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A FUNCTIONAL ANALYSIS OF LOCOMOTION
IN THE PRONGHORN ANTELOPE

by

ROBERT EARL BULLOCK

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

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EDMONTON, ALBERTA
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FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "A Functional Analysis of Locomotion in the Pronghorn Antelope" submitted by Robert Earl Bullock in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

A functional analysis of locomotion in the pronghorn antelope (Antilocapra americana) was conducted utilizing several different approaches for acquiring data. Motion picture film (16 mm) exposed at 80 frames per second was analyzed to identify the various gaits employed by the pronghorn and to record the relative positions in space of rapidly moving body structures, skeletal material was studied to give information on anatomical structure and body proportions, and field observations were conducted to collect information on aspects of behavior related to locomotion.

The repertoire of gaits employed by the pronghorn is varied and relatively extensive. The symmetrical gaits consist of the very slow, slow and fast diagonal walks and the slow, moderate and fast running trots. The transverse and rotary canters (lopes) and the rotogallop are the most frequently employed asymmetrical gaits. The rotogallop is the exclusive gait of pronghorn when running at fast speeds (speeds of up to 60 miles per hour have been reported). Although the bound, half-bound and bounding gallop (stotting included) are employed by pronghorn, they are rarely executed in their pure form. Until a fawn is about two weeks old its gait repertoire is limited to a rather awkward rotary canter and gallop and a feeble walk.

In the majority of pronghorn gaits an increase in speed is accomplished by increasing both length and rate of stride. In many fast galloping sequences, however, speed increase is a result of an increase in length of stride but a slight decrease in rate of stride. Total suspension time per stride increases with increased speed in walking and trotting gaits but decreases in cantering gaits. The fast gallop, with its

two periods of suspension, has a total suