. Source of Data

Three sequences of 6 strides of 295 frames of a galloping moose with no antlers. The film was taken from a plane by the Minnesota Department of Conservation.

ii. Description and Film Analysis

The moose's gallop is rather like that of a horse; there is no period of extended suspension.

The strides are analyzed in Table 15. All of the strides are executed in a rotary sequence. The longest suspension lasts about 0.14 seconds. The hind legs alone supported the moose slightly more than do the forelegs. The moose is supported by three legs only 9% of the time.

Table 15

Analysis of Six Galloping Strides of One Antlerless Moose 64 f.p.s.

Combinations of supporting legs not in the order in which they occur	Average time for a stride - in secs	Range of times - in secs	Average percentage of time of stride	
One foreleg on ground	0	0	0)	
Both forelegs on ground	.094	.031-.141	14)	35%
Lead foreleg on ground	.141	.063-.250	21)	
Flexed suspension	.037	0-.109	6	
One hind leg on ground	.069	.031-.125	11)	
Both hind legs on ground	.150	.109-.203	23)	38%
Lead hind leg on ground	.016	0-.078	4)	
Extended suspension	0	0	0	
Front and hind legs on ground - two legs	.080	.047-.094	12	
-three legs	.062	0-.047	9	
- four legs				
	.649	.516-.719	100	

7. Observations on Cervus canadensis

a. The Walk

i. Source of Data

Forty-three sequences of 131 strides of 2589[1] frames of the two elks in Waterloo Park filmed by the author

Eighteen sequences of 33 strides of 1009 frames from "The Olympic Elk"

Two sequences of 12 strides of 343 frames filmed in Assiniboine Park Zoo, Winnipeg

1 - One sequence of 66 frames of an elk of unknown sex was not used in Table 16.

Two sequences of 3 strides of 146 frames from "The Deer Family of North America."

One sequence of 1 stride of 40 frames filmed by the Michigan Department of Conservation

ii. Description and Film Analysis

A pair of young elk in Waterloo Park were filmed extensively during two successive seasons. The walk patterns of these individuals are given in Table 16, with the data so grouped that any changes due to body or antler size will be evident.

Table 16

Time Spent on Combinations of Supporting Legs for Two Elk in Waterloo Park

Elk	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs down	Total	Number of strides averaged
Female elk - 2 yrs.							
Frames observed	20	44	91	97	0	252	13
Percentage of stride	8	18	36	38	0	100	
Female elk - 3 yrs Sh. Ht. 129 cms							
Frames observed	159	287	349	388	0	1183	62
Percentage of stride	13	24	30	33	0	100	
Male elk - 2 yrs. spike antlers							
Frames observed	32	70	111	119	0	332	16
Percentage of stride	10	21	33	36	0	100	
Male elk - 3 yrs. small antlers Sh. Ht. 132 cms							
Frames observed	40	69	99	93	0	301	16
Percentage of stride	13	23	33	31	0	100	
Male elk - 3 yrs. large antlers							
Frames observed	56	107	135	157	0	455	21
Percentage of stride	12	24	30	34	0	100	

The three patterns of the male in Table 16 are similar (χ^2 test, $p = >.05$). The patterns of the male and female when they were two years old are similar (χ^2 test, $p = >.70$) as are those for these two animals when they were three years old (χ^2 test, $p = >.80$). However there is one unusual case; the pattern of the female at two years of age is highly significantly different from the pattern of the same female at three years of age (χ^2 test, $p = <.01$).

The walk patterns of elk from all film sources are included in Table 17. The walk patterns of adult Olympic elk without antlers are similar to those of the Olympic elk males with large antlers (χ^2 test, $p = >.30$). The pattern of the two Waterloo Park elk are highly significantly different from those of the Olympic elk (χ^2 test, $p = <.01$). Such a difference might have been expected as the Olympic elk are

Table 17

Time Spent on Combinations of Supporting Legs of Walking Elk

Animals	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs down	Total	Number of strides averaged
Waterloo Park male and female[1]							
Frames observed	273	513	669	728	0	2183	113
Percentage of stride	12	24	31	33	0	100	
Olympic elk males with large antlers							
Frames observed	51	137	240	222	6	656	24
Percentage of stride	8	21	36	34	1	100	
Olympic elk antlerless elk							
Frames observed	22	44	107	93	3	269	10
Percentage of stride	8	16	40	35	1	100	
All adult elk all sources - %	10	21	34	35	0	100	

1 - Excluding strides of female at two years of age

mostly older than those in Waterloo Park and the Olympic elk data are calculated from animals walking in their natural habitat which is less smooth than the ground in Waterloo Park.

The walk patterns for the elk in Waterloo Park are analyzed at different speeds and the results plotted in figure 12. The graph shows that the use of three supporting legs decreases at faster speeds while that of the diagonal legs increases drastically from 18 to 34% of the strides. The walk pattern at the fastest speed is highly significantly different than that at the slowest speed (χ^2 test, p =$\leqslant$.01). The limited Olympic elk data show these same trends.

One new-born calf with its umbilical cord still hanging walked so slowly and cautiously that it was never supported by only two legs; it balanced on three legs 82% of the time and on all four the rest of the time of the stride. These data are not included in the above tables.

The average speed of a walking stride for the female elk in Waterloo Park is 1.21 seconds (range 0.88 to 1.50, N sequences = 24). That of the male in Waterloo Park is 1.36 seconds (range 1.13 to 1.63, N sequences = 18). The female walked significantly faster than the male in these sequences (Student's t test, p =$\leqslant$.01).

b. The Trot

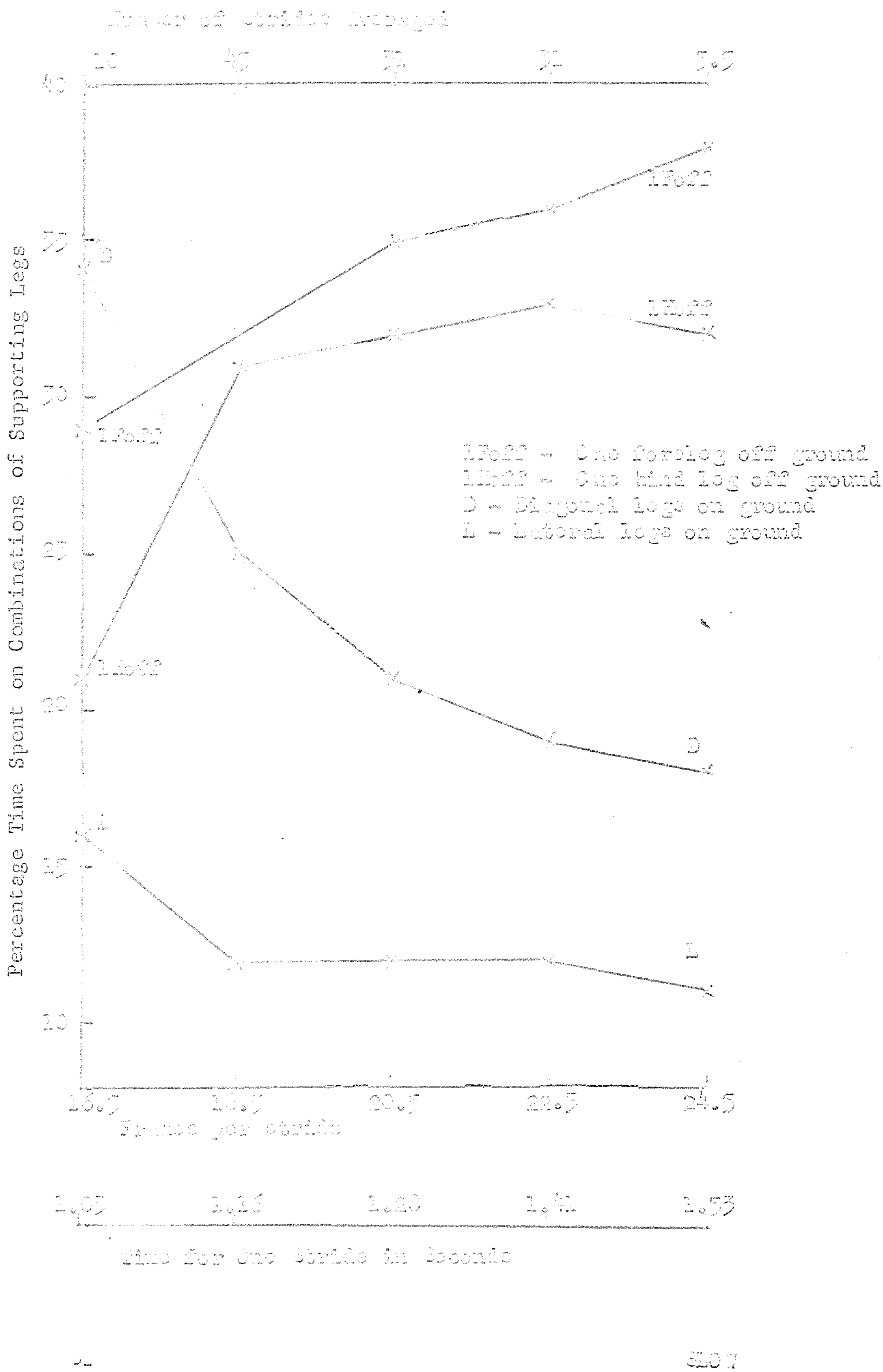
i. Source of Data

Eight sequences of 15 strides of 178 frames from "The Olympic Elk."

Seven sequences of 12 strides of 210 frames of the elk in Waterloo Park filmed by the author.

One sequence of 5 strides of 88 frames from "The Deer Family of North America."

Figure 10   Walking Patterns of Elk at Varying Speeds



ii. Description and Film Analysis

The elk has a flowing trot in which the head is held high with the muzzle stretched forward. The antlers sweep backward, sometimes almost touching the male's back.

The percentage of time spent on various supporting legs of an average stride (N strides = 15) is 75% on diagonal legs, 1% on lateral legs, 8% on three legs with one hind leg off, 12% on three legs with one fore off and 4% on all four legs. There are no periods of suspension in these strides, despite their springy appearance. The gait can include such suspensions however, as indicated by Muybridge (1957 - plate 154).

The time for a stride ranged between 0.63 and 0.75 seconds (average 0.70 seconds, N strides = 8) for the two elk in Waterloo Park.

c. The Gallop

i. Source of Data

Twelve sequences of 55 strides of 1494 frames filmed by the Michigan Department of Conservation of elk galloping on open rolling terrain.

Seven sequences of 9 strides of 113 frames from "The Olympic Elk."

ii. Description and Film Analysis

These animals commonly use both rotary (34 strides) and transverse (20 strides) series of impacts. Several elk execute both types in one sequence. For example, one gave three rotary, two transverse, two rotary, four transverse and then one rotary stride in that order. These changes are due in part to the elk's changes in lead, which occurred twice, during both types of suspension.

The gallop strides of the female elk were quite different from those of the bull, so they are analyzed separately. Those of the bull with large antlers (Table 18) are very symmetrical, with no period of suspension. The animal is always supported by either two or three feet.

Table 18

Analysis of Three Galloping Strides of One Male Elk with Large Antlers

Combination of supporting legs in the order in which they were used	Average time during one stride	Range of time	Percentage of time of stride	Totals
Two supports - lateral	.020	.016-.031	5	Laterals = 9%
Three supports - one fore off	.094	-	20	
Two supports - diagonal	.042	.031-.047	9	
Three supports - one hind off	.078	.063-.094	17	Diagonals = 17%
Two supports - lateral	.020	.016-.031	4	
Three supports - one fore off	.089	.078-.094	19	One fore off = 39%
Two supports - diagonal	.036	.031-.047	8	
Three supports - one hind off	.083	.078-.094	18	One hind off = 35%
	.463	.453-.469		

Those of the females are less symmetrical, with short periods of suspension (Table 19b.). They are supported by only one leg 45% of the time of the stride. Only three of the females' strides have extended suspensions. Two of these last .03 seconds each and the third lasts only half this time. Only one of these strides includes a flexed suspension.

The data are also analyzed to see if the patterns of the strides vary with the time of the flexed suspension in each stride. The strides are divided into four groups in which the number of frames during which there is a flexed suspension equalled none, one, two or three, as shown in Table 19a. With increased suspension times the use of three supporting

Table 19

Analysis of 52 Galloping Strides of Female Elk   64 f.p.s

19a Partial Analysis: Combinations of Supporting legs not in the order in which they occur	%age averages of frames where the number of frames of legs suspended and tucked in=				19b Total Analysis: Average time during one stride -in secs	Range of time - in secs	Percentage of time of stride
	0	1	2	3			
One foreleg on ground	7	1	3	0	.016	0-.109	4)
Both forelegs on ground	13	12	12	11	.052	0-.125	12) 39%
Lead foreleg on ground	22	24	23	22	.097	.047-.141	23)
Flexed suspension	0	4	7	11	.019	0-.047	5
One hind leg on ground	16	17	15	12	.064	0-.094	15)
Both hind legs on ground	19	12	16	12	.066	.016-.125	16) 34%
Lead hind leg on ground	7	0	2	0	.013	0-.094	3)
Extended suspension	1	0	0	0	.002	0-.031	0
Front and hind legs on ground - two	8	19	12	14	.049	0-.141	13
- three	7	11	10	18	.039	0-.109	9
Frames/stride	26	27	27	28	.417	.297-.484	100
No. of strides averaged	21	9	14	8			

legs increases and that of only forelegs or only hindlegs decreases.

The duration of each stride is also compared with the use of combinations of supporting legs for that stride, but no correlation is found.

d. The Bound

Murie (1951) states that on occasion elk can bound like mule deer.

There was no evidence of this gait in the film sequences examined for this study.

8. Observations on Eurasian Cervids

I was able to take photographs of the walks and occasionally of the trots and gallops of five captive species of deer from Europe and Asia, all at 16 f.p.s. This footage is analyzed here.

Dama dama

a. The Walk

i. Source of Data

Twenty-two sequences of 75 strides of 1202 frames from the Assiniboine Park Zoo, Winnipeg

Thirty-four sequences of 148 strides of 2464 frames from High Park Zoo, Toronto

Three sequences of 14 strides of 186 frames from Riverdale Zoo, Toronto

ii. Description and Film Analysis

Fallow deer inhabit woodlands by preference. They have a shoulder height of nearly one meter and a weight of about 75 kgs (Colby, 1966). The female is somewhat slighter with a back line sloping noticeably down from the hind quarters to the shoulders. The buck has large palmate antlers.

The analysis of the walking strides are given in Table 20. The walk patterns of the antlered males and of the females are similar (χ^2 test, p = $>$.20). The pattern of both adults is highly significantly different from that of the young fallow deer (χ^2 test, p = $<$.01).

The data for all the adults are grouped according to the speed at which each stride is taken (fig. 13). From this graph it is evident that during faster walks diagonal supporting legs are used more often and three supporting legs somewhat less.

The times of a walking stride for male and female adult fallow deer are similar. They average 1.07 seconds with a range of 0.88 to 1.38 seconds (N sequences = 47). Those of the half-grown fallow deer average 0.94 seconds with a range of 0.69 to 1.25 seconds (N sequences = 12).

Table 20

Time Spent on Combinations of Supporting Legs of Walking Fallow Deer

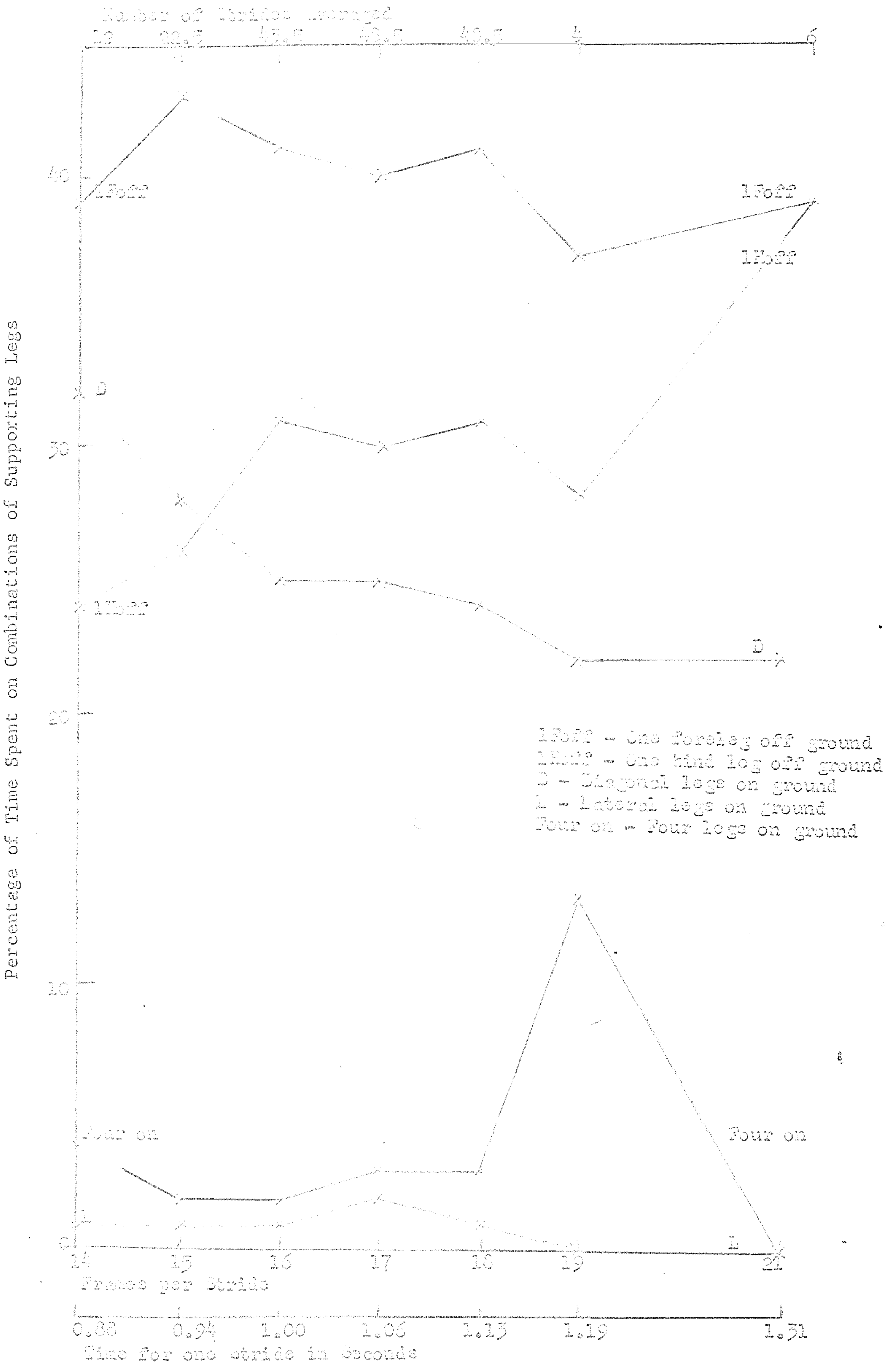
Animals	Lateral legs	Diagonal legs	One hind leg off	One fore leg off	Four legs on	Total	Number of strides averaged
Males with antlers							
Frames observed	10	280	361	481	43	1175	69
Percentage of stride	1	24	30	41	4	100	
Female adults							
Frames observed	20	466	516	717	48	1767	114
Percentage of stride	1	26	29	41	3	100	
Young - half grown							
Frames observed	10	226	219	261	9	725	51
Percentage of stride	1	31	31	36	1	100	
Total adults							
Percentage of stride	1	25	30	41	3	100	183

b. The Trot

i. Source of Data

One sequence of 3 strides of 21 frames of a half-grown fallow deer filmed at Riverdale Zoo, Toronto

Figure 15 Walking Patterns of Fallow Deer at Varying Speeds



One sequence of 6 strides of 44 frames of an adult female fallow deer filmed at Assiniboine Park Zoo, Winnipeg

ii. Description and Film Analysis

The trot of this species is springy, like that of Odocoileus, and the patterns of these two animals are similar. The average of the nine strides show that diagonal legs are used 72% of the time of the stride, three legs with one hind leg off 1%, three legs with one front leg off 8%, two forelegs off the ground 6% and only one hind leg on 5% of the time. The suspensions last 8% of the time of the stride.

The ranges of the times of the strides of these animals are the same, 0.38 to 0.50 seconds. The average time of the adult's six strides is 0.46 seconds and of the half-grown deer's three strides 0.44 seconds.

Cervus elaphus

a. The Walk

i. Source of Data

Eight sequences of 21 strides of 466 frames of red deer from Assiniboine Park Zoo, Winnipeg

ii. Description and Film Analysis

The European red deer is so closely related to the American elk that some authors feel they are conspecific (Ellerman and Morrison-Scott, 1951). However, it is smaller than the elk, standing about 140 cms at the shoulder and weighing about 115 kgs (Colby, 1966). The European red deer used to occupy a similar habitat to the elk, but today their range is greatly restricted. Like elk, they often undergo seasonal but not long distance migrations. The buck red deer, like the bull elk uses a characteristic stiff-legged gait during the rut (Darling, 1937).

The walk patterns of the red deer are given in Table 21. Those of males and females are similar (χ^2 test, p = $>$.30).

Table 21

Time Spent on Combinations of Supporting Legs for Red Deer

	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs down	Total	Number of strides averaged
Male with full antlers							
Frames observed	28	51	91	91	0	261	11
Percentage of stride	11	19	35	35	0	100	
Female adult							
Frames observed	16	44	68	77	0	205	10
Percentage of stride	8	22	33	37	0	100	
Adult red deer percentages	10	20	34	36	0	100	21

These patterns change markedly with speed, as shown in figure 14. The use of diagonal legs increases and the use of three legs decreases at faster speeds.

The strides last an average of 1.41 seconds (range 1.06 to 1.88 seconds, N sequences = 8) for these adults.

Cervus nippon

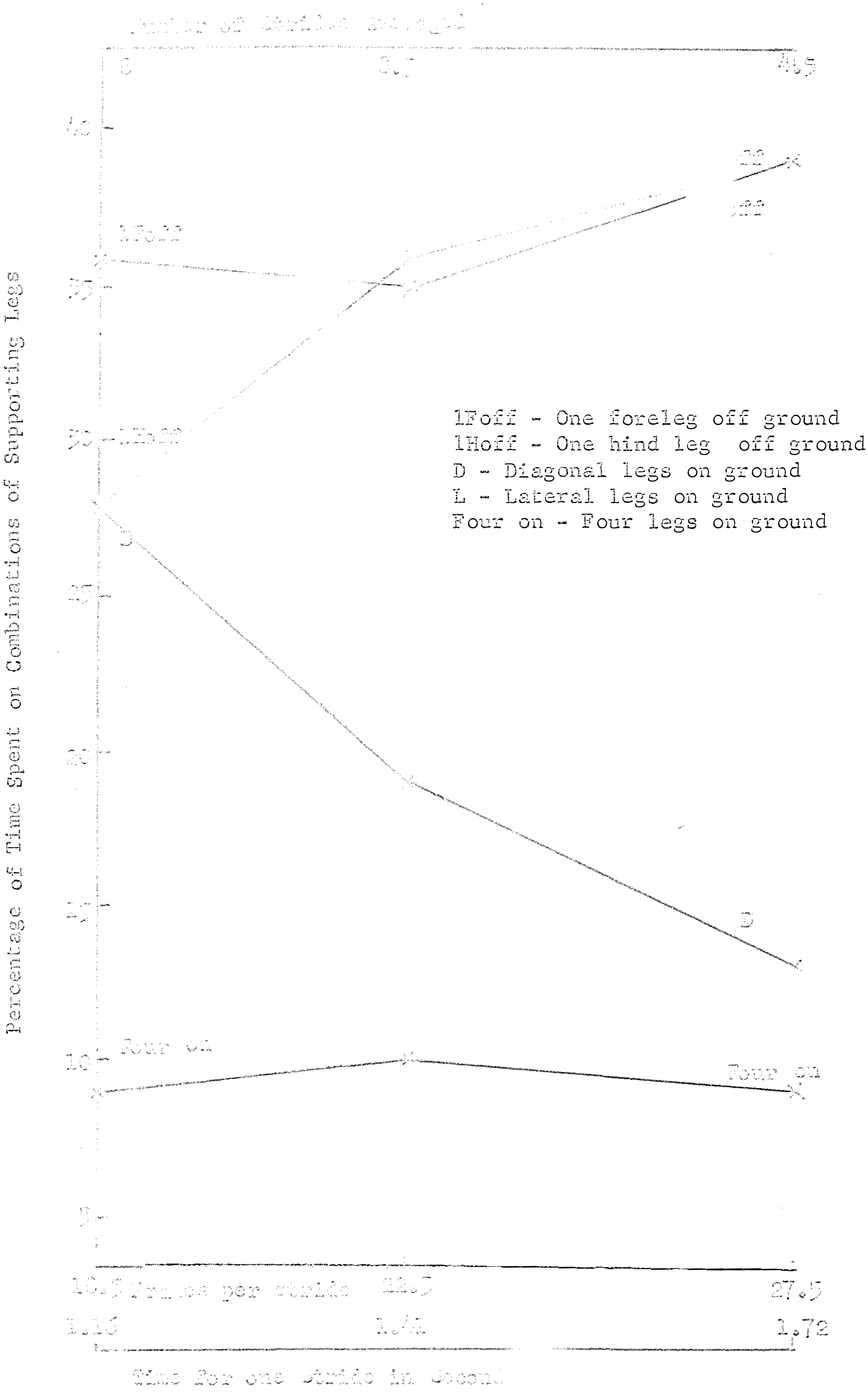
a. The Walk

i. Source of Data

Eight sequences of 21 strides of 405 frames of both Formosan and Japanese sika from Assiniboine Park Zoo, Winnipeg

ii. Description and Film Analysis

The Formosan and Japanese sika are races of the same species


Percentage of Time Spent on Combinations of Supporting Legs
1Foff - One foreleg off ground
1Hoff - One hind leg off ground
D - Diagonal legs on ground
L - Lateral legs on ground
Four on - Four legs on ground
Four on
D
Four on
27.5
1.72

and since the data are limited, the sequences of these two races are grouped together. Both races have a shoulder height of about 0.9 meters and both come from wooded areas of Asia.

The walk pattern for the sika deer adults is given in Table 22. A walking stride of the adults averages 1.20 seconds (range 0.94 to 1.38 seconds, N sequences = 6). That of a newborn fawn lasts 0.88 seconds.

Table 22

Time Spent on Combinations of Supporting Legs of Walking Sika Deer

Animal	Lateral legs	Diagonal legs	One hind leg off	One fore-leg off	Four legs on	Total	Number of strides averaged
Sika deer adults							
Frames observed	9	75	111	153	5	353	18
Percentage of stride	3	21	32	43	1	100	

b. The Trot

i. Source of Data

Two sequences of 4 strides of 47 frames from Assiniboine Park Zoo, Winnipeg.

ii. Description and Film Analysis

The trot of these animals appeared bouncier than that of any other cervid studied. It is possible to time the duration of the strides from the data. Those of a female adult Formosan sika last 0.75 and 0.88 seconds; those of a small fawn last 0.56 and 0.75 seconds.

c. The Gallop

i. Source of Data

Two sequences of 3 strides of adults from Assiniboine Park Zoo, Winnipeg

ii. Description and Film Analysis

The gallop of these animals was flat, exhibiting none of the bounds associated with the gallop of *Odocoileus*. There are not enough data to analyze this gait in detail. These strides all have rotary series of impacts. The suspensions are all flexed, the longest lasting 0.19 seconds.

Elaphurus davidianus

a. The Walk

i. Source of Data

Four sequences of 10 strides of 303 frames from the Assiniboine Park Zoo, Winnipeg

ii. Description and Film Analysis

At first glance Père David's deer looks less like a deer than an equid, with its stout legs, long tail, heavy body and hanging head. This impression is enhanced when the animal walks. Instead of the alert movements of most cervids the animal plods along slowly. This appearance of lethargy is very apparent in the Assiniboine Park animals and is also reported for a herd in England (Phillips, 1925).

The walk patterns of three adults and one fawn are given in Table 23. There are not enough data to compare these patterns. The average adult walking stride lasts 2.06 seconds (range 1.81 to 2.38, N sequences = 3). The stride of a calf lasts 1.38 seconds.

Table 23

Average Time Spent on Combinations of Supporting Legs of Walking Père David's Deer

	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs on	Total	Number of strides averaged
Adults							
Frames observed	21	5	115	108	10	259	8
Percentage of stride	8	2	44	42	4	100	
Calf							
Frames observed	3	8	15	17	1	44	2
Percentage of stride	7	18	34	39	2	100	

9. Discussion and Conclusions of Cervid Gaits

a. The Cervid Walk

i. The Walk Pattern

The walks of these species are expressed in walk patterns which give the percentage of time of the stride during which the animal is supported by each of the five possible combinations of legs. The walk patterns of ten cervids are listed in Table 24, in increasing order of size. Most of the patterns are highly significantly different (χ^2 test, p = $<$.01). The only ones that are similar are *Odocoileus virginianus* and *O. hemionus* (χ^2 test, p = $>$.30); *Cervus canadensis* and *C. elaphus* (χ^2 test, p = $>$.80); and *Odocoileus hemionus* and *Rangifer tarandus groenlandicus* (χ^2 test, p = $>$.05).

Table 24

Average Percentage of Time Spent on Supporting Combinations of Legs for Adult Cervids Walking on Flat Ground*

	Shoulder height - in m	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs down	No. of strides averaged
Dama dama	0.9	1	25	30	41	3	183
Cervus nippon	0.9	3	21	32	43	1	18
Odocoileus virginianus	1.0	5	18	38	39	0	212
Odocoileus hemionus	1.0	6	20	35	39	0	32
Rangifer t. groenlandicus	1.1	7	22	33	38	0	113
Rangifer t. caribou	1.4	8	31	35	26	0	17
Elaphurus davidianus	1.4	8	2	44	42	4	8
Cervus elaphus	1.4	10	20	34	36	0	21
Cervus canadensis	1.5	10	21	34	35	0	179
Alces americana	2.1	10	12	41	36	1	20

A. Diagonal Supporting Legs

Most of these cervids use diagonal legs for long periods, namely between 18 and 25% of the time of the stride. This cautious, stable walk may be attributed to the wooded environment of these animals where sound is as important as sight in identifying danger. We will later contrast this with the walk of the pecoran species that inhabit open plains and rely primarily on their sight.

*The single exception is the pattern of Rangifer tarandus caribou which is for rough terrain.

There are three species for which the use of diagonal legs does not lie between these 18 and 25% limits. Among these three exceptions, Père David's deer walked so slowly that they used diagonal legs for only 2% of each stride. Their apparent lassitude is likely connected with their previous mode of life. Even though the original distribution of these deer is unknown there is little doubt among zoologists that its habitat comprised swamps and reedy areas; their broad toes spread widely when they are set down and their dewclaws are close to the ground, both features ideal for supporting an animal in soft and swampy areas. As well, these animals love water so much that if it is available they will submerge themselves up to their necks for hours at a time. In an animal that spends most of its time in swamps there is little possibility of using an alert walk; at best it can only move forward as fast as it can pull its feet free of the mud.

The second exception is the moose, which uses two diagonal legs while on smooth ground only 12% of the time. The moose has relatively long legs in proportion to its body length (fig. 4). If it used diagonal supporting legs for an extended period, the front leg would still be planted on the ground, impeding the swing of the hind leg on the same side as it moves forward. The moose does not compensate for its reduced use of diagonal supporting legs by an increased use of lateral legs, implying a slower walk than it might have. Possibly an extended use of lateral legs would be too unlike the inborn cervid walk pattern.

The woodland caribou, the third exception, uses diagonal legs nearly one third of the time. This extended use of diagonal legs occurs since in the films used for these data the caribou are walking in their rough natural habitat where diagonal legs are necessary in maintaining a walk of any speed while maneuvering through water and around obstacles. The variation in the walk pattern because of the terrain is discussed below.

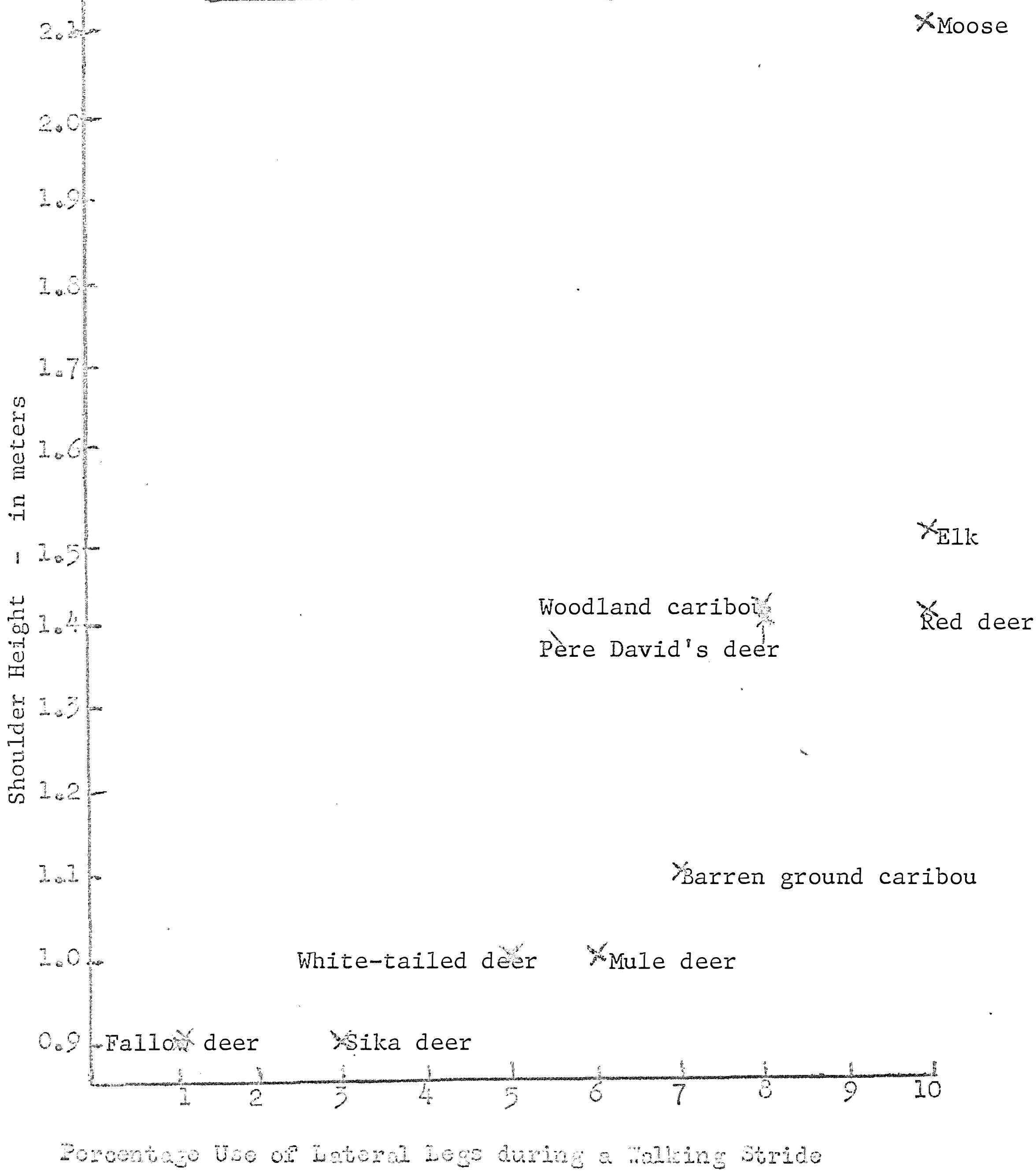
B. Lateral Supporting Legs

The use of lateral legs is correlated with the shoulder height of these cervids in Table 24. This is illustrated in figure 15 where the shoulder height of the cervids is plotted against the percentage use during a stride of lateral legs. All cervids use lateral legs at least one percent of the time, as they must to allow the hind hoof to be set down where the forehoof on the same side was. The larger cervids use lateral legs for proportionately longer periods. The larger an animal is, the longer its legs generally are absolutely and the better able it is to balance its centre of gravity over two lateral legs. As extreme examples, a dachshund with its short legs is virtually unable to balance itself on two lateral legs at all; the long-legged giraffe by contrast spends about 40% of a walking stride on lateral legs.

C. Three Supporting Legs

For all animals walking on flat ground, three legs were used for over two-thirds of each stride. Seven of these species were supported by hind legs more than by forelegs during their use of three legs. Therefore, as a foreleg is swung forward in these species it swings either higher than a hind leg or more slowly. The former movement would be advantageous in passing over long vegetation or other obstacles. By the time the animal has set down its foreleg it is aware if such obstacles are present. If they are not, the hind leg need not be lifted as high as it swings forward. The latter slow movement of the foreleg would enable the cervid to be extra careful in the placement

Figure 15 Shoulder Height of Cervids Plotted against their Use of Lateral Legs during a Walking Stride



of its forehoof; if any small impediment or soft patch in the substrate were present it could be avoided. However three species were supported by their forelegs longer than by their hindlegs - the moose, the woodland caribou and Père David's deer. The relative use of front and hind legs varied within several species and could not be correlated with other features of these cervids.

D. Four Supporting Legs

Few cervids are supported by all four legs during a walking stride. Those that are, are the two smallest species (the sika and the fallow deer), the largest (the moose) and the slowest (Père David's deer). These also use two legs the least during the walk and they perhaps need this increased support.

ii. Variation in the Walk Pattern

This work assesses for the first time the variations present in the walking strides of mammals. The walk patterns must be based on as many data as possible, since there is considerable variation in the use of supporting legs even in sequences of the same individual walking at the same speeds (see discussion for the white-tailed deer). In spite of the variations in the data, there are in most cases highly significant differences in the walk patterns of different species.

A. Variation with the Speed of the Walk

All of the cervids examined (*Odocoileus virginianus*, *Odocoileus hemionus*, *Alces americana*, *Cervus canadensis*, *Cervus elaphus* and *Dama dama*) use diagonal supporting legs more often and three supporting legs less often as the speed of their walks increases. The walk at the fastest speed is usually highly significantly different from that at the slowest speed. The use of lateral legs is relatively independent of speed.

B. Variation with the Terrain

Examples of variation in the walk pattern caused by the nature of the terrain are available for the moose and for the woodland caribou. The walking strides of the moose on flat surfaces and through water or snow indicate that diagonal legs are used longer in rough terrain where stability is essential. If the terrain is very rough the use of two legs is greatly decreased and the use of three and four legs make up most of the stride, as illustrated for an individual woodland caribou. The general walk pattern for the woodland caribou (Table 24) was calculated for animals walking through shallow mud and water.

C. Variation with Antlers

Those species with the heaviest antlers in relation to their body weight (moose and caribou, Table 4) have walk patterns that are significantly different between the antlered males and the antlerless adults. In these two species diagonal supporting legs are used less in the walk of the animals with heavy antlers, since these need the support of the three legs that replace the diagonal supports.

Elk have proportionately the next heaviest antlers, but their presence on bulls does not change their walk pattern significantly. Nor do the presence of antlers affect the walk patterns of fallow deer, red deer, mule deer or white-tailed deer.

D. Variation with Age

The young of a species of cervid generally have proportionately longer legs than the adults (fig. 4) and they may also have significantly different walk patterns. For the three species in which enough data are present to compare adequately the fawns with the adults, the white-tailed fawns have a highly significantly different pattern than the adults, with a decreased use of lateral legs; the fallow deer fawns have a highly significantly different pattern than their adults with an increased use of diagonal supporting legs and the barren ground caribou fawns have a walk pattern similar to that of their adults. In these three species, if the walk pattern of the fawns differs from that of the adults, it does so in a direction of greater stability, either with a decreased use of lateral supporting legs or with an increased use of diagonal supporting legs.

iii. Comparative Times for a Walking Stride

The average time for the walking strides of the animals of each species studied are given in figure 16, together with the range of times for the strides. Several observations can be made from these data:

A. Each species has a wide range of times for a walking stride. A slow stride may last over twice as long as a fast stride.

B. The taller mammals tend to have strides that last longer than those of the shorter mammals, as is evident in figure 17 where the shoulder height of an animal is plotted against the average speed of its walking stride. Since the legs are appendages that swing forward more or less like pendulums, this difference is to be expected; the longer a pendulum is, the longer is its period.

C. The particularly slow walk of the Père David's deer is underlined in figure 17. The speed is much slower than that of other cervids of similar size.

Figure 16 Average Time and Range of Times for Walking Strides of Cervids

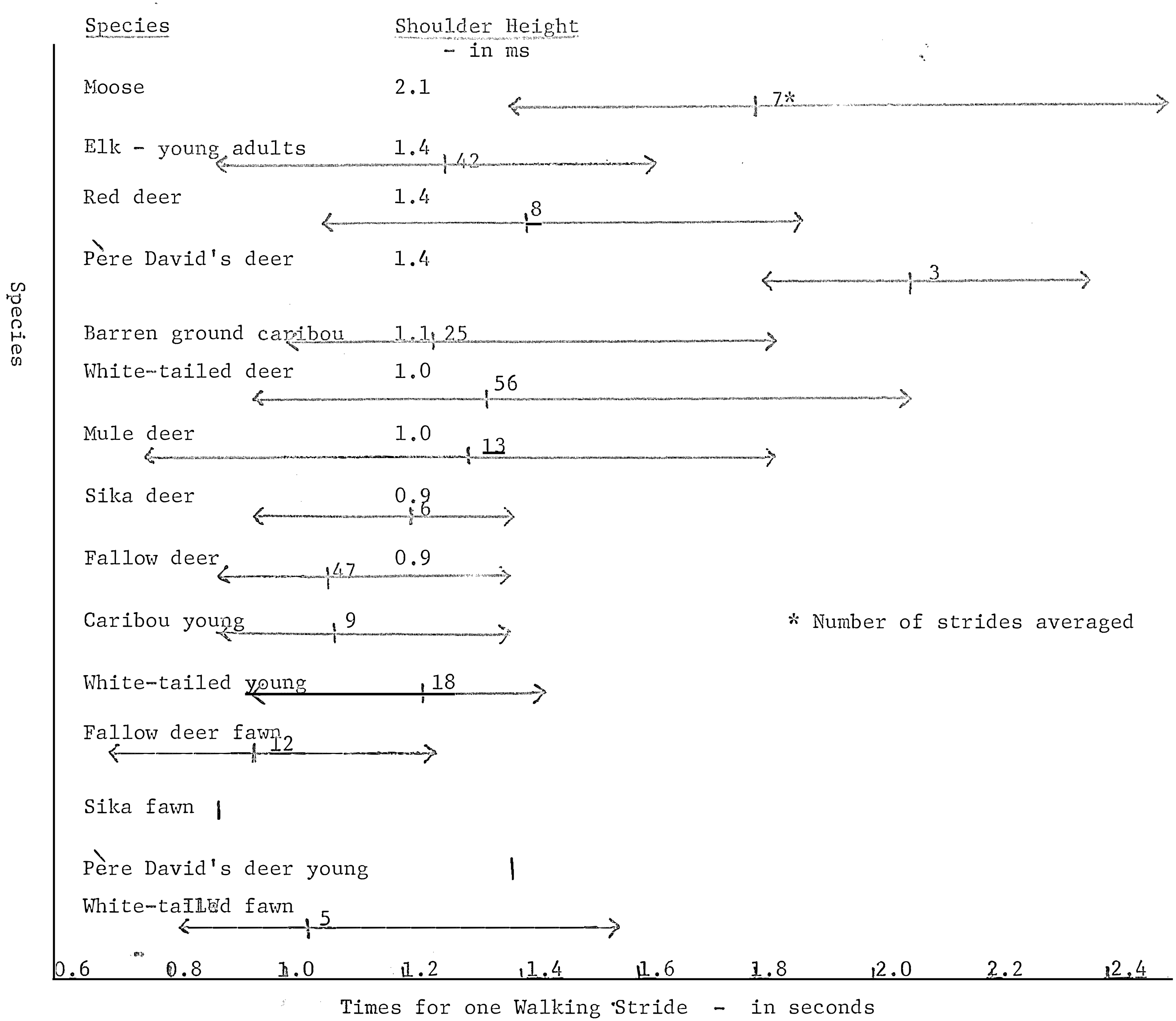
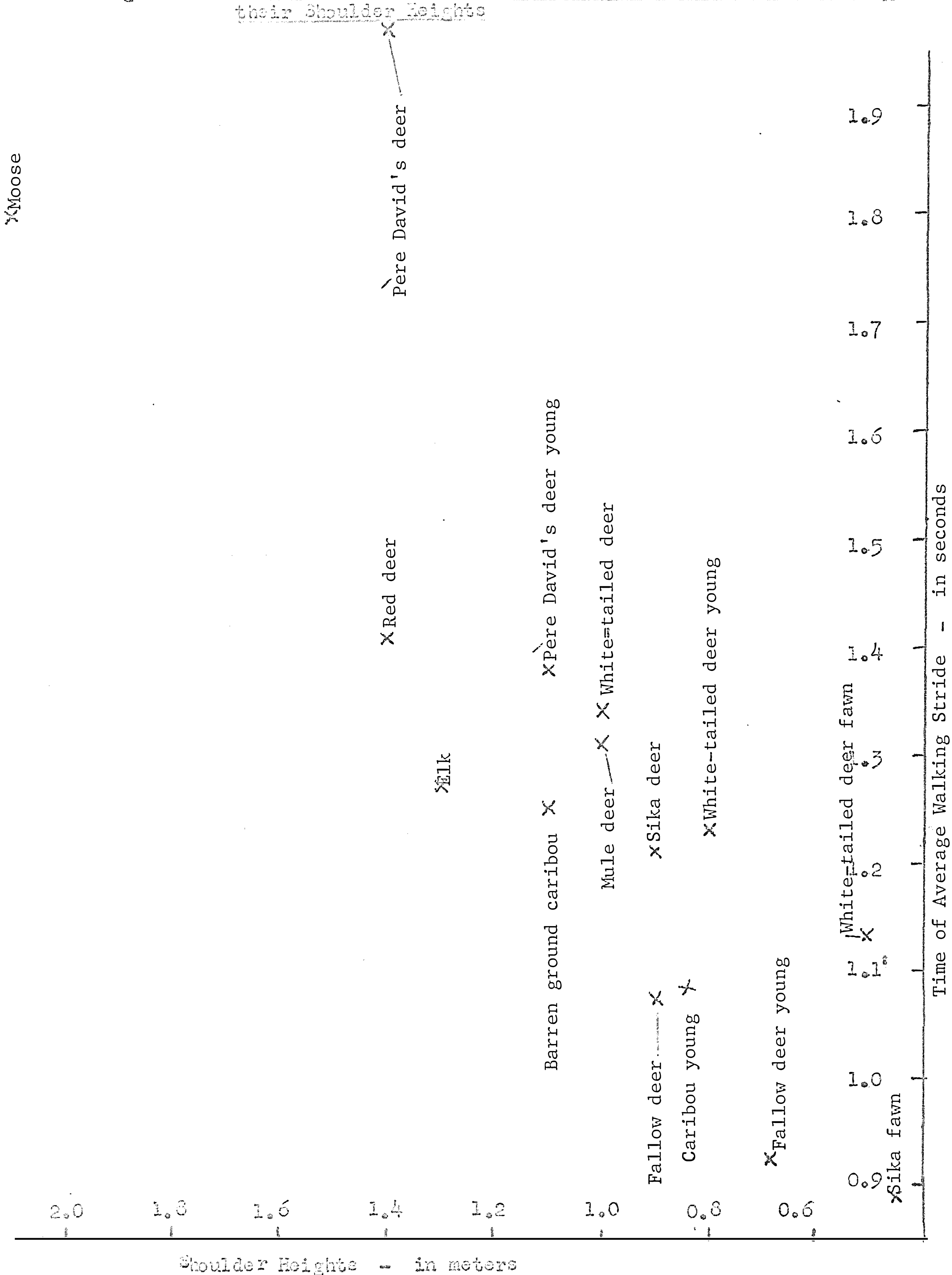


Figure 17 Average Time of Walking Strides of Cervids Plotted Against their Shoulder Heights



b. The Cervid Trot

Several general conclusions can be drawn for the trot of these cervids.

i. A species can trot at either fast or slow speeds. The ranges and average time for a trotting stride are given in figure 18.

ii. The average time for one trotting stride is roughly proportional to the shoulder height and therefore also to the leg length of a species. This is shown in figure 19. The considerable spring in the trot of the sika deer is reflected in the long average time of their strides.

iii. The ranges of the times for the strides are not in general as large as those for the walking strides. An average trotting stride for a species usually lasts somewhat more than half the time of an average walking stride.

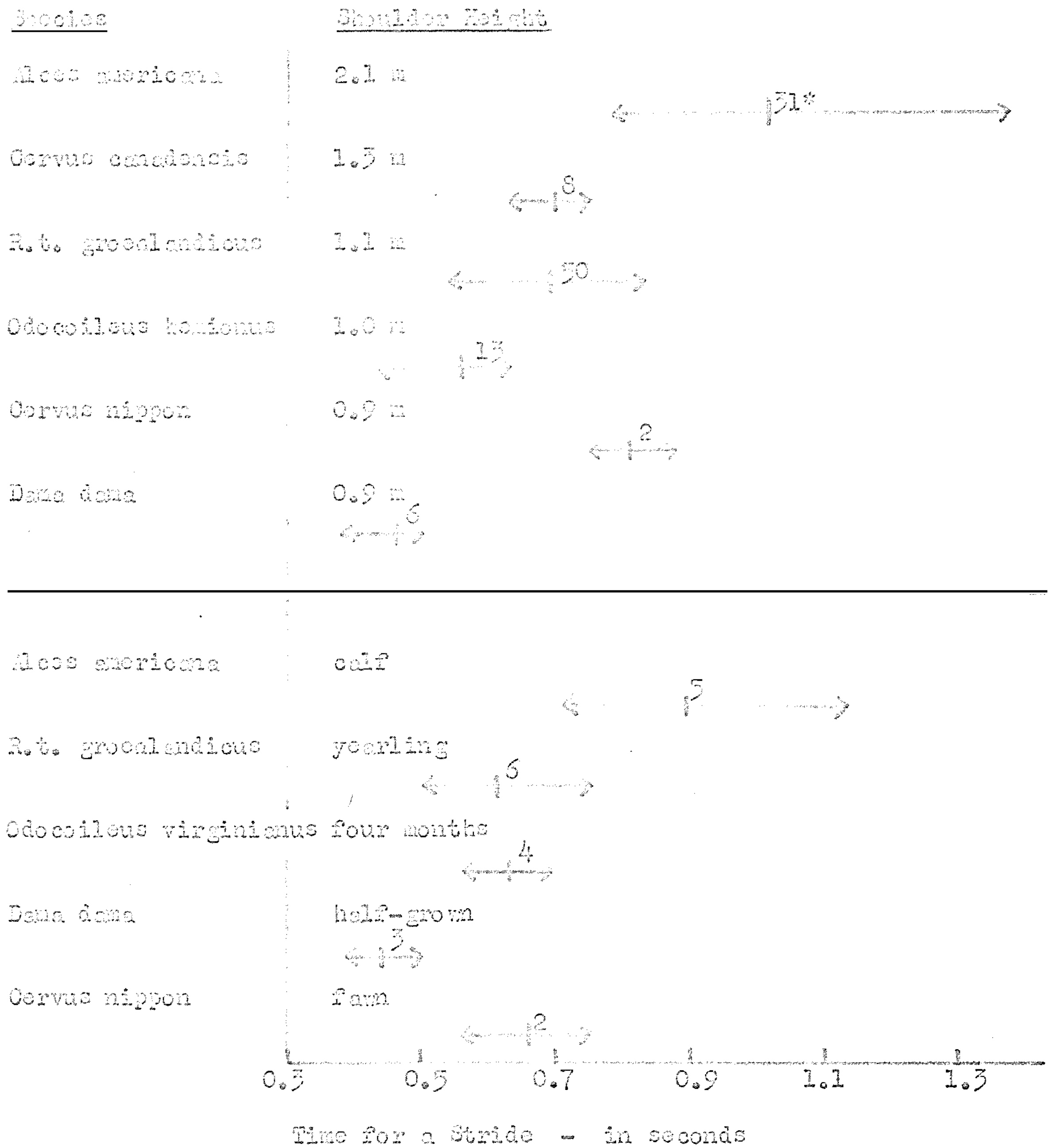
More particularly, if we examine the combinations of supporting legs used in the trots of these species as set out in Table 25, we can draw several further conclusions.

Table 25

Average Percentage Time Spent on Combinations of Supporting Legs for Trotting Cervids

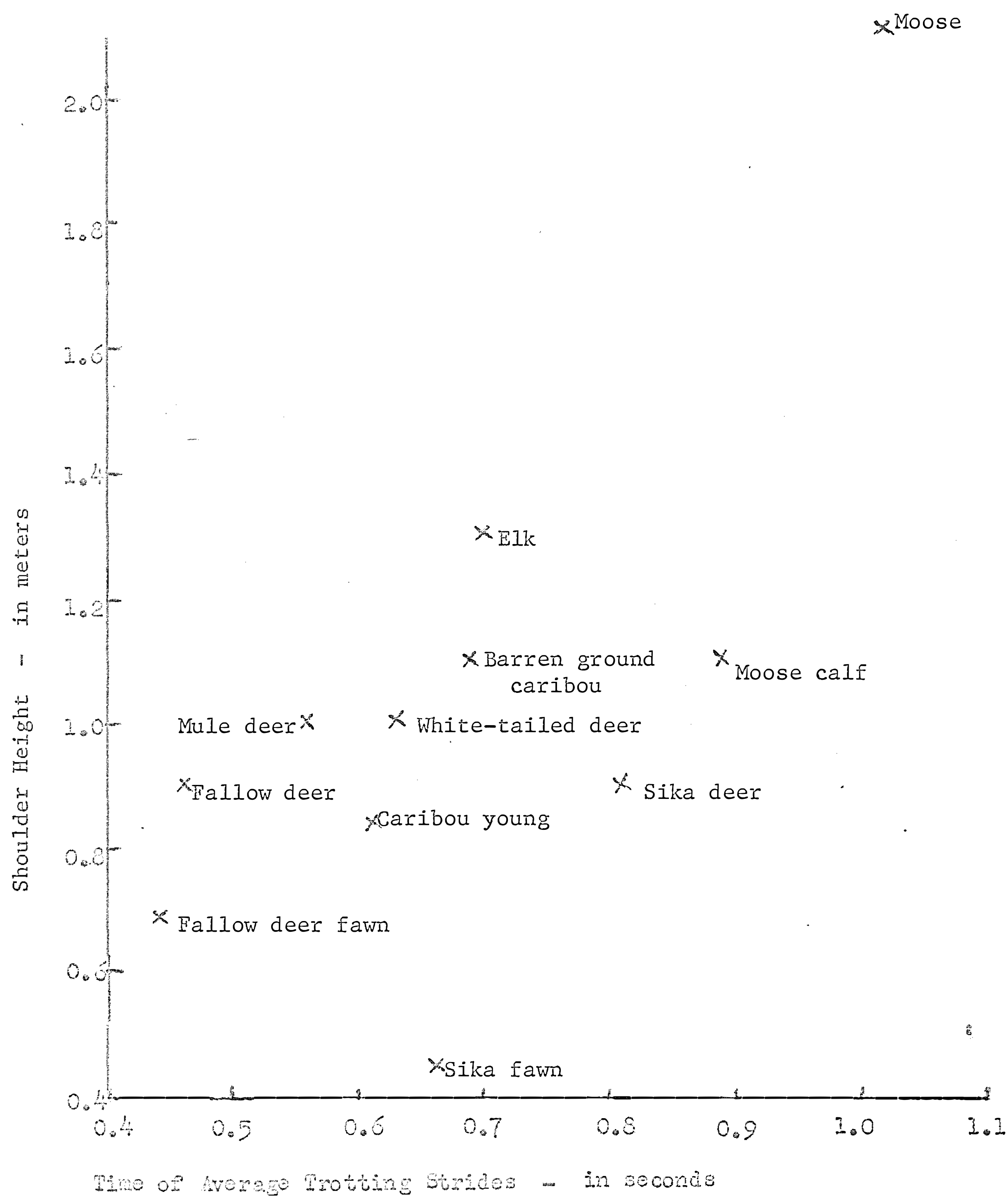
Combinations of supporting legs, not in order	Moose	Elk	Barren-ground Caribou	Mule deer	Fallow deer	White-tailed deer-4 mos.
Lateral legs on ground	0	1	0	0	0	0
Diagonal legs on ground	80	75	83	86	72	77
One hind leg off ground	6	8	1	0	1	3
One front leg off ground	13	12	5	6	8	5
Four legs on ground	1	4	1	1	0	0
One hind leg on ground	0	0	3	2	5	0
One front leg on ground	0	0	0	2	0	0
Two hind legs off ground	0	0	0	0	0	0
Two front legs off ground	0	0	0	0	6	0
Suspension	0	0	7	3	8	15
No. of strides averaged	13	15	43	13	9	4

Figure 18 Average Time and Range of Times for Trotting Strides of Cervids



* Number of strides averaged

Figure 19 Average Time of Trotting Strides of Cervids Plotted Against their Shoulder Heights



iv. The smaller of these species have periods of suspension while the two largest species do not. It is probable that heavier animals have greater difficulty in attaining suspensions and for this reason they may use them less often.

v. Perhaps also for this reason the heaviest two species use three supporting legs for longer periods than the other cervids. Three supporting legs are used about one-fifth of the time of a stride by the moose and the elk but never more than 9% of a stride by the smaller cervids.

vi. Although most of each trotting stride is spent on diagonal supporting legs in each species, they may have a large number of other supporting legs during the remainder of the stride. Such irregular supporting combinations are especially common in the smaller cervids.

vii. For each species the forelegs spend more time in the air than the hind legs. This is expected, since in a fast trot especially the forelegs cannot push off at the same time as the hind legs as they are shorter than the hind legs (Howell, 1944).[1] The forelegs leave the ground fractionally earlier and the hind provides support for the animal until it too pushes off from the ground.

The trotting gaits of all cervids are highly serviceable but of all the animals studied the trotting gait of the caribou is especially suitable for travelling long distances. Indeed only by being able to

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[1] The sum of the measurements of the front leg bones was less than 85% that of the hind leg bones in four cervid species reported in Murie (1870) and in four individuals of other cervid species measured by the author at the Royal Ontario Museum. From photographs it is obvious that the hind legs are also longer in other cervid species as well.

trot long distances has the barren ground caribou been able to occupy a habitat where movement is an essential way of life. Although this may be interpreted as a speculative statement, it seems that the caribou has evolved in directions that favour an effective trot. For example its legs tend to be relatively short in relation to its body length (figure 4). Dog breeders are well aware that these are good body proportions in German shepherd dogs bred for their show-ring trot. Relatively long legged animals that have no period of suspension often have to swing their hind legs forward to one or the other side of their forelegs, which adversely affects the speed and stamina of their gait.

The caribou is smaller than one might expect it to be, since it lives in regions where the average daily temperature during the winter falls to -50°F (Symington, 1965). In general, northern cervids like elk and moose tend to be large so that they will have a proportionately reduced surface area relative to their body weight - a factor which helps them to withstand low temperatures. One might explain the relatively small size of caribou as a possible correlation between this feature and that of endurance; certainly smaller horses have been found to have more endurance than larger ones (Smith, 1921). It must be mentioned, however, that races of caribou on the Arctic islands tend to be smaller than those of the mainland (Banfield, 1961), a difference that does not seem related to their locomotion.

As compared to other cervids, the extreme flexibility of the feet of the caribou illustrated in figure 3 serves this species well in pawing through the snow, in swimming, in bringing the dewclaws nearer to the ground for increased support on snow or tundra and, what is of greatest concern here, in the production of a springy trot. This springiness can best be seen in a comparison of the average times of a trotting stride for the barren ground caribou and for the mule deer, two species which have about the same shoulder height and therefore more or less the same leg lengths. Despite their similar height and the fact that the caribou is much the heavier (Table 4), the caribou's average trotting stride lasts 19% longer than that of the mule deer. These longer trotting strides have longer periods of suspension (Table 25).

As an indication that long periods of suspension are advantageous in the trot, we may consider trotting horses. The best Standardbred trotters are those with the greatest thrust and the longest periods of suspension; because of the decreased number of foot impacts the legs move relatively slowly and less often and the gait is less tiring (Bracket, 1961). Undoubtably these same criteria apply to cervids too and the caribou with its flexible feet is able to attain a strong thrust and a long suspension in each trotting stride.

A final anatomical feature that implies an especially effective trot is the straight horizontal back of caribou, particularly noticeable since the back is long. Contrast this with the top lines of the fallow deer whose croups are slightly higher than their shoulders and with the moose whose shoulders are the higher. A horizontal back is best for the trot since this is a symmetrical gait in which the forequarters and hindquarters produce about equal emounts of power simultaneously, as a front and a back leg swing through the same distance at the same time.

The springiness of the caribou's trot allows the hind hoof to be set down on the ground ahead of the imprint of the forehoof of the same side. These animals have a high leg action, with the knees bent up to 90°. This action shortens the leg and gives it a faster natural swing.

The shape of caribou seems to have developed in such a manner that the species can travel long distances with its trotting gait. On the other hand, moose inhabit a forest environment where they have evolved long legs to help them manoeuver in deep show, in stepping over ubiquitous windfalls, in wading into deep water and in reaching high browse. Nevertheless these long legs do not preclude a fast trot over short distances.

c. The Cervid Gallop

Several general conclusions can be drawn from the data in Table 26, in which the average time spent on the various combinations of supporting legs are given for the five species whose gallops were analyzed in detail.

i. All of these species can spend at least 5% of the time of a stride in suspension. The extended suspensions are virtually restricted to Odocoileus, where these bounds are valuable from a survival point of view. They enable a deer to leap over both high and wide obstacles that are often found in its varied habitat, they allow it to see over vegetation from the highest point of its leap where the best route of escape lies or where its pursuer is and during the bound the rump is necessarily lifted high into the air so that the white underside of the tail when it is lifted can serve as a distinctive signal. One such bound lasted 55% of the stride in Odocoileus virginianus. The larger cervids use flexed suspensions. These are never present for

Table 26

Average Percentage Time of a Stride Spent on Combinations of Supporting Legs for Galloping Cervids.

Combinations of supporting legs, not in order	Alces americana	Cervus canadensis fem.	Cervus canadensis male	Rangifer t. groenlandicus	Odocoileus hemionus	Odocoileus virginianus
One foreleg on ground	0	4	0	1	15	14
Both forelegs on ground	14	12	0	12	11	16
Lead foreleg on ground	21	23	0	19	9	5
Flexed suspension	6	5	0	9	0	9
One hind leg on ground	11	15	0	5	2	2
Both hind legs on ground	23	16	0	19	15	25
Lead hind leg on ground	4	3	0	2	11	4
Extended suspension	0	0	0	1	15	21
Fore and hind legs on ground						
- two	12	13	26	6	7	2
- three	9	9	74	24	13	2
- four	0	0	0	2	2	0
No. of strides averaged	6	52	3	23	5	29
Average time for a stride - in seconds	0.65	0.42	0.46	0.47	0.40	0.38

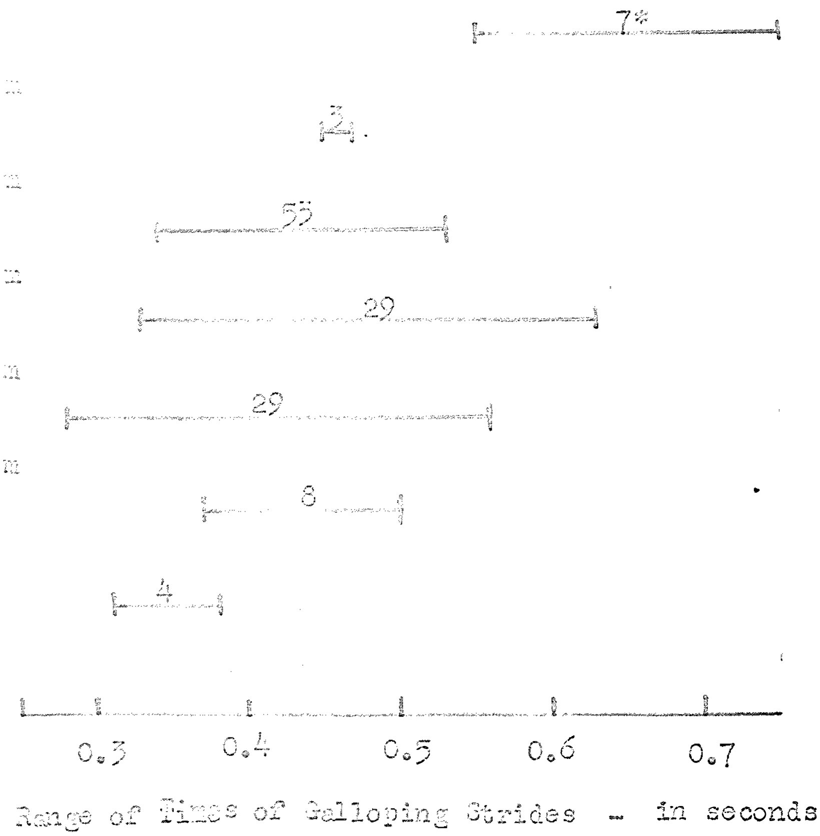
more than 9% of the time of a stride.

ii. The front legs support these cervids for longer periods than the hind legs in all cervids but the moose. However, the support of the front legs is not related to the strength of the push-off or to the type of suspension present in the stride.

iii. The range of times for galloping strides varies considerably for the strides (fig. 20). Generally the times are longer

Figure 20 Range of Times for Galloping Strides of Cervids

Species	Shoulder Height
Alces americana	2.1 m
Cervus canadensis male	1.5 m
Cervus canadensis female	1.4 m
R.t. groenlandicus	1.1 m
Odocoileus virginianus	1.0 m
Odocoileus hemionus	1.0 m
Odocoileus virginianus three week fawn	



* Number of strides averaged

for those species with the greater shoulder heights and therefore the longer legs.

d. The Use of the Trot and the Gallop

Merrill (1916) writes that moose rarely gallop except when they are startled or when they are charging an adversary. They usually trot when they are in a hurry. These observations hold to a lesser extent in elk. In early spring, young and old elk may gallop about aimlessly as if in pure exuberance of spirits and elk often stampede from real or imagined danger, but they rarely flee over any great distance (Murie, 1951). Green (1933) reports that elk will gallop when first startled but, if not pursued, they will soon revert to a fast trot. He also states that heavily antlered elk always trot rather than gallop and that a trot is used mainly when in timber and heavy bush. Caribou also rarely gallop unless closely pursued (Flerov, 1952; Harper, 1955). In contrast *Odocoileus* always gallop away if there is danger near.

It is apparent that some cervids prefer the trot and some the gallop for their fast gait. If we compare these two gaits, we may perhaps explain these preferences:

i. Quadrupeds can gallop faster than trot, but the trot is less tiring than the gallop and can therefore be continued for longer periods. This is evident in racing horses. Standardbred horses can trot seven one-mile heats in an afternoon at speeds of 30 m.p.h. and repeat this performance several times a week (Emerson, 1951); a thoroughbred gallops up to 43 m.p.h., but it is fit for only about one race a week.

ii. The trot is more stable than the gallop, since two diagonal legs support the animal for most of each stride. One leg rarely supports an animal by itself, although this is a common phase of the gallop.

iii. The centre of gravity of an animal changes drastically during the course of each galloping stride. The animal's equilibrium is less disturbed in the symmetrical trot.

iv. A trotting animal with periods of suspension pushes off with two legs and lands on two legs nearly simultaneously. In the gallop an animal usually pushes off and lands with one foot.

v. Since the trot is a symmetrical gait, each stride has either no or two periods of suspension. The asymmetrical gallop may have 0, 1, 2 or 3 periods of suspension.

vi. The gallop is a faster gait to attain from a standing position. In this gait the entire power of the animal can be channelled into the initial plunge forward from the two hind legs.

There are several possible reasons, based on these gait differences, to explain why moose, elk and often caribou may use the trot as a fast gait rather than the gallop. For one thing in deep snow, swamp or soft tundra the underfooting is usually too yielding for a gait like the gallop in which the entire weight of an animal rests on only one hoof both while it is taking off and while it is landing, if there is a period of suspension. For example, in the case of a moose, one hoof carries the 385 kg weight (Table 2) for a pressure of 264,000 newtons per square m of hoof plus the additional thrust needed for the locomotion. Such pressures could force the hoof so far into the substrate that the animal would have trouble extricating it. The difficulties of sustaining a gallop under such conditions are formidable. The moose and the caribou that live where swamps are common and snow may be deep are the species most affected by these conditions. These two species are also the ones that need a stable gait to manoeuvre among the logs and windfalls that pervade the boreal forests and taiga.

The heavier the animal, the greater is its difficulty in launching itself into a period of suspension, especially when all the weight must be launched from one foot. For example a white-tailed deer fawn may have three periods of suspension during one gallop stride, while an elephant is never in suspension (Muybridge, 1957). The moose requires proportionately more effort to sustain a gallop than does the far lighter white-tailed deer.

Another factor is the proportionately heavy antlers of moose bulls, caribou and to a lesser extent elk bulls. The heavier the antlers, the more they weigh down the forequarters, upsetting the animal's normal balance, and the more difficult it is for the animal to hoist them up into the air during each gallop stride. The symmetrical trot is a preferable gait for heavily antlered cervids, since the centre of gravity changes less radically in this gait than in a stride of the gallop and the heavy head is more easily controlled. Whether trotting or galloping, these antlered cervids all hold their heads well back and rigidly so that their centres of gravity are as far back and as stable as possible.

Finally there is evidence for the moose at least that natural selection is not working in this species to produce gaits of increasing speed. Mech (1966) reports that on Isle Royale, where wolves killed a moose about every three days, those that ran from these predators were more likely to be killed than those that did not. Of 41 moose that ran from the wolves, five were killed; of 36 that were forced to stand at bay because they did not realize their danger soon enough to run, none were brought down and killed.

Part III. Gaits of the Antilocapridae

1. Factors Related to the Gaits of Antilocapridae

a. Recorded Speeds

Einarsen (1948) reports that pronghorns[1] run at speeds of up to 61 m.p.h. Young (in Howell, 1944) timed a buck for half a mile at 55 m.p.h. and Belden (in Howell, 1944) checked these animals many times over a two mile course at 60 m.p.h. Other top speeds have been cited as 53 m.p.h. (McLean, 1944), 45 m.p.h. (Cottam & Williams, 1943), 43 m.p.h. (DeVore, quoted by Seton, 1953), 40 m.p.h. (Chapman, 1948; Bridge, 1942) and 35 m.p.h. (Seton, 1953). Such speeds are not always sprints. Carr (1927) observed four pronghorns galloping at 30 m.p.h. for seven miles and Jaeger (1961) and McLean (1944) report that these animals can run 30-40 m.p.h. for miles. Howell (1944) cites young pronghorns that ran 27 miles at an average speed of 36 m.p.h. Even a fawn one or two days old can run at 20 m.p.h. for short distances (Ormond, 1958), something that cervid young can not do.

b. Jumping Ability

The pronghorn can jump 1.5 m vertically, although it has no need to do so except in fenced areas (Howell, 1944). One male running down a road made a sudden leap into the air every time he came to the shadow of a telephone pole across his path (Jewett, 1946). Sometimes pronghorns (like saigas) give a jump into the air or a "spy hop" to look for danger (Seton, 1953).

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[1]This species is here referred to colloquially as the pronghorn. The word antelope is reserved for members of the Bovidae examined later.

c. Habitat Frequented

Antilocaprids have evolved in North America since the Miocene (Colbert, 1961). They inhabit the flat plains of the continent where there are no trees or bushes, often undergoing seasonal migrations.

d. Anatomical Characteristics

i. Feet

The pronghorn does not have any dewclaws. It encounters neither deep snow nor bogs on the wind-swept plains where it lives, so it has no need to increase the diameter of its foot for support or to ensure a large gripping surface for dodging around bushes or trees.

The hooves are smaller but similar in shape to those of *Odocoileus* (figure 2). Seton (1925) gives measurements of 76 by 51 mms for a hind hoof print and 64 by 57 mms for a front hoof print.

ii. Proportions of Body Length to Shoulder Height

This ratio is similar to that of *Odocoileus*, namely the legs are somewhat longer than the trunk.

iii. Sexual Differences

Both sexes have horns. Those of the male are the larger, measuring about 30 cm. The males have a shoulder height of 90 cm and a weight of up to 57 kg (Burt, 1952). The female is about 10% smaller (Seton, 1953).

2. Observations on *Antilocapra americana*

a. The Walk

i. Source of Data

Five sequences of 8 strides of 140 frames filmed by L. Linnard

Three sequences of 12 strides of 211 frames filmed by the author at Assiniboine Park Zoo, Winnipeg

ii. Description and Film Analysis

The legs on one side of the pronghorn swing forward more nearly together than they do in the cervids. The foreleg has swung forward well before the hind foot on the same side finishes its swing to step onto the ground where the forehoof has been.

The time spent on the different combinations of supporting legs is given in Table 27. The data for males and females are grouped together because in five of the sequences it is difficult to tell the sex of the animal being studied.

The walk patterns are calculated for three different speeds with the limited data available, as shown in figure 21. This graph

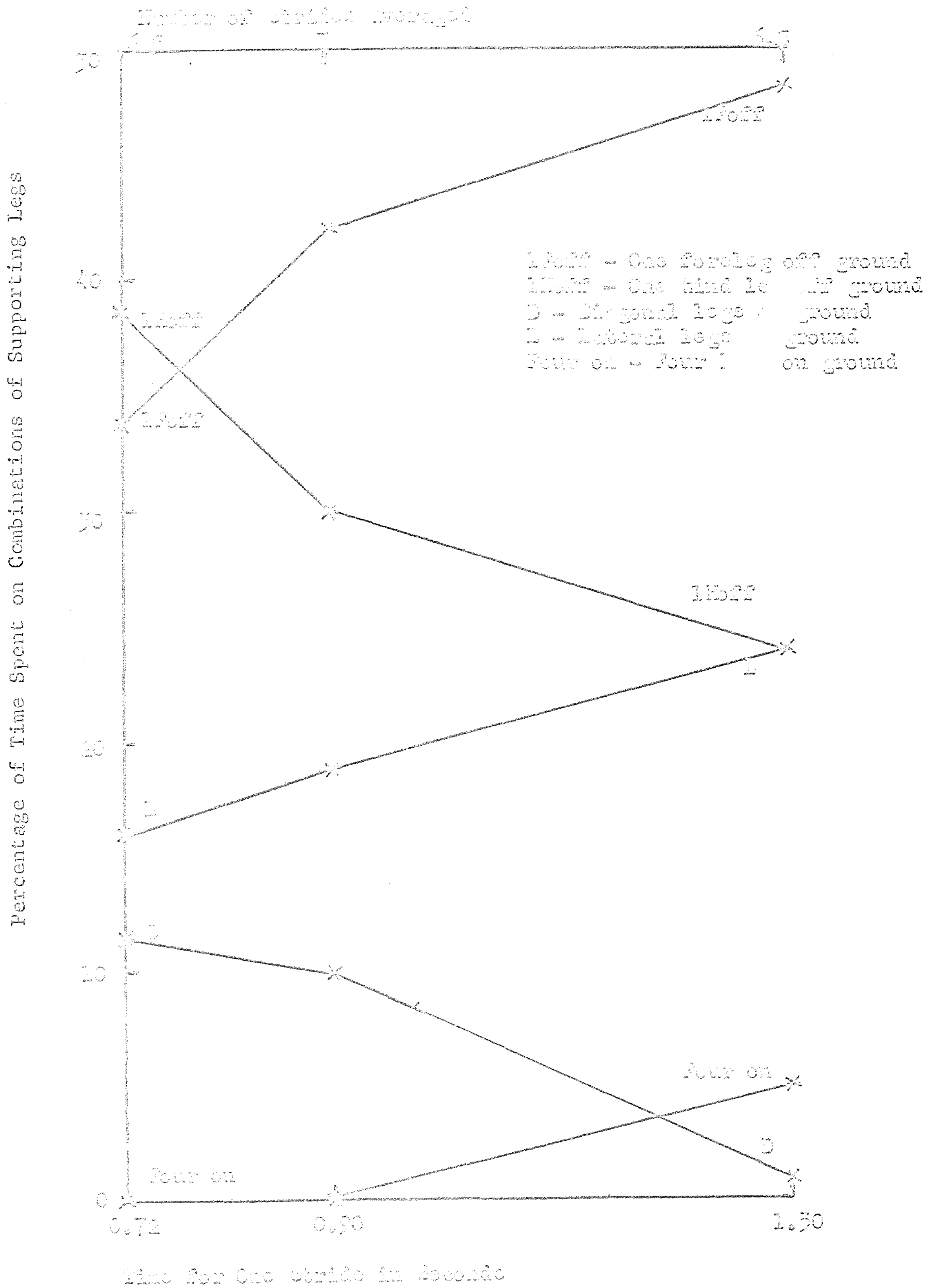
Table 27

Time Spent on Combinations of Supporting Legs of Walking Pronghorn Antelope

	Lateral legs	Diagonal legs	One hind leg off	One fore-leg off	Four legs on	Total	Number of strides averaged
Pronghorn adults							
Frames observed	68	25	106	145	7	351	20
Percentage of stride	20	7	30	41	2	100	

indicates that the use of diagonal legs increases at faster speeds as does that of three supporting legs with one hind leg off. The use of three supporting legs with one foreleg off and of lateral legs decrease with increasing speed. The walk pattern at the fastest speed is highly significantly different than that at the slowest speed (χ^2 test, p = $\leq$.01).

Figure 21 [illegible]


Percentage of Time Spent on Combinations of Supporting Legs
Time For One stride in Seconds
0.72
0.90
1.50
0
10
20
30
40
1Foff
1Hoff
D
L
Four on
1Foff - One foreleg off ground
1Hoff - One hind le ff ground
D - Diagonal legs ground
L - Lateral legs ground
Four on - Four l on ground

The average walking stride of the pronghorns studied lasts 0.94 seconds (range 1.44 to 0.63, N sequences = 8).

b. The Trot

I was unable to obtain footage of pronghorns trotting. In zoos it was impossible for me to arouse them beyond a walk; in the wild, if they are close enough to be photographed they are frightened enough

d. Audubon & Bachman (1856) describe the trot as "elegant and graceful". The steps are mincing and the head is held high (Seton, 1953) so that the animal moves slowly but always alertly.

c. The Gallop

i. Source of Data

Eighteen sequences of 18 strides of 633 frames from "Large Animals that once roamed the Plains"

Six sequences of 13 strides of 465 frames from "Escape in Mammals."

ii. Description and Film Analysis

The gallop of the pronghorn is a smooth gait, with each leg in turn supporting the body and pushing it forward. Both types of suspension are present in roughly equal durations.

The 31 complete galloping strides and various incomplete strides are recorded for 23 individuals galloping in three herds. The gallop patterns of the male, female and yearling pronghorns are similar so these are grouped together for the analysis in Table 28.

The sequence of foot impacts is rotary in 37 strides and transverse in six. In one large herd eight out of ten pronghorns have the same lead foot during the several strides observed, supporting Howell's

(1944) observation that the individuals galloping in a herd tend to have the same lead at the same time. Individuals change leads during both kinds of suspension and during strides of varying duration.

Table 28

Analysis of 31 Galloping Strides of Pronghorns

Combinations of supporting legs not in the order in which they occur	Average duration of a stride - in secs	Range of times - in secs	Percentage time of a stride	
One foreleg on ground	.043	.023-.070	16)	
Both forelegs on ground	.024	.008-.047	9)	41%
Lead foreleg on ground	.044	.023-.070	16)	
Flexed suspension	.033	.008-.070	12	
One hind leg on ground	.034	.016-.055	12)	
Both hind legs on ground	.039	.016-.094	14)	36%
Lead hind leg on ground	.032	.008-.047	11)	
Extended suspension	.028	0-.070	10	
Fore- plus hind leg on ground	.001	0-.016	0	

Both suspensions are important in the pronghorn's gallop, with the flexed suspension used longer. The forelegs rest on the ground longer than the hind legs, but the lead foot in either case is on the ground the same length of time as the non-lead foot. The duration of a stride can not be correlated with the length of either type of suspension, nor is the length of a suspension related to the amount of time that forelegs or hind legs are used in any stride.

These strides of pronghorns illustrate the simplest as well as the fastest form of the gallop. In four phases the animal is a) supported by the forefeet, b) in a flexed suspens c) supported by the hind feet and d) in an extended suspension. In the pronghorn each leg is more or less equal important in supporting the animal and in pushing it forward. If it finishes an extended suspension on the right foreleg, this leg supports the animal for about one-sixth of the time of the stride before the left foreleg touches the ground. Both legs remain on the ground while the body continues to plunge forward and then the left leg supports it alone for another one-sixth of the stride. This left leg then launches the pronghorn into the flexed suspension from which it lands on its left hind leg. The body propels itself forward on this leg for 12% of the stride before the right hind leg is set down and it in turn supports the animal for an equal length of time by itself before it launches the pronghorn on the extended suspension.

d. The Bound

i. Source of Data

Two sequences of 5 strides of 240 frames from "Escape in Mammals."

ii. Description and Film Analysis

These bounds resemble those of the mule deer. The pronghorn executed them while rushing up a rocky slope. Although the exact foot impacts of the animal were difficult to determine because of the rocks and the tussocks of grass often obscuring the feet, the four hooves seemed to touch and leave the ground together. During the suspension the legs hung down, parallel to each other and somewhat bent. When the pronghorn reached the top of the hill, its feet began to move asymmetrically and the bound gradually changed into a gallop. Seton 953) compares these bounds in the pronghorn with "spy-hops" in that they increase the vision of the animal.

During these five strides the pronghorn spends an average of .160 seconds with all four feet on the ground (range .133 to .180 secs) and .216 seconds suspended in the air (range .180 to .258 seconds). The strides average .385 seconds (range .320 to .438 seconds).

Discussion and Conclusions

The most interesting features of the gaits of the pronghorn are the flat speedy gallop and the relatively long use of lateral legs during the walk compared to their limited use in the cervids. These features will be compared in detail with those of the members of other families in Part VI.

Part IV Gaits of the Giraffidae

1. Factors Related to the Gaits of the Giraffidae

a. Recorded Speeds

Giraffes can run at speeds of up to 35 m.p.h. (White, 1948). Maxwell (1925) timed several giraffes galloping over several miles at 28-32 m.p.h. and Akeley (1929) reports that a young giraffe ran two miles with its mother at 15 m.p.h.

The speed of the okapi is unknown. This species can walk and gallop but it is not known if it can trot or pace (Chicago Zool. Park, corres., 1966).

b. Jumping Ability

Adult giraffes in general step over fences up to 1.5 m high rather than jump them (Dagg, 1962), although one medium-sized male giraffe leaped over a fence in full flight, pushing off with his hind legs (Churcher, pers. comm.). Okapis are such poor jumpers that pits built to catch them need not be excessively deep (Grzimek, 1956).

c. Habitats Frequented

The giraffe lives in lightly forested areas throughout much of Africa. It is entirely a browser (Innis, 1958). The okapi which also browses exclusively lives in the dense rain forests of the Congo. Vision there is limited and hearing more important, a fact reflected in the relatively larger ears and tympanic bullae of the okapi compared to the giraffe (Pocock, 1936).

d. Anatomical Characteristics

i. Feet

The feet of both the giraffe and the okapi are as specialized as those of any of the ungulates, with the second and the fifth digits (Frechkop, 1953). When these animals walk or run their toes spread apart. Both giraffids have hard, rounded hooves; those of the giraffe are illustrated in figure 22. The hoof print and tracks of a galloping giraffe are shown in figure 23. The hoof print of a male may measure over 305 mms long and 230 mms wide. Those of the females are somewhat smaller.

ii. Pertinent Measurements

In general ruminants have hind legs that are longer than the forelegs but in the giraffe the forelegs are the longer while in the okapi these legs are about the same length (Forsyth Major, 1902a). Both species have backs that slope down to the rump, but this slope is steeper in the giraffe than in the okapi.

The shoulder height of an okapi is about 1.6 m. An adult male at death weighed 227 kgs (Crandall, 1964). The shoulder height of a young 2.5 m tall giraffe is about 1.5 m and that of an adult 5 m tall about 3 m. One two month old male weighed 150 kgs (Black, 1915) and an adult may weigh 900 kgs or more.

2. Observations on Giraffa camelopardalis

a. The Walk

i. Source of Data

Fifty-eight sequences of 120 strides of 5687 frames filmed by the author.

Three sequences of 17 strides of 890 frames from "CBC-Web of Life."

Two sequences of 2 strides of 168 frames filmed by L. Linnard.

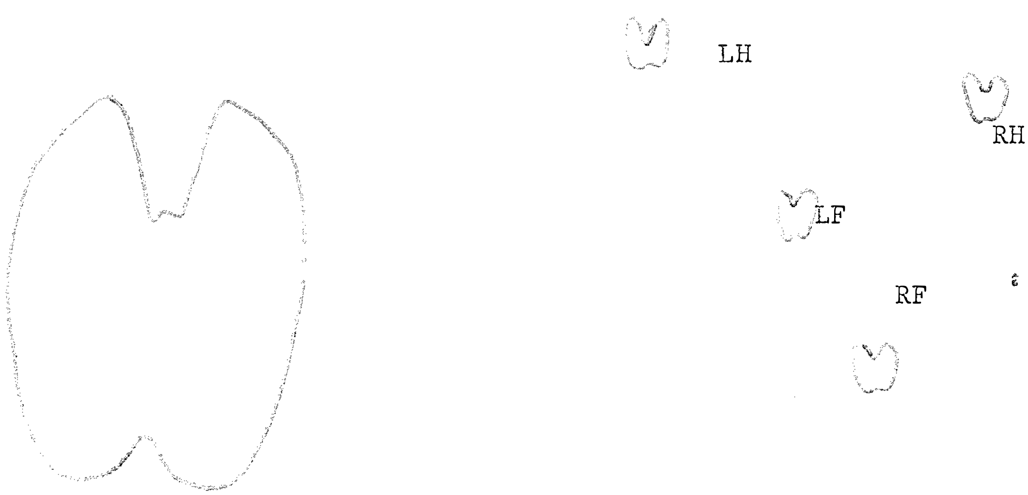
Figure 22

Hooves of Giraffe

Photo by J. B. Foster, 1966.

Figure 23

Giraffe Hoofprint and Tracks of the Gallop - after Jaegar, 1948



ii. Description and Film Analysis

Various authors have mentioned the unusual walk of the giraffe, in which the two legs on one side of the body swing forward nearly in unison. One writer remarked upon it as early as the fourth century (Mongez, 1827). Bourlière (1955) refers to this walk as an amble.

The walk patterns for adult giraffes (over 3 m tall) and for young giraffes (under 3 m) are given in Table 29. The patterns are similar (χ^2 test, $p = > .10$).

Walk patterns are calculated at different speeds for both young and adult giraffes. These are plotted in figures 24 and 25. From these graphs it is evident that with increased speed lateral legs tend to be

Table 29

Time Spent on Combinations of Supporting Legs for Walking Giraffe.

	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs on	Total	Strides averaged
Adult giraffe							
Frames observed	1984	4	999	1272	736	4995	92
Percentage of stride	40	0	20	25	15	100	
Young Giraffe							
Frames observed	728	3	317	426	238	1712	46
Percentage of stride	43	0	18	25	14	100	

used more and three legs less for both adult and young giraffes. The use of four legs is considerable and independent of speed. In these graphs forelegs are off the ground for a period of at least four per cent longer than hind legs.

The fastest walk pattern is highly significantly different than the slowest walk pattern (χ^2 test, $p = < .01$) for both the adult and the young giraffes.

Figure 24 Walking Patterns of Young Giraffe at Varying Speeds

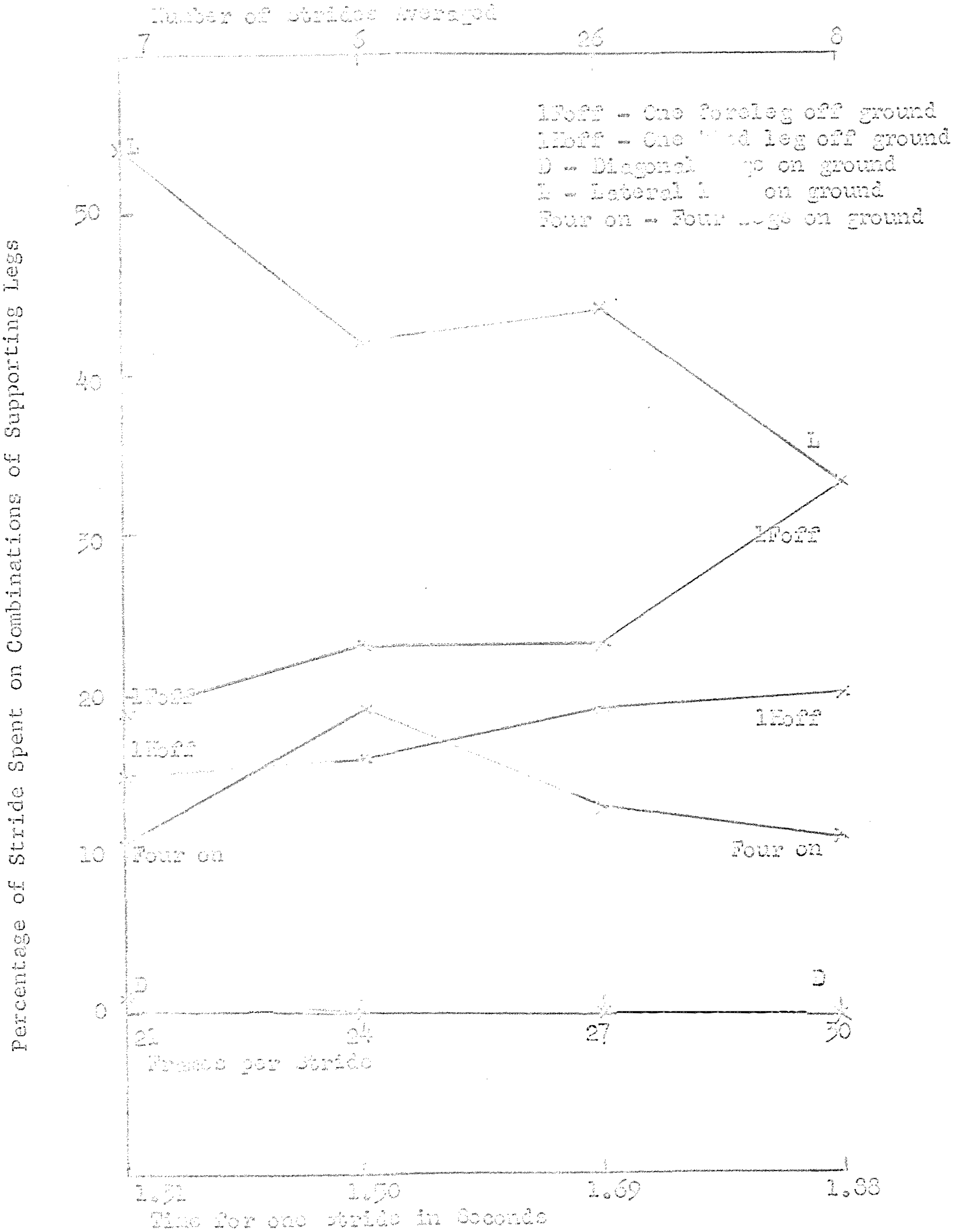
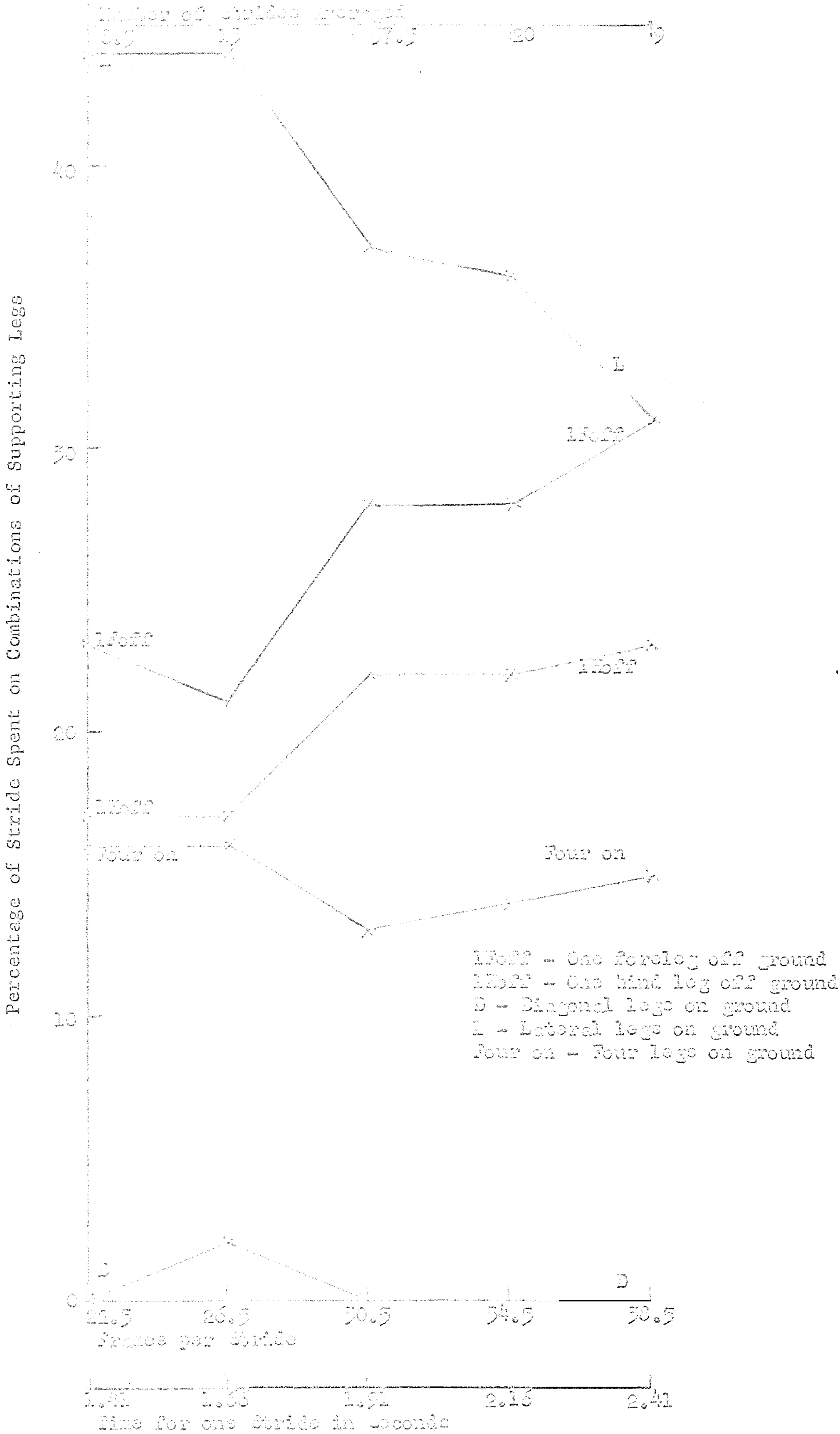


Figure 25 Avg. Walking Patterns of Adult Giraffe at Varying Speeds



The average walking stride of the young giraffes lasts 1.69 seconds (range 1.25 to 2.00, N = 23 sequences). That of the adults lasts 1.94 seconds ange 1.31 to 2.69, N = 36 sequences). From these data it seems that and small giraffe have similar fast walking strides but that the giraffe can walk much more slowly than the young giraffe. Apparently a large giraffe can walk more slowly because of its longer legs, its increased weight and its greater inertia.

b. The Gallop

i. Source of Data

Six sequences of 17 strides of 952 frames from CBC-"Web of Life."

Two sequences of 2 strides of 70 frames filmed by the author

Two sequences of 2 partial strides filmed by A. Keast

One sequence of 1 stride of 101 frames from "Africa Untamed."

ii. Description and Film Analysis

This gait is a remarkable one to watch. As the giraffe rushes along its head and neck stretch forward and back in time with the stride and the hind legs reach forward outside of the forelegs before they are set down upon the ground. Two phases of the gallop of a giraffe are illustrated in figures 26 and 27.

Twenty-one of the galloping strides are rotary and one is transverse. An analysis of 18 galloping strides of adult giraffes and two galloping strides of a giraffe under six months old are given in Table 30.

Figures 26 and 27

Phases of the Galloping Stride of a Giraffe   Photos by J. B. Foster

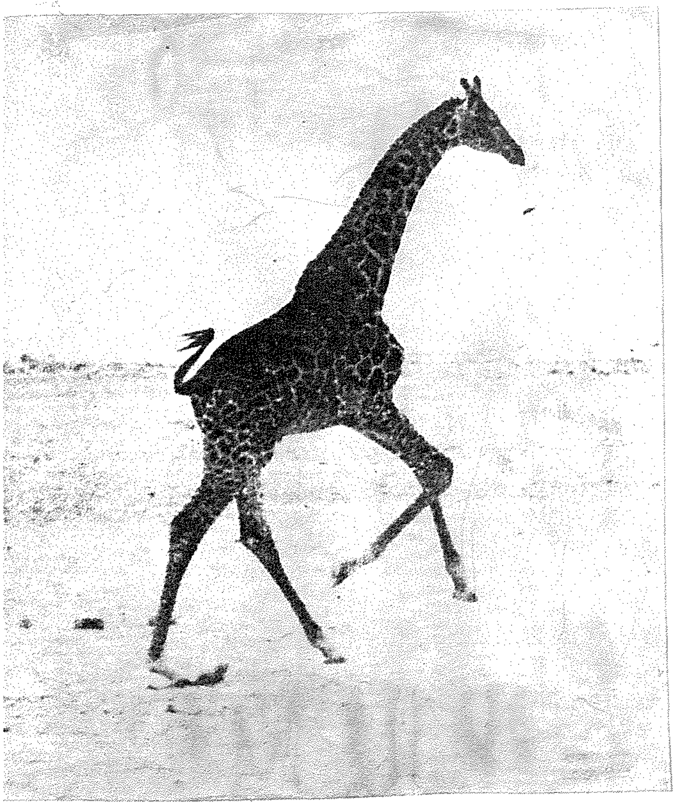


Table 30

Percentage Time Spent on Combinations of Supporting Legs of Adult and Young Galloping Giraffes.   Unknown camera speed

Combinations of supporting legs, not in the order in which they occur	Adults %age time of stride	Young Giraffe %age time of stride
One foreleg on ground	4	12
Both forelegs on ground	19	8
Lead foreleg on ground	16	22
Flexed suspension	0	10
One hind leg on ground	3	22
Both hind legs on ground	14	10
Lead hind leg on ground	1	9
Extended suspension	0	7
Fore and hind legs on ground - 2	29	0
Fore and hind legs on ground - 3	14	0
Number of strides averaged	18	2

In these data the gallop of the young giraffe is supported less than that of the adults. Both types of suspension are present in the young giraffe's gallop but none are found in the 18 strides of the adults. These data are undoubtedly correlated with the fact that the lighter young tend to be faster than the adults; if a group is stampeded the young giraffe usually lead the troop in flight.

3. Observations on *Okapia johnstoni*

a. The Walk

i. Source of Data

Six sequences of 18 strides of 443 frames filmed by the author at the New York Zoological Park

ii. Description and Film Analysis

The similarity of the walk of the okapi to that of the giraffe was noted in 1960 (Dagg, 1960). Both species use lateral supporting legs only for a large part of each stride. The walk pattern of one adult okapi is given in Table 31.

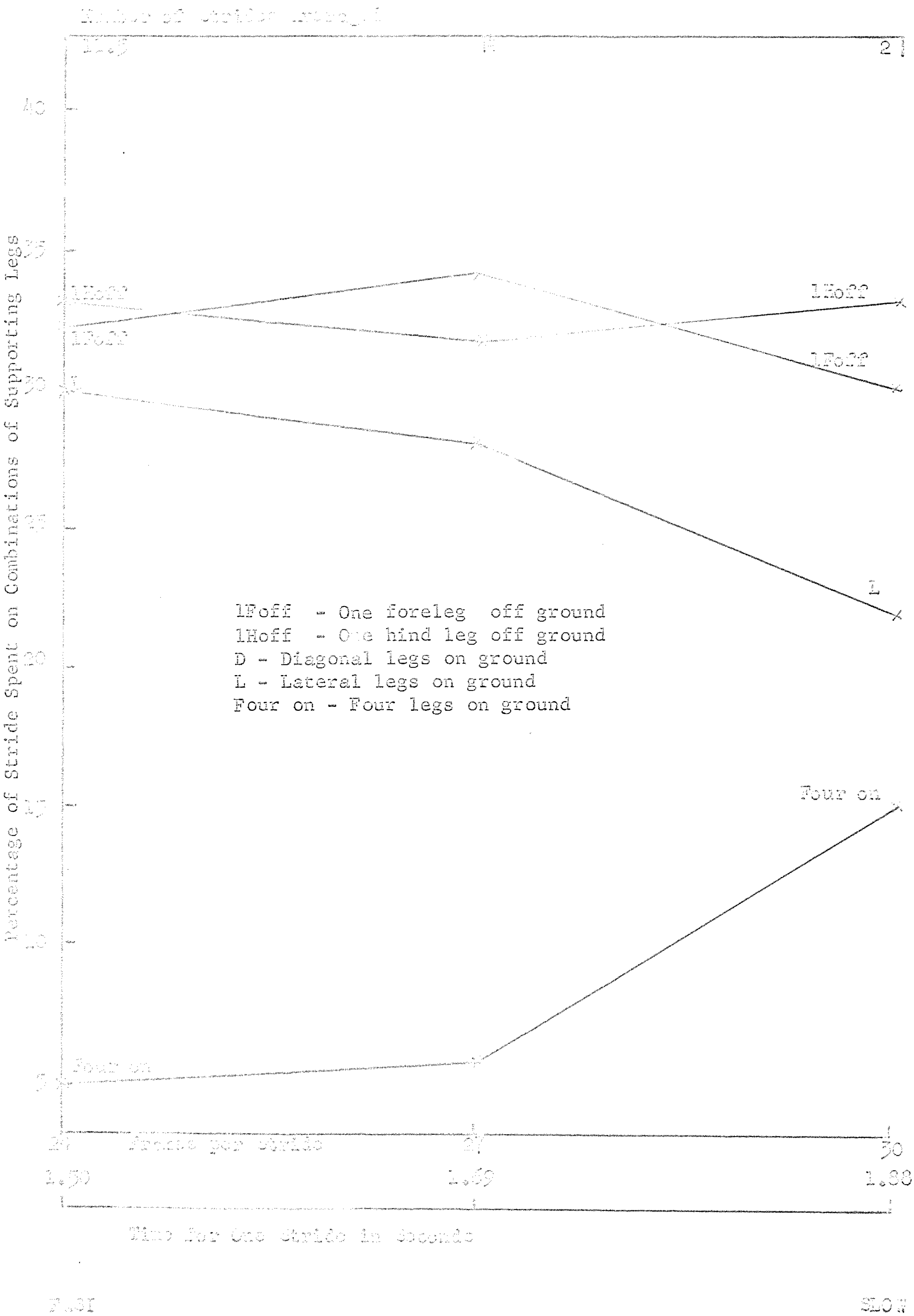
Table 31

Time Spent on Combinations of Supporting Legs of a Walking Adult Okapi

	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs on	Total	Strides averaged
Adult Okapi							
Frames observed	126	0	145	143	29	443	18
Percentage of stride	28	0	33	32	7	100	

The walk patterns, calculated at three different speeds, are given in figure 28. This graph shows that lateral legs are used less and four supporting legs more at slower speeds.

Figure 20 [illegible]



Percentage of Stride Spent on Combinations of Supporting Legs
40
35
30
25
20
15
10
5
2
1Hoff
1Foff
L
Four on
1Foff - One foreleg off ground
1Hoff - One hind leg off ground
D - Diagonal legs on ground
L - Lateral legs on ground
Four on - Four legs on ground
27
30
1.50
1.69
1.88
FAST
SLOW

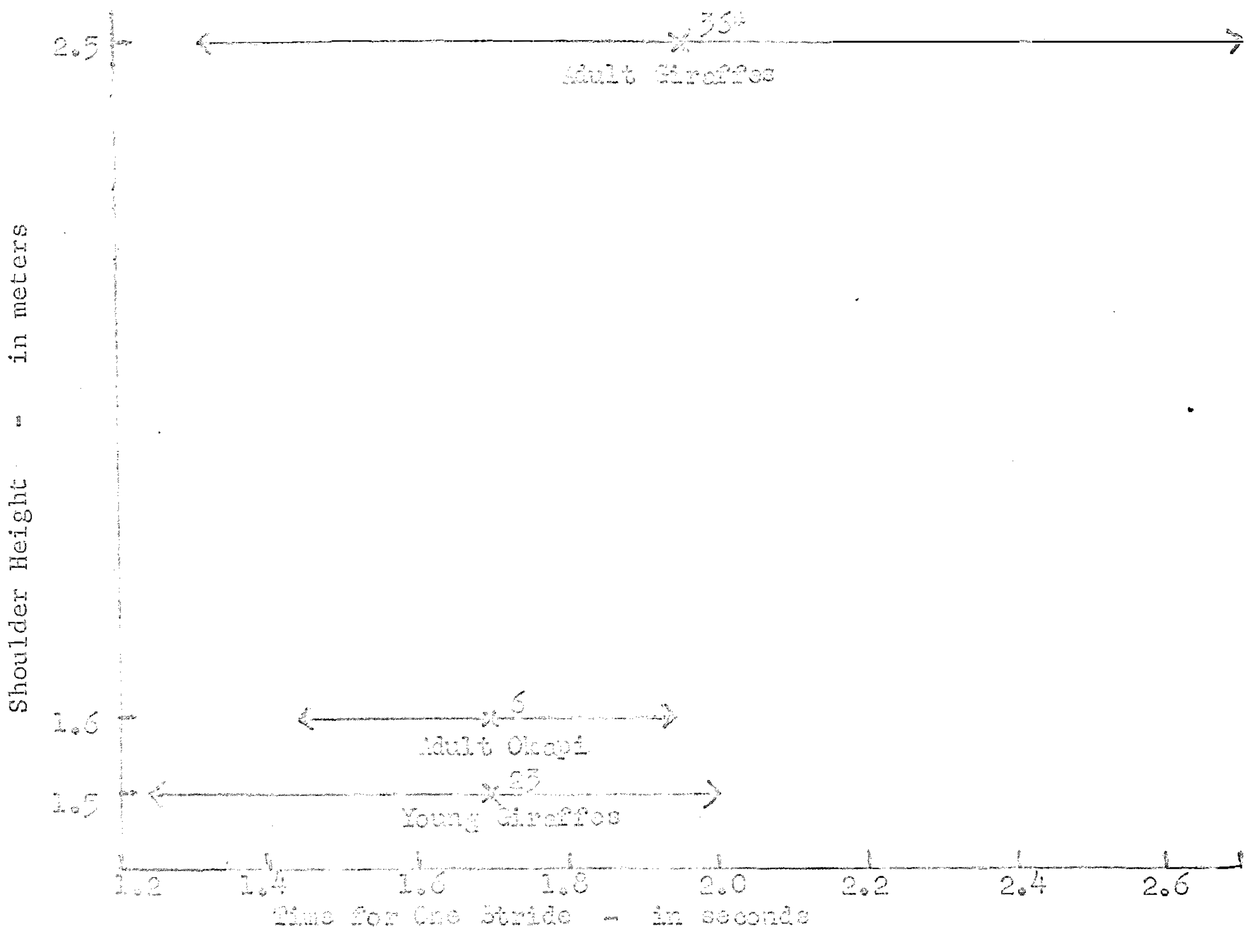
The average speed of a walking stride of this individual is 1.68 seconds (range 1.44 to 1.94, N sequences = 6).

4. Discussion of the Giraffid Walk

A comparison of the walk patterns of the giraffe and the okapi reveals that the giraffe uses lateral supporting legs for longer than does the okapi. This is true also for the young giraffe which has a shoulder height and therefore a leg length similar to that of the okapi. The more stable walk of the okapi can be correlated with its more densely wooded habitat. This animal must be able to stop instantly to detect danger.

The speed of a walking stride can vary considerably. Figure 29 indicates that the average speed is related to the shoulder height of these species.

Figure 29 Average Time and Range of Times for Walking Strides of Giraffids



* - Number of strides averaged

Part V. The Gaits of Antelope (Bovidae)

1. Factors Related to the Gaits of Antelope

a. Recorded Speeds

The difficulty of measuring the speed of these animals, particularly those that live in or near swamps where vehicles dare not venture, is reflected in the paucity of data. In general the fastest antelopes run at about 50 m.p.h. The largest antelopes (the kudu and the eland) and the Reducinae are probably much slower than this, although no exact measurements are available. Speeds that have been reported in the literature are listed in Table 32.

b. Jumping Abilities

The impala is a champion jumper among the antelopes. It can jump over 13 m horizontally and 3 m vertically (Stevenson-Hamilton, 1947). Elands, although much heavier, are agile enough to jump over each other (Percival, 1924). The kudu can leap 5 m horizontally (Percival, 1924) and 2.4 m vertically (Stevenson-Hamilton, 1947). Various antelopes give small leaps when alarmed and before running off. These include lechwe, impala and waterbuck (DeVos & Dowsett, 1966).

c. Habitats Frequented

The bovids are the most advanced group of ruminants. They evolved in northern Eurasia during and after the Pliocene, first migrating into Africa in the late Pliocene (Colbert, 1961). Unlike the cervids that are frequently browsers, the African antelopes are more often grazers.

The saiga is found on the desert and steppe areas west of the Gobi Desert (Bannikov, 1958). Because of the severe climatic conditions in these areas, especially in the winters, this species must often undergo vast migrations.

Table 32

Recorded Speeds of Antelope

Scientific name	Common Name	Speed	Reference
Saiginae			
Saiga tartarica	Saiga antelope	-38 m.p.h.	Walker, 1964
		-50 m.p.h.	Murie, 1870
		-50 m.p.h.	Grzimek, 1966
Gazellinae			
Gazella thomsonii	Thomson's gazelle	-50 m.p.h.	Guggisberg, 1961
		-over 50 m.p.h. for ½ a mile	Johnson in Howell, 1944
Gazella granti	Grant's gazelle	-over 50 m.p.h. for ½ a mile	Johnson in Howell, 1944
Aepyceros melampus	Impala	-35 m.p.h. for ½ a mile	Alberts, 1964
		-swifter than tsessebe	Kirby in Howell, 1944
Reduncinae			
Redunca arundinum	Reedbuck	-"not fast"	Trewhela, 1960
Kobus kob	Kob	-	
Kobus leche	Lechwe	-	
Kobus ellipsiprymnus	Waterbuck	-	
Alcelaphinae			
Damaliscus lunatus	Tsessebe	-"Fastest South African Antelope"	Selous in Howell, 1944
Alcelaphus buselaphus cokii	Kongoni	-barely 30 m.p.h.	Grzimek, 1960
Alcelaphus buselaphus	Hartebeest	-40 m.p.h.	Walker, 1964
Gorgon taurinus	Wildebeest	-50 m.p.h. for ¼ mile	Johnson in Howell, 1944
		-over 50 m.p.h.	Cockrum, 1962
		-over 35 m.p.h. at one wk. of age	Talbot & Talbot, 1963
Hippotraginae			
Hippotragus niger	Sable antelope	-36 m.p.h.	Walker, 1964
Strepsicerosinae			
Strepsiceros strepsiceros	Greater kudu	-	
Taurotragus oryx	Eland	-"slow"	Walker, 1964

Both species of gazelles considered are found on the open grasslands of East Africa. The impala which has a more widespread distribution in Africa inhabits areas of open bush (Dasmann & Mossman, 1962). Unlike the gazelles, the impala browses as well as grazes.

The Reduncinae are also known as marsh-antelopes, a name which corresponds roughly with their habitats. The lechwes are the most water-loving of the four species examined. They inhabit shallow grassy flood-plains that border open water and neighbouring swamps and lagoons (Maberly, 1959). They often swim or wade in the water. Reed-bucks also live near water, but they generally prefer the grasslands or open forests adjacent to the water. If disturbed they often flee into the marsh or reedbeds for safety. The kob inhabits both the flood plains of rivers and the edges of the light woodlands bordering them. The waterbuck, despite its name, is the species that may be found farthest from the water. Although it will take to the water if pursued, it also ranges into forested areas several miles from water (DeVos & Dowsett, 1966).

The alcelaphine antelopes are gregarious animals that inhabit open grasslands. They are primarily grazers.

The sable antelope ranges over much of Africa, inhabiting thinly forested and grassy country. It too grazes by preference.

The kudu is the only one of these animals that inhabits densely wooded areas by preference. It may be found in forested hilly areas or in dense bush veld. The eland is also a browser but it inhabits lightly forested regions or grassy areas with scattered bushes.

d. Anatomical Characteristics

i. Feet

The feet of the antelopes are more highly evolved than are those of the cervids, with the dewclaws in a more advanced state of reduction (Colbert, 1961). In the impala, as in the pronghorn, the dewclaws are no longer present at all. In members of the genus Kobus the dewclaws are relatively large as an adaptation to their riparian environment (Walker, 1964).

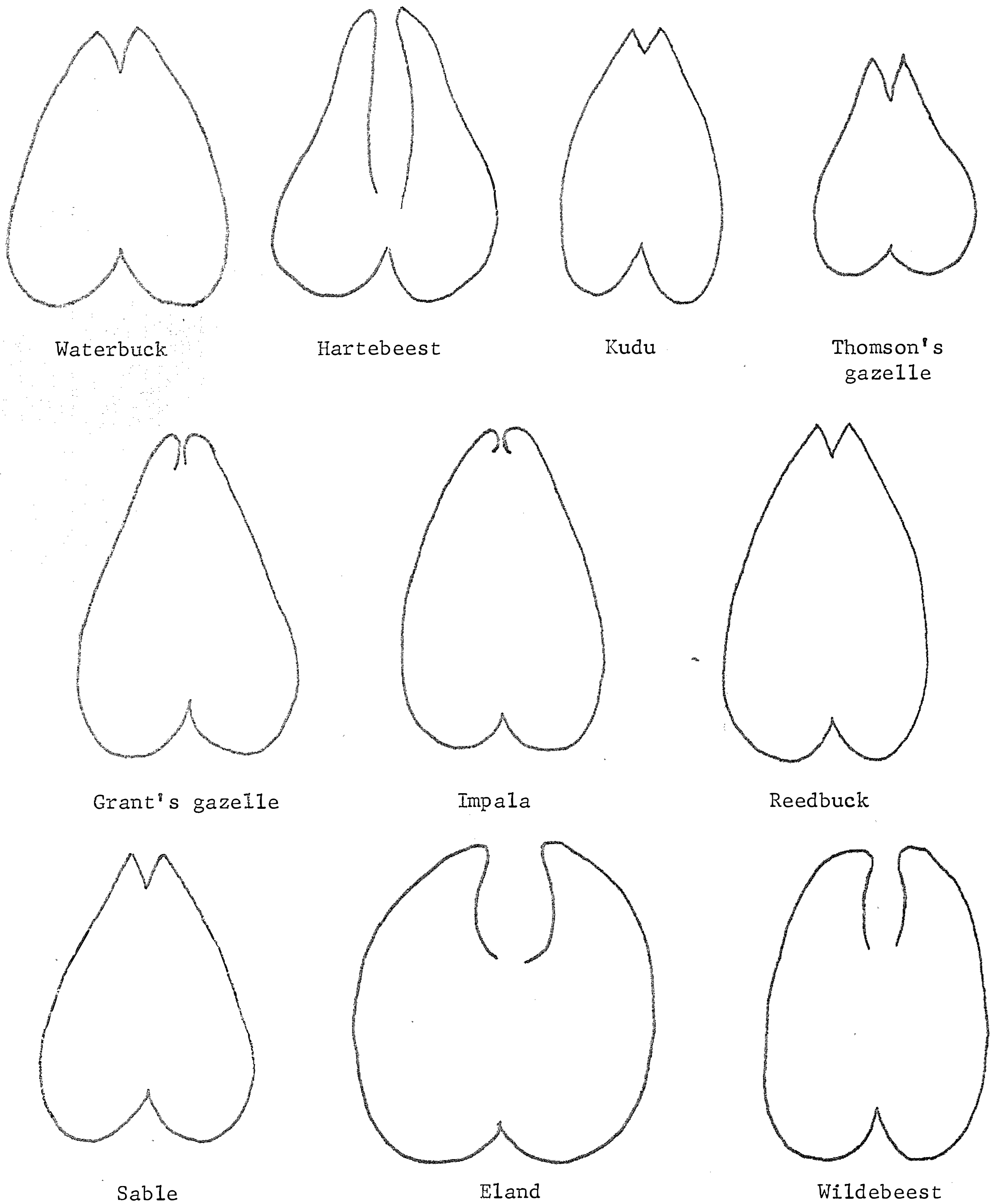
The standing hoof imprints of ten bovids are outlined in figure 30. The toes of the bovids splay out somewhat when the animals run (Hesse, 1957) and the dewclaws, if present, touch the ground as illustrated in figure 31.

ii. Pertinent Measurements

Measurements and observations that may affect the gaits of these species are presented in Tables 33 and 34.

Figure 30

Hoofprints of Some African Antelope - after Hesse, 1957



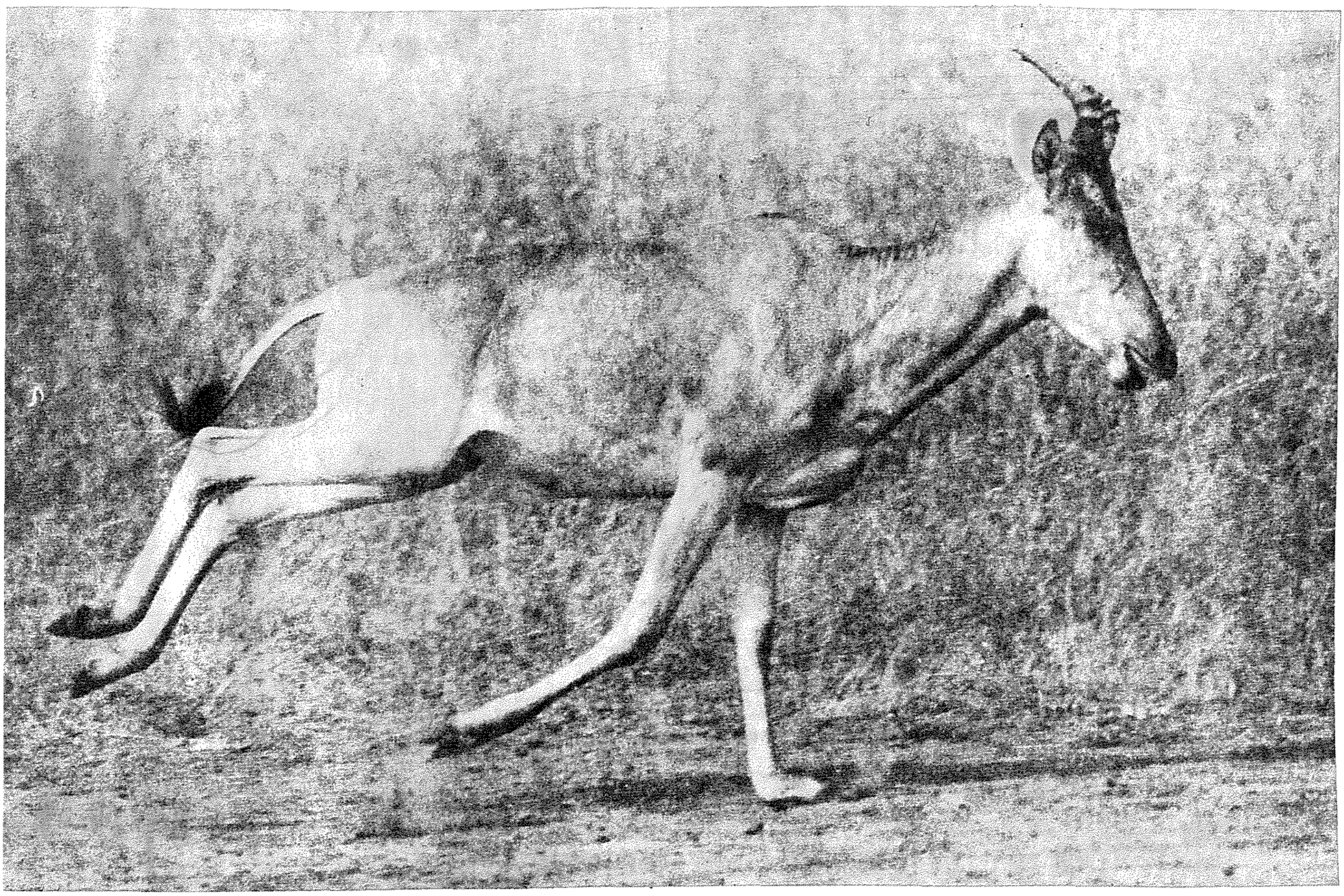


Figure 31

Galloping Hartebeest Showing the Use of the Dewclaws
Photo by J. B. Foster

Table 33

Presence of Horns and General Body Conformation of Antelopes

Species	Horns	Body Conformation
Saiga	Male only, to 25 cms (Walker, 1964)	Sheeplike
Thomson's gazelle	Male and female	Resembles the shape of the pronghorn
Grant's gazelle	Male and female	
Impala	Male only	
Reedbuck	Male only	Dama-like, with the rump higher than the shoulders (see figure 32)
Kob	Male only	
Lechwe	Male only - to 80 cms (DeVos, pers. comm.)	
Waterbuck	Male only	
Hartebeest	Male and female	Shoulders higher than rump, so back sloping. (see figure 32)
Kongoni	Male and female	
Tsessebe	Male and female	
Wildebeest	Male and female	
Sable	Male and female	-
Kudu	Male only	-
Eland	Male and female	Cow-like

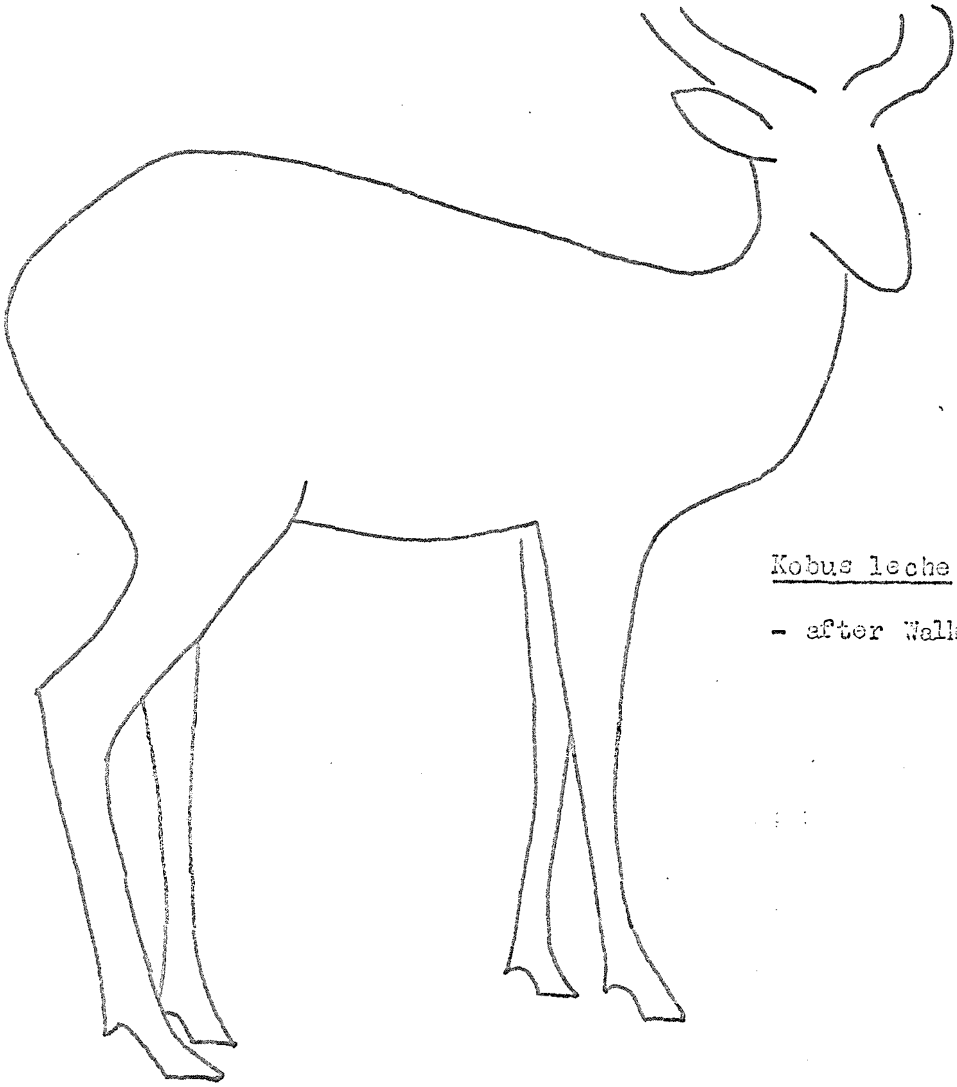
Table 34

Shoulder Heights and Weights of Antelopes

Species	Shoulder Height - in cms	Ref.	Least adult weight - in kgs	Reference
Saiga	80	Walker, 1964	36	Walker, 1964
Thomson's gazelle	66	Meinertzhagen, 1938 *N = 39	22	Bourlière, 1963
Grant's gazelle	98	Meinertzhagen, 1938 N = 20	60	Bourlière, 1963
Impala	100	Walker, 1964	60	Bourlière, 1963
Reedbuck	93	Meinertzhagen, 1938 N = 8	40	Bourlière, 1963
Kob	97	Meinertzhagen, 1938 N = 5	70	Bourlière, 1963
Lechwe	112	Meinertzhagen, 1938 N = 1	--	
Waterbuck	116	Meinertzhagen, 1938 N = 24	150	Bourlière, 1963
Hartebeest	119	Meinertzhagen, 1938 N = 30	160	Walker, 1964
Kongoni	--		140	Bourlière, 1963
Tsessebe	122	Stevenson-Hamilton, 1947	136	Stevenson-Hamilton, 1947
Wildebeest	133	Meinertzhagen, 1938 N = 14	200	Bourlière, 1963
Sable	130	Meinertzhagen, 1938 N = 3	204	Walker, 1964
Kudu	142	Meinertzhagen, 1938 N = 3	250	Bourlière, 1963
Eland	164	Meinertzhagen, 1938 N = 6	300	Bourlière, 1963

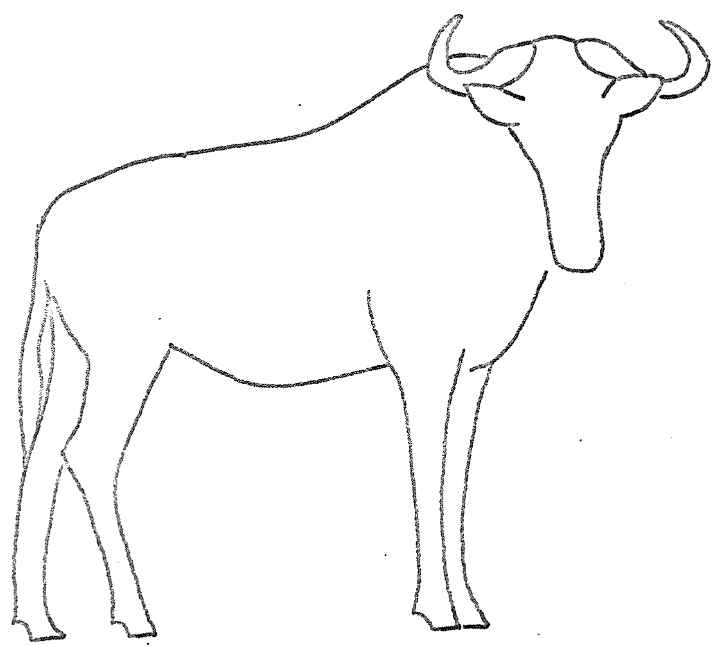
*N = No. of individual measurements averaged.

Figure 32 Body Conformations of Two Antelopes



Kobus leche

- after Walker, 1964



Gorgon taurinus

- from Kruger National Park souvenir booklet

2. Observations on Saiga tartarica

a. The Walk

i. Source of Data

Nine sequences of 18 strides of 229 frames filmed by the author at Assiniboine Park Zoo, Winnipeg.

ii. Description and Film Analysis

The saiga walks in a shambling fashion, with its head hung forward rather than carried alertly up. The walk patterns of one adult male and of one adult female saiga are given in Table 35.

Table 35

Time Spent on Combinations of Supporting Legs of Walking Adult Saiga Antelopes.

	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs	Total	Number of strides averaged
Male							
Frames observed	37	8	31	45	3	124	11
Percentage of stride	30	7	24	36	3	100	
Female							
Frames observed	31	1	26	41	6	105	7
Percentage of stride	29	1	25	39	6	100	
Total adults							
Percentage of stride	30	4	25	37	4	100	18

The walk patterns of the male and of the female are similar (χ^2 test, $p = > .10$).

The of a stride for the male and the female are similar. They average 0.84 seconds (range 0.63 to 1.13 seconds, N sequences = 9).

b. The Trot

i. Source of Data

Two sequences of five strides of 42 frames filmed by the author at Assiniboine Park Zoo.

ii. Description and Film Analysis

The sequence of the male and that of the female are similar. During their average trotting stride these saiga antelopes are supported by diagonal legs for 84% of the time of the stride, by lateral legs 2%, by three legs with one front leg off the ground 2% and by no legs 12% of the time of the stride.

The average time for a trotting stride is 0.53 seconds (range 0.44 to 0.63 seconds, N strides = 5).

c. The Gallop

i. Source of Data

One sequence of 2 plus strides of 11 frames filmed by the author at Assiniboine Park Zoo.

ii. Description and Film Analysis

The series of foot impacts of these slow strides are both rotary. The strides last 0.31 and 0.38 seconds. The female spends 36% of the stride on 3 legs, 36% on one foreleg and 28% on one hind leg. There are no periods of suspension.

3. Observations on Gazella thomsonii

a. The Walk

i. Source of Data

One sequence of 7 strides of 129 frames filmed by A. Keast

ii. Description and Film Analysis

The walk of this genus is alert and graceful. The walk pattern of an adult is given in Table 36.

Table 36

Time Spent on Combinations of Supporting Legs of a Walking Adult Thomson's Gazelle

	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs on	Total	Number of strides averaged
Adult Thomson's gazelle							
Frames observed	57	0	34	23	15	129	7
Percentage of stride	44	0	26	18	12	100	

The average walking stride of this sequence lasts 0.75 seconds.

b. The Trot

i. Source of Data

One sequence of 2 strides of 46 frames filmed by A. Keast

ii. Description and Film Analysis

The Thomson's gazelle is supported by diagonal legs 92% of the time of the stride, by three legs with one foreleg off the ground 4% and by two hind legs 4% of the time of the stride. There is no period of suspension.

4. Observations on *Gazella granti*

a. The Walk

i. Source of Data

One sequence of 8.5 strides of 515 frames from "CBC - Web of Life."

ii. Description and Film Analysis

The walk pattern of the adult is given in Table 37.

Table 37

Time Spent on Combinations of Supporting Legs of a Walking Adult Grant's Gazelle

	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs on	Total	Number of strides averaged
Adult Grant's gazelle							
Frames observed	167	20	148	178	2	515	8.5
Percentage of stride	32	4	29	35	0	100	

5. Observations on Aepyceros melampus

a. The Walk

i. Sources of Data

Six sequences of 8 strides of 282 frames filmed by L. Linnard

One sequence of 0.5 strides of 14 frames filmed by A. Keast

ii. Description and Film Analysis

The walk patterns for the horned male impala and for the half-grown impala are given in Table 38.

Table 38

Time Spent on Combinations of Supporting Legs of Walking Impalas

	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs on	Total	Number of strides averaged
Male adult							
Frames observed	83	8	68	64	13	236	6.5
Percentage of stride	35	3	29	27	6	100	
Young impala							
Frames observed	22	0	18	19	1	60	2
Percentage of stride	37	0	30	32	1	100	

The patterns for the adult male and for the half-grown young are similar (χ^2 test, $p = > .30$). The two sequences for the half-grown impala last 1.08 and 1.33 seconds. Those for the male average 1.44 seconds (range 1.17 to 1.67 seconds, N sequences = 5).

b. <u>The Trot</u>

i. <u>Source of Data</u>

One sequence of 1.5 strides of 18 frames filmed by P. C. Lent.

ii. <u>Description and Film Analysis</u>

This female is supported by diagonal legs 72% of the time of the stride, by lateral legs 22%, and by three legs with one hind leg in the air 6%. The strides average 0.50 seconds.

c. <u>The Gallop</u>

i. <u>Source of Data</u>

Fifteen sequences of 17 strides of 259 frames filmed by P. C. Lent.

One sequence of 1 stride of 13 frames filmed by A. Keast.

ii. <u>Description and Film Analysis</u>

The bounding gallop of the impala is spectacular. Krieg (in Hediger, 1951) felt that this method of locomotion was so "extravagant" that it was beyond efficacy the function of the high leaps apparently being to confuse the predator.

The sequences filmed show impala does leaping high into the air during flight. In at least two sequences of suspensions following a push-off with the forefeet an animal sailed through the air with its tail on a higher level than its head. The brilliant whiteness of the animal's belly during the leap was striking to an observer behind the animal. The bounds can cover up to 13 m horizontally and 3 m vertically (Stevenson-Hamilton, 1947).

So many of these strides are symmetrical, with the impala launching itself from and landing onto two front or two hind legs at once, that the sequence of foot impacts can only be determined for five strides; four of these sequences are rotary and one is transverse. These strides often resemble bounds because of their symmetry, but the animals are never supported by all four legs at once and all of the strides are therefore considered as galloping ones. The average stride lasts 0.63 seconds (range 0.29 to 0.88 seconds, N strides = 18).

The analysis of these strides is given in Table 39.

Table 39

Analysis of 18 Galloping Strides of Impala. 24 f.p.s.

Combinations of supporting legs not in the order in which they occur	Average time per stride - in secs	Range of times - in secs	Average percentage time of stride
One foreleg on ground	.016	0-.083	3
Both forelegs on ground	.118	.042-.250	19
Lead foreleg on ground	.047	0-.208	7
Flexed suspension	.227	.042-.458	36
One hind leg on ground	.018	0-.083	3
Two hind legs on ground	.116	.083-.208	18
Lead hind leg on ground	.004	0-.083	1
Extended suspension	.067	0-.583	11
Fore and hind legs on ground			
-two	.009	0-.083	1
-three	.007	0-.083	1
	.629	.292-.792	100

6. Observations on Redunca arundinum

a. The Gallop

i. Source of Data

Two sequences of nearly 3 strides of 40 frames filmed by P. C. Lent.

ii. Description and Film Analysis

The tails are held upright when reedbucks gallop or bound off so that the white underside is exposed. The hind quarters are thrown into the air at each stride, creating a distinctive "rocking horse action," that is accentuated by the high rump of the antelope. Reedbucks do not run far before hunting for cover to hide in (Walker, 1964).

The three strides all have rotary sequences of foot impacts. The average stride lasts 0.58 seconds. These females spend 8% of the time of the average stride on the non-lead forefoot, 10% on both forefeet, 15% on the lead forefoot, 15% on the non-lead hind foot, 20% on both hind legs, 8% on the lead hind leg and 5% on a front and a hind leg. The reedbucks spend 16% of the stride in a flexed suspension and 3% in an extended suspension.

b. The Bound

i. Source of Data

Five sequences of 3 complete strides of 41 frames and several incomplete strides filmed by P. C. Lent.

ii. Description and Film Analysis

The strides average 0.56 seconds (range 0.50 to 0.67 seconds). During these bounds by female reedbuck the animals are supported by two front legs at the end of the period of suspension 15% of an average stride, by four legs 7% and by two hind legs at the beginning of the leap 25%. The suspension lasts 46% of the time of the stride. The three leaps themselves last 0.21, 0.29 and 0.29 seconds. This gait is not completely symmetrical as one hind leg supports a reedbuck by itself 5% and three legs support it 2% of the time of an average stride.

7. Observations of Kobus kob

a. The Walk

i. Source of Data

Three sequences of 7.5 strides of 433 frames from "CBC- Web of Life."

ii. Description and Film Analysis

The walk pattern of these male adult Uganda kobs is given in Table 40.

Table 40

Time Spent on Combinations of Supporting Legs of Walking Uganda Kobs.

	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs on	Total	Number of strides averaged
Uganda kob							
Frames observed	169	34	135	88	7	433	7.5
Percentage of stride	39	8	31	20	2	100	

b. The Gallop

i. Source of Data

Three sequences of 41 strides of 1151 frames from "CBC - Web of Life."

ii. Description and Film Analysis

There are 40 rotary sequences of foot impacts and one transverse sequence. The strides, all taken of males galloping on flat ground, are divided into groups to see if the pattern of the gallops varied with the speed. When the strides are grouped from fast to slow by the number of frames required for a stride (26, 27, 28 and 29-30 frames), the average number of frames spent in a flexed suspension decrease (2.1, 1.9, 1.3 and 0.8 respectively,) although at any speed strides have from 0 to 3 or 4 frames of flexed suspension.

The strides are grouped according to whether they have 0, 1, 2 or 3-4 frames of suspension in Table 41a. From these data is it evident that those strides with longer periods of suspension use three supporting legs less. The analysis of all the strides is given in Table 41b.

Table 41

Analysis of 41 Galloping Strides of Uganda Kobs. Unknown camera speed

Combinations of supporting legs not in the order in which they occur

a. Analysis of strides grouped for increased use of the flexed suspension					b. Analysis of all strides		
	Slow to fast Number of frames				Aver. No. of frames	Range of frames	Aver. %age of time of stride
One foreleg on ground	0	1	2	1	0.2	0-1	1
Both forelegs on ground	6	8	9	10	2.4	1-4	8
Lead foreleg on ground	24	28	26	24	7.0	6-10	25
Flexed suspension	0	4	7	12	1.6	0-4	6
One hind leg on ground	15	15	17	16	4.4	3-6	16
Two hind legs on ground	3	9	10	11	2.4	0-5	8
Lead hind leg on ground	0	0	0	0	0	-	0
Extended suspension	0	0	0	0	0	-	0
Fore plus hind legs on ground -two	17	11	13	16	4.2	1-7	15
-three	35	24	16	10	5.9	0-13	21
	100	100	100	100	28.1	26-30	100
Number of frames examined	12	8	9	12	41		41

8. Observations on Kobus leche

a. The Walk

i. Source of Data

Twenty-three sequences of 36 strides of 1075 frames filmed by P. C. Lent.

ii. Description and Film Analysis

The walk patterns for large horned males, for female adults and for fawns are given in Table 42.

Table 42

Time Spent on Combinations of Supporting Legs of Walking Lechwes.

	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs on	Total	Number of strides averaged
Males							
Frames observed	170	5	158	180	23	536	17
Percentage of stride	32	1	29	34	4	100	
Females							
Frames observed	158	23	127	156	8	472	16.5
Percentage of stride	33	5	27	33	2	100	
Fawns							
Frames observed	24	0	22	21	0	67	2.5
Percentage of stride	36	0	33	31	0	100	
Total Adults percentage of stride	33	3	28	33	3		33.5

The walk pattern of the fawns is similar to that of the females (χ^2 test, p = $>$ .20), which are hornless and it is similar to that of the horned males (χ^2 test, p = $>$.05). The walk pattern of the females is highly significantly different from that of the males (χ^2 test, p = $<$.01).

The walk patterns were calculated at different speeds for the male and for the female lechwes. The results were similar. These data are grouped together and the walk patterns of these adults executed at different speeds are given in figure 33. This graph shows that the walk pattern does not change decisively with the speed at which the walk is executed.

The two walking stride sequences of the lambs last 1.13 and 1.17 seconds. Those of the males are similar in duration to those of the females. The adult walking strides average 1.26 seconds (range 1.08 to 1.42 seconds, N sequences = 20).

b. The Trot

i. Source of Data

Six sequences of 6 strides of 75 frames filmed by P. C. Lent.

ii. Description and Film Analysis

The posture of these trotting lechwes is unusual as compared to other members of the genus *Kobus*. They move with their heads stretched forward and low to the ground.

In an average stride these animals are supported by diagonal legs 74% of the time of the stride, by only one hind leg 15% and by no legs 11% of the time of the stride.

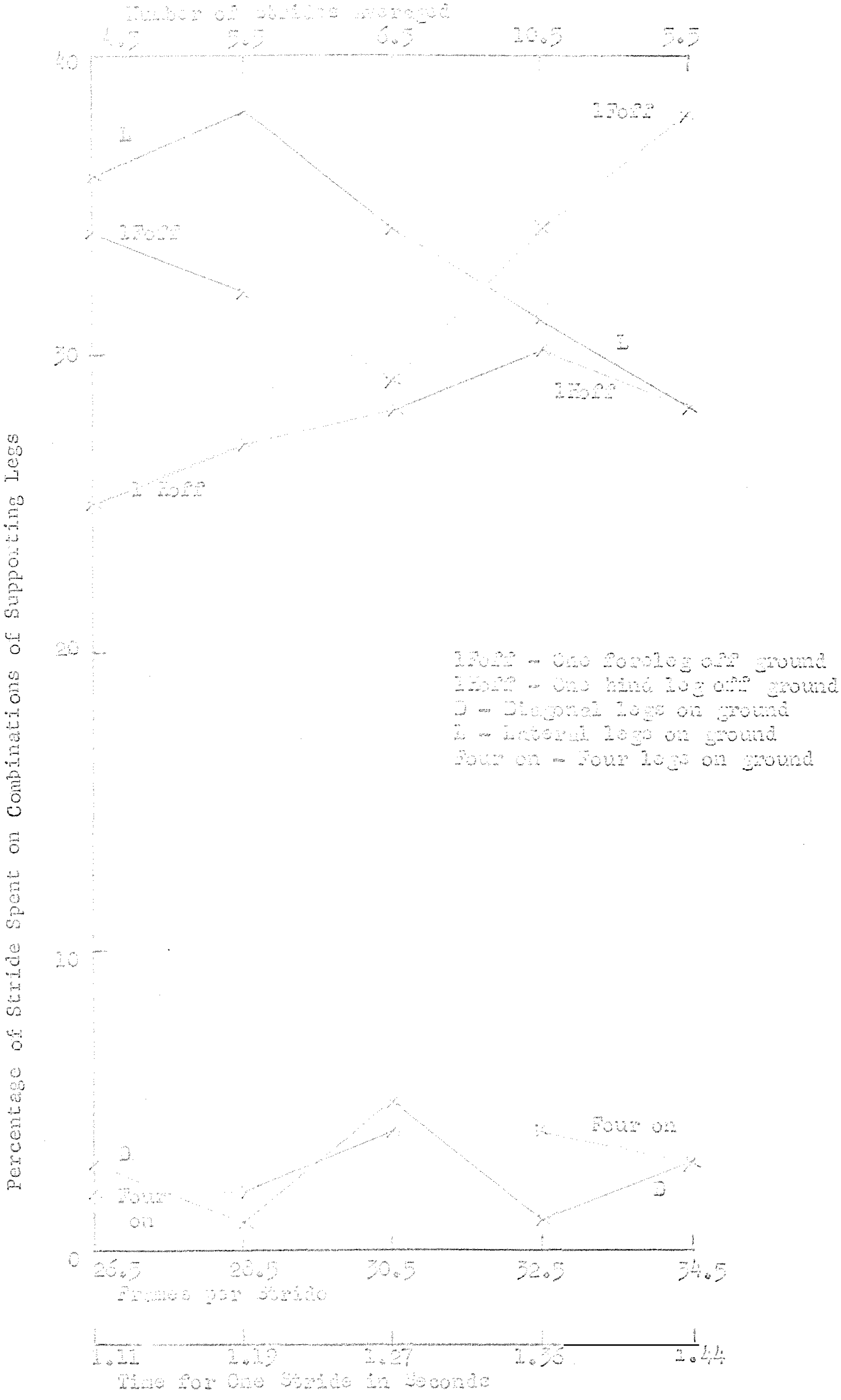
The average stride lasts 0.52 seconds (range 0.50 to 0.58 seconds, N strides = 6).

c. The Gallop

i. Source of Data

Thirteen sequences of 17 strides of 216 frames plus incomplete strides filmed by P. C. Lent.

Figure 35 Walking Patterns of Lechwe at Varying Speeds



ii. Description and Film Analysis

The gallop of this species is often referred to as a "rocking horse gait" because of the rollicking manner in which the rump and then the shoulders are thrust into the air during each stride. During these strides a rotary sequence of foot impacts is used five times and a transverse sequence six times. The two strides of lambs both last 0.42 seconds; those of the adults average 0.54 seconds (range 0.46 to 0.63 seconds, N strides = 15).

The gallop patterns of the adults and lambs are similar so these are grouped together. The analysis of all these strides is given in Table 43.

Table 43

Analysis of 17 Galloping Strides of Lechwes. 24 f.p.s.

Combinations of supporting legs not in the order in which they occur	Average time per stride - in secs	Range of times - in secs	Average percentage of times of stride
One foreleg on the ground	0.65	0-.125	12
Two forelegs on the ground	.052	0-.125	10
Lead foreleg on the ground	.118	.083-.208	22
Flexed suspension	.090	0-.208	17
One hind leg on the ground	.045	0-.125	8
Two hind legs on the ground	.079	.042-.125	14
Lead hind leg on the ground	.010	0-.083	2
Extended suspension	.030	0-.208	6
Foreleg plus hind leg on ground			
- two	.028	0-.167	5
- three	.023	0-.167	4
	.540	.417-.625	100

d. The Bound

i. Source of Data

Seven sequences of 4 strides plus incomplete strides filmed by P. C. Lent.

ii. Description and Film Analysis

During a bound, the head is raised high so that the lechwes can see well ahead. The legs hang down under the body and parallel to each other. The four strides last an average of 0.57 seconds (range 0.38 to 0.67, N strides = 4).

The lechwes are supported during an average bound by two front legs following the leap 13% of the time of the stride, by four legs 18% and by two hind legs prior to the suspension 13% of the stride. Three legs are used an average of 3% of the stride. The periods of suspension average 53% of the stride. The seven leaps that are filmed last 0.17, 0.25, 0.33, 0.38, 0.42, 0.46 and 0.50 seconds or an average of 0.36 seconds.

9. Observations on Kobus ellipsiprymnus.

a. The Walk

i. Source of Data

One sequence of 2 strides of 150 frames from "CBC - Web of Life."

ii. Description and Film Analysis

The walk pattern of this male waterbuck is given in Table 44.

Table 44

Time Spent on Combinations of Supporting Legs of a Walking Waterbuck

	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs on	Total	Number of strides averaged
Waterbuck							
Frames observed	27	34	53	36	0	150	2
Percentage of stride	18	23	35	24	0	100	

b. The Trot

i. Source of Data

One sequence of 1.5 strides of 64 frames from "CBC - Web of Life."

ii. Description and Film Analysis

This male is supported by diagonal legs 79% of the time of an average stride, by three legs with one front and with one hind leg off the ground each 9% and with all four legs on the ground 3% of the time.

10. Observations on *Damaliscus lunatus*

a. The Walk

i. Source of Data

Seven sequences of 14 strides of 179 frames filmed by P. C. Lent.

ii. Description and Film Analysis

The walk pattern for tsessebe adults and for a newly-born fawn are given in Table 45.

Table 45

Time Spent on Combinations of supporting legs of walking Tsessebes.

	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs on	Total	Number of strides averaged
Adult							
Frames observed	78	18	66	79	0	241	9
Percentage of stride	32	8	27	33	0	100	
Newly born fawn							
Frames observed	45	0	32	46	6	129	5
Percentage of stride	35	0	25	36	4	100	

The patterns of the adults and of the newly-born fawn are highly significantly different (χ^2 test, $p = < .01$).

The strides of the fawn last 1.08 seconds (N sequences = 2). Those of the adults average 1.15 seconds (range 1.08 to 1.33 seconds, N sequences = 5).

b. The Gallop

i. Source of Data

One sequence of 1 plus strides of 13 frames filmed by P. C. Lent.

ii. Description and Film Analysis

Although this gait is reported to be fast, it appears lumbering. The single sequence of foot impacts is rotary. The stride lasts 0.54 seconds. The tsessebe is supported by the lead forefoot 31% of the stride, by the non-lead hind leg 23%, by both hind legs 8%, by a front and a hind leg 7% and by three legs 23%. It is in a flexed suspension 8% of the time of the stride.

II. Observations on *Alcelaphus buselaphus cokii*

a. The Gallop

i. Source of Data

Three sequences of 9 strides of 130 frames filmed by L. Linnard.

ii. Description and Film Analysis

Four sequences of the foot impacts of these galloping kongonis are rotary and four are transverse. The average stride lasts 0.60 seconds (range 0.50 to 0.71, N strides = 9). An analysis of the galloping strides is given in Table 46.

Table 46

Analysis of Nine Galloping Strides of Kongonis. 24 f.p.s.

Combinations of supporting legs not in the order in which they occur	Average time per stride - in secs	Range of times - in secs	Average percentage of times of stride
Two forelegs on the ground	.051	0-.125	9
Lead foreleg on ground	.111	.042-.167	18
Flexed suspension	.146	.042-.250	25
One hind leg on ground	.070	0-.125	11
Two hind legs on ground	.097	0-.208	16
Fore and hind legs on ground			
- two	.009	0-.042	2
- three	.116	0-.250	19
	.600	.500-.708	100

12. Observations on Alcelaphus buselaphus

a. The Walk

i. Source of Data

Three sequences of 8.5 strides of 454 frames from "CBC - Web of Life."

ii. Description and Film Analysis

The walk pattern of these adults is given in Table 47.

Table 47

Time Spent on Combinations of Supporting Legs of Walking Hartebeests.

	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs on	Total	Number of strides averaged
Adult hartebeest							
Frames observed	130	0	101	161	62	454	8.5
Percentage of stride	29	0	22	35	14	100	

The duration of the two walking strides is 1.21 and 1.42 seconds.

13. Observations on Gorgon taurinus

a. The Walk

i. Source of Data

Five sequences of 11 strides of 384 frames filmed by A. Keast

Two sequences of 1 stride of 70 frames from "CBC- Web of Life."

One sequence of 1 stride of 22 frames filmed by P. C. Lent

ii. Description and Film Analysis

The wildebeest carries its head low as it walks. The walk pattern for these adults is given in Table 48.

Table 48

Time Spent on Combinations of Supporting Legs of Walking Wildebeests

	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs on	Total	Number of strides averaged
Wildebeest adults							
Frames observed	120	21	149	163	12	465	13
Percentage of stride	26	4	32	35	3	100	

The average walking stride lasts 1.40 seconds (range 0.92 to 1.67 seconds, N sequences = 6).

b. The Gallop

i. Source of Data

Two sequences of 14 strides of 438 frames from "CBC - Web of Life."

ii. Description and Film Analysis

The analysis of these strides is given in Table 49. In this slow gallop the series of foot impacts are rotary in three and transverse in five strides. The foreleg on the same side as the first supporting hind leg is set down before the second hind leg in two strides and the diagonal foreleg is placed on the ground before the second hind leg but after the first hind leg in one stride.

Various observers of wild wildebeests have remarked upon the skittish nature of their gallop. The irregularities of this gait are explained in part by the varied sequences of foot impacts in a stride, as well as by the large number of combinations of supporting legs used in these strides and by the frequent change of lead. In nine consecutive strides an individual changed its lead foot three times. Perhaps these unusual variations help in eluding prey or perhaps they are connected with the frequent massive infestations of dipteran larvae which irritate the nasal passages and upset the animals (Lydekker, 1908).

Table 49

Analysis of 14 Galloping Strides of Wildebeests unknown camera speed

Combinations of supporting legs not in the order in which they occur	Average number of frames per stride	Range of number of frames	Average percentage of stride
Two front legs on ground	1.0	0-2	3
Lead front leg on ground	7.7	4-10	25
Flexed suspension	3.9	0-7	13
One hind leg on ground	6.2	3-10	20
Two hind legs on ground	1.1	0-4	4
Front and hind legs on ground			
- two	3.0	0-7	9
- three	8.1	5-12	26
- four	0.1	0-2	0
	31.1	26-34	100

14. Observations on *Hippotragus niger*

a. The Trot

i. Source of Data

One sequence of 3.5 strides of 70 frames filmed by P. C. Lent

ii. Description and Film Analysis

During an average trotting stride this animal is supported by diagonal legs 77% of the time of the stride, by only one foreleg 3% and by no legs 20% of the time of the stride.

The strides last an average of 0.83 seconds (range 0.79 to 0.88 seconds, N strides = 3).

15. Observations on *Strepsiceros strepsiceros*

a. The Walk

i. Source of Data

One sequence of 5 strides of 188 frames filmed by A. Keast

ii. Description and Film Analysis

The walk of the kudu, especially the male, is stately. The walk pattern of a bull with large horns is given in Table 50.

Table 50

Time Spent on Combinations of Supporting Legs of a Walking Kudu.

	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs on	Total	Number of strides averaged
Kudu							
Frames observed	13	15	61	99	0	188	5
Percentage of stride	7	8	32	53	0	100	

The time for an average walking stride in this sequence averages 1.75 seconds.

16. Observations on Taurotragus oryx

a. The Walk

i. Source of Data

Two sequences of 5.5 strides of 266 frames filmed by L. Linnard

ii. Description and Film Analysis

The walk pattern of the adult eland is given in Table 51.

Table 51

Time Spent on Combinations of Supporting Legs of a Walking Adult Eland

	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs on	Total	Number of strides averaged
Adult eland							
Frames observed	36	30	93	106	1	266	5.5
Percentage of stride	14	11	35	40	0	100	

The duration of an average walking stride in these two sequences is 1.88 and 2.04 seconds.

17. Discussion and Conclusions of Antelope Gaits

a. The Antelope Walk

i. The Walk Pattern

The walk patterns of the adult species are given in Table 52, arranged in increasing order of shoulder height.

Table 52

Walk Patterns of Adult Antelopes

Percentage Time Spent on Combinations of Supporting Legs							
Shoulder height -in cms	Species	Lateral legs	Diagonal legs	One hind leg off	One front leg off	Four legs on	Number of strides examined
66	Thomson's gazelle	44	0	26	18	12	7
80	Saiga antelope	30	4	25	37	4	18
97	Kob	39	8	31	20	2	7.5
98	Grant's gazelle	32	4	29	35	0	8.5
100	Impala	35	3	29	27	6	6.5
112	Lechwe	33	3	28	33	3	33.5
116	Waterbuck	18	23	35	24	0	2
119	Hartebeest	29	0	22	35	14	8.5
122	Tsessebe	32	8	27	33	0	9
133	Wildebeest	26	4	32	35	3	13
142	Kudu	7	8	32	53	0	5
164	Eland	14	11	35	40	0	5.5

The following pairs of antelope have walk patterns that were similar

(χ^2 test):

Saiga and Grant's gazelle	$p = > .01$
Saiga and Impala	$p = > .10$
Saiga and Lechwe	$p = > .30$
Saiga and Wildebeest	$p = > .30$
Grant's gazelle and Tsessebe	$p = > .30$
Grant's gazelle and Wildebeest	$p = > .01$
Impala and Lechwe	$p = > .10$
Lechwe and Wildebeest	$p = > .02$
Tsessebe and Wildebeest	$p = > .01$
Kudu and Eland	$p = > .02$

There is a tendency for the larger antelopes to use lateral legs less than the smaller antelopes. All use diagonal legs for only short periods of a walking stride, if at all. The larger animals tend to balance on two legs for shorter periods than do the smaller ones. In general when three legs are used a foreleg is off the ground for longer than a hind leg. This is true for all species but the Thomson's gazelle, the kob and the impala. Four legs support an antelope for short periods if at all.

ii. Variations in the Walk

A. Variation with Speed

For the lechwe, in which species there are enough data to calculate the walk patterns at different speeds, the patterns do not change decisively.

B. Variation with Horns

The walk patterns of male and female saiga are similar while those of the male and female lechwe are not. This difference may be because of the relatively larger horns in the lechwe compared to its size (Table 33). The male lechwe which have fully grown horns use two supporting legs for a shorter period and four legs for a longer period than do the females. This apparent need for more support in its walk may be attributable to the relatively heavy horns of the male lechwe.

C. Variation with Size

The lambs of the impala and of the lechwe, all of which are at least several months old, have walk patterns similar to that of their adults. The walk of the newly-born tsessebe is highly significantly different from that of the adult tsessebe, with a decreased use of two legs and an increased use of four legs. This lamb is presumably young enough to need this increased support for its early walking efforts.

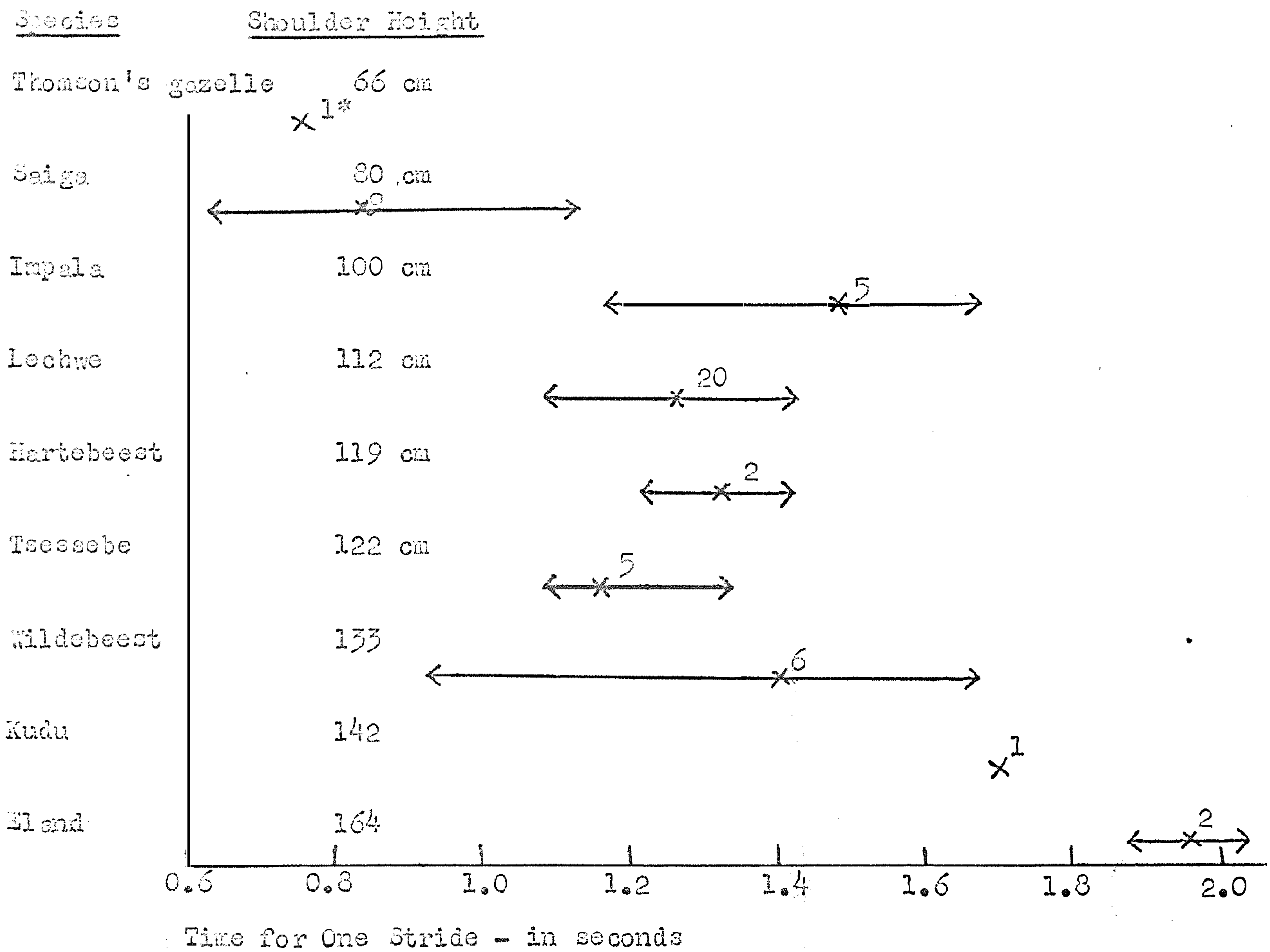
ii. Time of a Walking Stride

The average time of a walking stride in the sequences examined is given in Figure 34 together with the range of times for each species. This range can be wide. The average times are plotted against the shoulder height of each species in figure 35. In this graph it is evident that in general the taller species and therefore those with the longer legs have longer-lasting walking strides.

b. The Antelope Trot

The percentage of time of an average trotting stride that the various combinations of supporting legs are used for six species of antelope are given in Table 53. The average duration and range of times of trotting stride for four species plotted against shoulder height are given in figure 36.

Figure 34 Average Times and Range of Times of Walking Strides of Antelopes



* Numbers of strides averaged

Figure 35 Average Times of Walking Strides Plotted Against Shoulder Heights of Antelopes

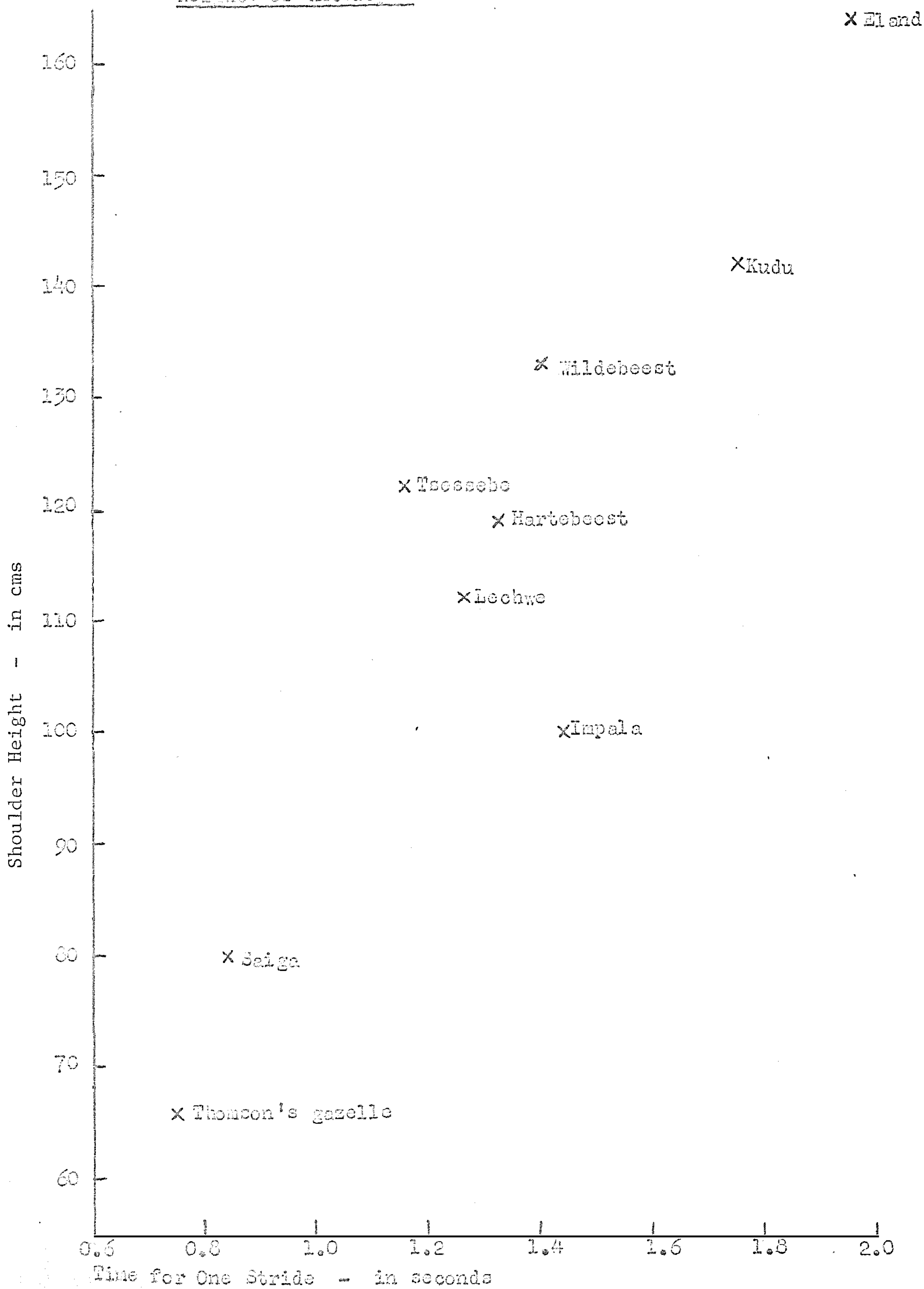
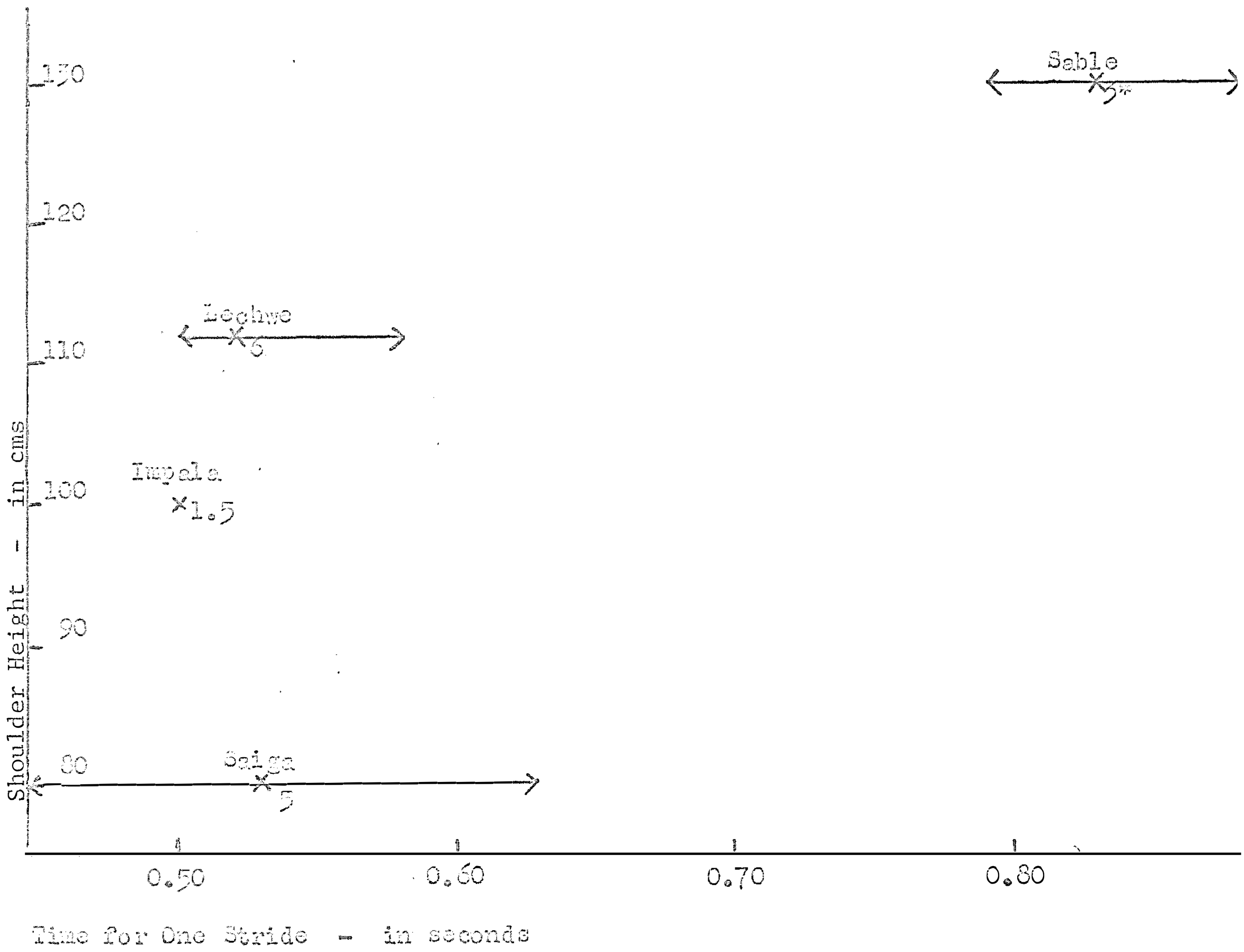


Figure 36 Average Time and Range of Times for Trotting Strides of Four Antelopes, Plotted against their Shoulder Heights



* - Number of strides averaged

Table 53

Percentage Time Spent on Combinations of Supporting Legs for Six Trotting Antelopes.

Combinations of supporting legs, not in the order in which they occur	Saiga antelope	Thomson's gazelle	Impala	Lechwe	Water-buck	Sable
Lateral legs on ground	2	0	22	0	0	0
Diagonal legs on ground	84	92	72	74	79	77
One hind leg off ground	0	0	0	0	9	0
One front leg off ground	0	4	0	0	9	0
Four legs on ground	0	0	0	0	3	0
Two forelegs off ground	0	4	0	0	0	0
Only one hindleg on ground	0	0	6	15	0	0
Only one foreleg on ground	2	0	0	0	0	3
Suspension	12	0	0	11	0	20
Number of strides averaged	5	2	1.5	6	1.5	3.5

Periods of suspension occur in both the smallest (saiga) and the largest (sable) of the antelopes examined. Such suspensions do not necessarily increase the time of a stride as the average duration of a stride for the lechwes shows. This species spends 11% of the time of a stride off the ground and yet its strides last for a shorter time than one expects from its size (fig. 36).

During these strides the antelopes have their forelegs in the air for longer than their hind legs in general, as one would expect since the hind legs are longer than the forelegs (Howell, 1944)[1]. The

[1] The sum of the measurements of the hind leg bones of Saiga tartarica, Hippotragus sp. and Gazella sp. in each case is at least one-tenth greater than that of the forelegs (Murie, 1870). From photographs it is obvious that the hind legs are also longer than the forelegs in other species of antelopes too.

diagonal legs support these antelopes for from 72 to 92% of a stride; a variety of other combinations of legs support them for short periods.

c. The Antelope Gallop

The percentage time per galloping stride spent on the different combinations of supporting legs for eight antelopes are given in Table 54. Care must be takin in generalizing about these data, as for some species few strides are available and as the speed at which each species is travelling may vary greatly.

In all of these antelopes the flexed suspension is used to a far greater extent than the extended suspension. An extended suspension is never used by the three species of Alcelaphinae, perhaps because of the shape of these antelope. Their shoulders are considerably higher and more muscular in appearance than their rumps (fig. 32). The hind legs may not be powerful enough to launch these animals into the air for an extended suspension. Correlated with the absence of extended suspensions in the tsessebe, kongoni and wildebeest is the absence of a single supporting lead hind leg to launch an antelope into such a suspension and the absence of one non-lead forefoot on which it would have landed following an extended suspension.

The gallop pattern of the kob is more like that of the alcelaphine antelopes than that of the lechwe or the reedbuck to which it is more closely related. Perhaps this correlates with the relatively flatter back of the kob compared to the more sloping backs of the lechwe and reedbuck. From these data it is impossible to characterize what has been called the "lumbering shoulder gallop" of the alcelaphine antelopes and the "rocking horse gait" of the reedbuck. It may be that these

Table 54

Percentage Time Spent on Combinations of Supporting Legs for Eight Galloping Antelope Species

Combinations of supporting legs, not in the order in which they occur	Saiga	Impala	Reed-buck	Kob	Lechwe	Tsessebe	Kon-goni	Wilde-beest
One foreleg on ground	0	3	8	1	12	0	0	0
Two forelegs on ground	0	19	10	8	10	0	9	3
Lead foreleg on ground	36	7	15	25	22	31	18	25
Flexed suspension	0	36	16	6	17	8	25	13
One hind leg on ground	28	3	15	16	8	23	11	20
Two hindlegs on ground	0	18	20	8	14	8	16	4
Lead hindleg on ground	0	1	8	0	2	0	0	0
Extended suspension	0	11	3	0	6	0	0	0
Front and hind legs - two	0	1	5	15	5	7	2	9
- three	36	1	0	21	4	23	19	26
	100	100	100	100	100	100	100	100
Number of strides averaged	2	18	3	41	17	1	9	14
Average time of stride in seconds	0.35	0.63	0.58	-	0.54	0.54	0.60	-
Range of times for a stride - in seconds	0.31-0.38	0.29-0.88	-	-	0.46-0.63	-	0.50-0.71	-

movements, which are distinctive to see, are connected entirely with the conformation of these animals and are not reflected in the manner in which each is supported during a galloping stride.

The duration of a stride is very variable in the impala particularly, because of the variation in number and length of the suspensions present in any one stride.

d. The Antelope Bound

Bounds in which four legs support the antelope in each stride occur in lechwe and reedbuck. These gaits are analyzed in Table 55. This gait is apparently one that serves mainly to launch an antelope into the air where it can see better. The head position of the lechwe seems to confirm this. While running, the lechwe holds its head low so that it can run through vegetation without becoming entangled in reeds or branches; while bounding it holds its head high during the periods of suspension. Four legs supporting an animal at once indicates a slow gallop but not a slow bound.

Table 55

Percentage Time Spent on Combinations of Supporting Legs for Two Bounding Antelope Species.

Combinations of supporting legs in the order in which they occur	Reedbuck	Lechwe
Suspension	46	53
Two forelegs on the ground	15	13
Four legs on the ground	7	18
Three legs on the ground	2	3
One hind leg on the ground	5	0
Two hind legs on the ground	25	13
	100	100

Part VI. Final Discussion and Conclusions

The data of the previous sections have pointed up the correlation between the locomotion of the Pecora and their environment. This may be expected since the locomotion of an individual depends upon its anatomy and its neurophysiology and during the evolution of a species these have been profoundly affected by the habitat in which the species lives.

1. The Walk

Despite the basic similarity in the shape of various Pecora, their walking gaits are different. The effect of the environment is so strong that the members of cursorial Pecora that live in woodlands where vision is limited have evolved a distinctly more stable walk than those that live on open grasslands. The woodland Pecora tend to use either diagonal supporting legs in preference to lateral legs or three or four legs in preference to two legs to provide such stability. With increased stability an animal can quickly pause to listen for danger and can move more quietly. The walk patterns within the families of the Pecora are discussed below.

In the cervids, most of which are woodland species, diagonal supporting legs are used to a large extent in each stride. Of particular interest is the barren-ground caribou, an animal that has a typically cervid walk even though it spends the summer on the tundra where vision is not limited. Here the evolutionary pattern is largely adapted to winter conditions where the concept of "survival of the fittest" is the most poignant. The barren-ground caribou's walk pattern, together with its relatively poor vision, suggest that this species evolved in woodlands as did the other cervids. Caribou developed either in the temperate zone of North America (Flerov, 1952) or in Eurasia (Colbert, 1961). During the Pleistocene they acquired specific adaptations for life in the Arctic and became disseminated circumpolarly.

On examining the walk patterns of the antelopes, the walk pattern of the kudu is found to be that with the greatest stability. This is the only species examined that lives in rather densely wooded areas, a habitat preference indicated by its large ears. The eland and the waterbuck, the two species next most likely to be encountered in open wooded areas, are the two antelopes with the next most stable walks.

If we consider the walk patterns of the giraffe and the okapi, we find that the okapi uses two legs less than the giraffe and therefore has the more stable walk. Both species live in wooded areas, but the habitat of the giraffe is less dense than that of the okapi.

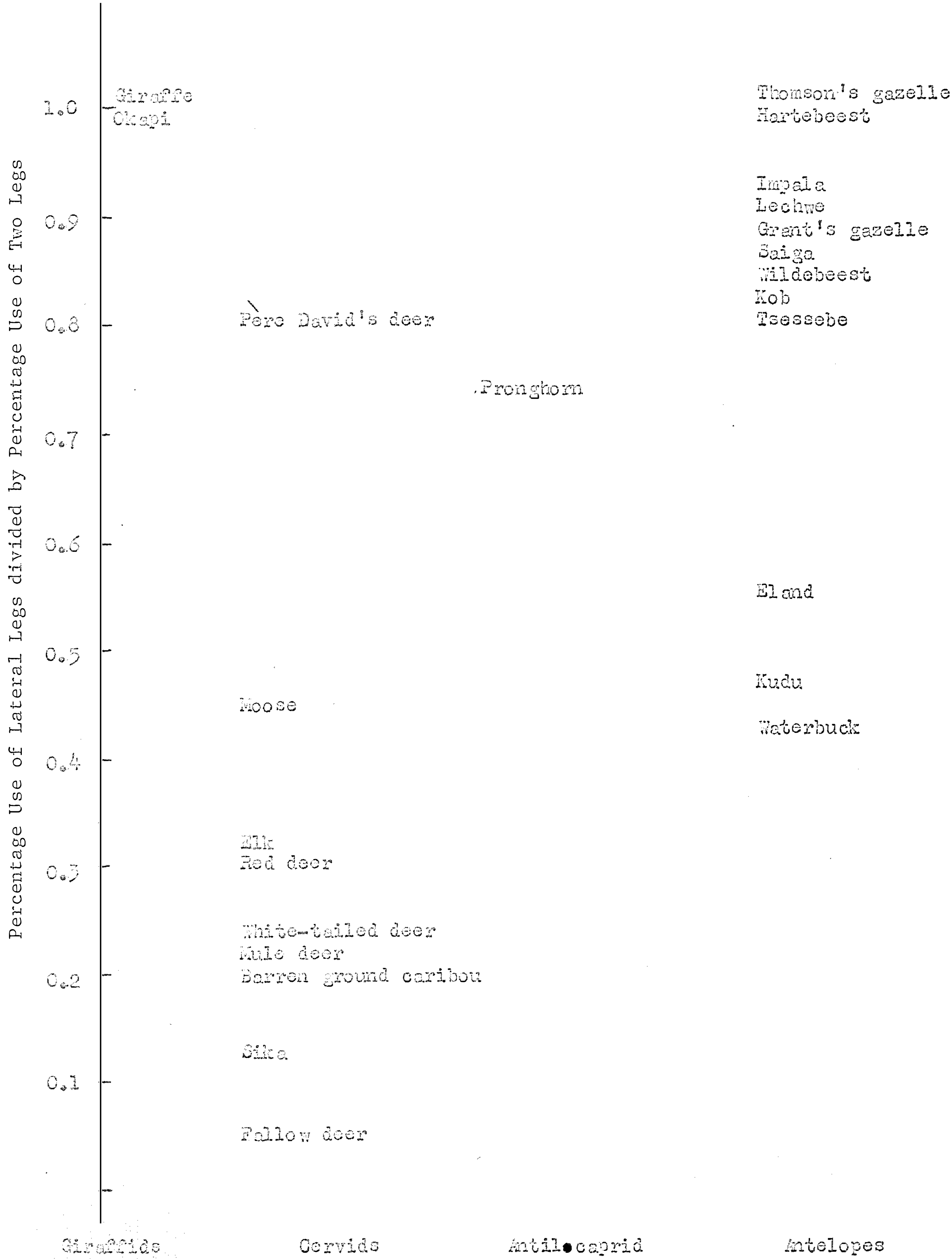
Pecora that live on open grasslands generally have such keen eyesight that they can spot danger at a great distance. These species have evolved walking patterns that need not be particularly cautious, since listening for danger is an insignificant part of their daily lives. As well, grassland animals are less likely to encounter obstacles on the ground and they do not need to follow winding woodland trails, both factors that imply less emphasis on a stable gait.

The increased use of lateral supporting legs in open country animals where stability is less vital suggests that this makes a more efficient gait than one in which diagonal supporting legs are used more. The step of the hind leg can be longer when the foreleg on the same side is not still planted on the ground as the hind leg moves forward, effectively terminating its swing. As well, the muscular efforts of an animal may be easier if the muscles on one side of the body contract more nearly together than they do in the walks where the use of diagonal legs is prominent.

The extensive use of lateral legs in both the antelopes and the pronghorn implies that the ancestors of these two groups evolved on open grasslands. This can also be said of the giraffid ancestors. The giraffe uses lateral legs for two-fifths of the time of each stride. This may be partially because of the giraffe's size but it is mostly because of its long legs and relatively short body. The stride of the hind leg would be severely curtailed if the foreleg did not swing forward well before the arrival of the hind leg on the same side.
The use of lateral legs is not correlated with size alone, for the Thomson's gazelle uses lateral legs for an even longer duration of its walking stride, despite its small size. Nor does the distinctive and virtually non-existent use of diagonal legs in both the giraffe's and in the okapi's walks seem to be correlated with their sloping backs; in the tsessebe and wildebeest, species which also have a top-line sloping down to the rump, diagonal legs support the animals 8% of the time of the strides respectively.

In summary, and partially illustrated in figure 37 where the percentage use of lateral legs divided by the percentage use of two legs is plotted for each of the species studied, it is apparent that each of these families have distinctive walk patterns. Within each family (with the partial exception of the cervids where the use of lateral legs is correlated with height), the members that use a more stable walk are those that live in wooded areas and those that use a

Figure 37 Percentage Use of Lateral Legs / Percentage Use of Two Legs of Pecoran Species



relatively less stable walk live in more open areas.

The distinctiveness of the walk patterns of the cervids and of the antelopes is reflected in their habitats. These habitats are more varied in the cervids, so that only three pair of the ten cervids examined have statistically similar walk patterns. For the twelve antelope studied, ten pairs have similar patterns. Most of these antelopes live in similar habitats of relatively open savannah country or grasslands.

For the first time the variation of the pattern of walking strides within a species is assessed. The walk pattern for the fastest walk is highly significantly different from that of the slowest walk for at least one species of three of these four families. The walk pattern can vary significantly on smooth as opposed to rough terrain, as illustrated by moose and woodland caribou. It can be significantly different in those individuals with heavy horns and antlers as opposed to individuals of the same species without them. Moose, caribou and lechwes possess a significantly more stable walk in those individuals which have antlers or horns as opposed to those animals that do not; the individuals of elk, red deer, mule deer, white-tailed deer, giraffe and saiga have similar walk patterns whether or not they bear horns or antlers. Young animals sometimes have significantly different walks than the adults of the same species and always in the direction of increased stability. These variations underline the necessity of collecting as many data as possible on which to base the walk pattern of a species.

The average duration of a walking stride is longer in the taller species. These animals have longer legs which have a slower natural frequency of swing. However, the leg's swing is not passive like that of a pendulum, as shown in Table 56. A front leg swings forward about twice as fast as it would if it swung freely like a cylindrical pendulum. For the trot, the swing is even faster. Muscles therefore play an important part in pulling the leg forward in even a slow walk.

Table 56

Times for the Swing of a Foreleg as it Really is in the Walk and the Trot and as it Would be if it Swung Passively Like a Cylindrical Pendulum of the Same Length.[1]

Species	Length of fore-leg - in cms	Time if a cylindrical pendulum[2]	Walk			Trot		
			Time of stride - secs	% one fore-leg in air	Time for swing of fore-leg	Time of stride - secs	%one fore-leg in air	Time for swing of fore-leg
Saiga*	54	.60	0.84	35.5	.30	0.53	56	.30
Fallow deer*	61	.64	1.07	33.5	.36	0.46	59	.27
Reindeer*	69	.68	1.25	33.5	.42	0.69	57	.39
Pronghorn	74	.70	0.94	34	.32			
White-tail	80	.73	1.34	32.5	.44			
Elk	112	.87	1.36	33	.45	0.70	44	.31
Moose	143	.97	1.80	29	.52	1.02	47	.47
Giraffe*	179	1.09	1.94	32.5	.63			

[1] The values in this table indicate the order of magnitude of the differences but they are necessarily approximate since the leg measurements were taken from only one specimen each.

[2] The swing of the foreleg as a pendulum is taken as

$$\frac{T}{2} = \frac{\sqrt{2/3\, l}}{10}$$

*These measurements were recorded for single individuals by Murie, 1870. The other measurements were taken on single specimens by the author at the Royal Ontario Museum of Zoology.

2. The Trot

The trot is a gait intermediate in speed between the walk and the gallop. The effect of the environment is important only in the case of caribou, since they must trot great distances during their lifetime. This species has evolved an especially effective trotting gait. Some cervids prefer the trot to the gallop, because of the soft underfooting where they live, because of their wooded environment, because of their large size or because of their heavy antlers. Among antelopes, two species that trot by preference are the eland and the waterbuck (Dagg, 1961). The animals are both large, the male waterbuck at least bearing heavy horns. Both of these animals prefer to inhabit wooded areas. The eland, but not the waterbuck, is a great traveller for which the trot provides an enduring gait. None of the lighter antelopes are noted for their trotting abilities, even though some, like the reedbuck and the lechwe, inhabit relatively moist areas and some, like the saiga and the pronghorn, often migrate long distances. The latter two animals generally gallop during such migrations.

3. The Gallop

The environment has had an important role in determing the type of gallop that each Pecoran species has evolved. In turn the anatomy of the species has evolved so that it can execute this gallop.

Animals that live in woodlands and that are light enough to leap over obstacles, like the white-tailed deer and the mule deer, use an extended suspension more than a flexed suspension in their gallops. Other light Pecorans that live in relatively open areas, like the impala, lechwe, reedbuck, young giraffe and pronghorn have both extended and flexed suspensions as prominent parts of their gallops. The first three species often bound high, too, to clear vegetation so that the extended suspension can serve to lift the animal vertically into the air rather than horizontally. The pronghorn, the fastest of this group of animals, uses both the extended and the flexed suspensions as low leaps to cover ground quickly.

It is interesting that the pronghorn, and also the saiga antelope that occupies similar ecological niches but on a different continent, were once believed unable to jump at all, since if they came to a fence they squeezed through or under the wire strands rather than jumped over it. Now it is known that the pronghorn can jump over 1.5 m if necessary (Howell, 1944). Its early hesitation to jump was caused by inexperience and previous lack of necessity rather than by inability. Similarly, giraffe in Africa needed several years to become used to fences encroaching into their wild lands. Originally they broke through fences but at present they usually step over them (Innis, 1958).

A third group of Pecoran species use flexed suspensions predominantly and often entirely. These animals are often heavy, like moose and elk, or they have backs that slope down from their shoulders to their rumps, like tsessebe, kongoni and wildebeest. These latter three animals are not noted jumpers, nor are the giraffe and the okapi which have similarly sloping backs and relatively weak hindquarters.

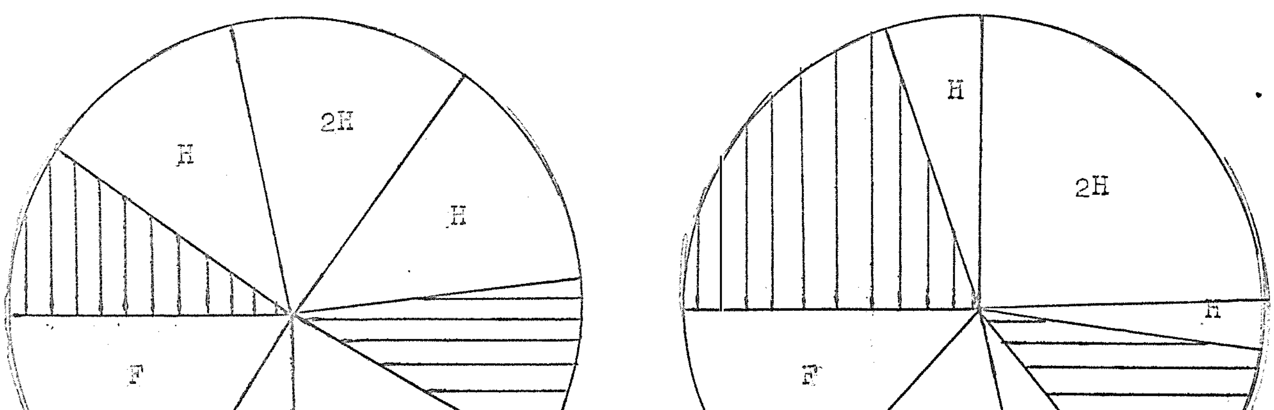
A final group have no suspensions at all, because of their bulk (adult giraffe and elk with full antlers) or because of the slowness of the strides studied (saiga).

A comparison of a galloping stride of the pronghorn and the white-tailed deer, given in figure 38, illustrates why the pronghorn is the faster of these two species. The four legs of the pronghorn touch the ground at more regular intervals, each in its turn supporting the body and pushing it forward. Because of this there is a considerable distance between foot impacts and one stride covers a longer distance than it does in the deer. Since relatively few impacts are present, the gait is less tiring than it would otherwise be. Deer have longer periods in their stride when two front or two hind legs support the animal at once. This decreases the work that one foot alone might do and hence the speed of the gait, although it is doubtless necessary to give the deer enough thrust to launch it into a longer period of suspension. Theoretically the fastest gait would be one in which two legs never supported an animal together at all. There is a second point of comparison between these two species. Both are gregarious, so that if danger threatens an individual will warn others nearby. When a white-tailed deer perceives danger in its woodland environment, the danger is usually close. The deer bounds off, lifting its tail so that the undersurface flashes white during its leaps, warning other deer. One may reason that as the pronghorn does not make such high bounds, it has had to evolve a more complex way to signal danger to other individuals. It has muscles in its rump which enable it to raise long white hairs there even while standing still. Fellow pronghorns up to a mile away are alerted of danger by this means.

4. The Bound

Howell (1944) describes the bound (as here defined) as unique to the mule deer, but it can be executed by other cervids, by the pronghorn and by various antelopes. Murie (1870) describes this gait for the saiga, which uses it when pursued. The pronghorn, the mule deer and possibly the elk use this gait to climb up slopes where vegetation is thick or the ground rough. The reedbuck and the lechwe use the bound on flat ground, apparently both to navigate in thick reedbeds and to see better. In each of these latter four species the gait is similar, with the periods of suspension lasting between 46% and 57% of the time of the stride.

Figure 38 Percentages of Strides that Galloping Pronghorns and White-Tailed Deer Spend on their Four Legs



Antilocapra americana Odocoileus virginianus

The legs are indicated as spokes in the wheels. The circles represent one stride

F - One foreleg on ground
H - One hind leg on ground
- Extended suspension
- Flexed suspension

Appendix A

Besides the footage photographed by the author, sequences from the following films were examined for this study.

1. Personal film loans from:

		Speed of film
Carrick, W.	Ontario Waterfowl Research Foundation	24 f.p.s.
Foster, J. B.	University of East Africa	mostly 24 f.p.s.
Geist, V.	University of British Columbia	24 f.p.s.
Innis, D. Q.	Geneseo State College, New York	16 f.p.s.
Keast, A.	Queen's University, Ontario	24 f.p.s.
Lent, P. C.	Memorial University, Newfoundland	24 f.p.s.
Linnard, L.	Maumee, Ohio	mostly 24 f.p.s.

2. Institutional film loans from:

	Michigan Department of Conservation - deer and elk	64 f.p.s.
	Minnesota Department of Conservation - moose	64 f.p.s.

3. Completed Films:

Africa Untamed	-
Animals - Ways they Move - Encyclopaedia Britannica	-
Behaviour of the Barren-Ground Caribou	24 f.p.s.
Caribou Hunters, The	-
Caribou Mystery	24 f.p.s.
Deer Family of North America	-
Escape in Mammals - Ealing Film Loop	128 f.p.s.
Expedition Moose - Carling Conservation Film	-
High Arctic - National Film Board	-
Large Animals that Once Roamed the Plains - Walt Disney Productions	-
North to Hudson Bay	-
Olympic Elk, The - Walt Disney Productions	-

Appendix A

3. Completed Films: cont'd.

On the Edge of the Barrens	-
Survival Perilous - Carling Conservation Film	-
Web of Life - Canadian Broadcasting Corporation	mostly 24 f.p.s.

Appendix B

So that the walks of these artiodactyls can be compated with those of other quadrupeds using Hildebrand's gait formula (1965), these have been calculated from the walk pattern of each species as follows:

Gait Formula = X : Y

where X = the percent of the stride interval that each hind foot is on the ground

$= \frac{1}{2}(L) + \frac{1}{2}(D) + \frac{1}{2}(1\ H\ off) + (1\ F\ off) + (4\ on)$

and where

Y = the percent of the stride interval that the footfall of a forefoot lags behind the footfall of the hind foot on the same side of the body

$= \frac{1}{2}(D) + \frac{1}{2}(1\ F\ off).$

Gait Formula (Hildebrand, 1965)		Number of strides averaged
Dama dama	72:33	176
Cervus nippon	72:32	18
Odocoileus virginianus	70:29	212
Odocoileus hemionus	70:30	32
Rangifer t. groenlandicus	69:30	138
Cervus elaphus	68:28	21
Rangifer t. caribou (rough ground)	63:28	25
Cervus canadensis	67:28	179
Alces americana	69:24	20
Elaphurus davidianus	73:22	8
Antilocapra americana	71:24	20
Okapia johnstoni	70:16	18
Giraffa camelopardalis	70:13	92
Saiga tartarica	71:20	18
Gazella thomsonii	65:9	7
Gazella granti	68:20	9
Aepyceros melampus	67:15	7
Kobus kob	61:14	8
Kobus leche	68:18	34

Appendix B. cont'd.

Gait Formula ..brand, 1965)		Number of strides averaged
Kobus ellipsiprymnus	62:24	2
Alcelaphus buselaphus	75:18	9
Damaliscus lunatus	67:21	9
Gorgon taurinus	69:20	13
Strepsiceros strepsiceros	77:31	5
Taurotragus oryx	70:26	6

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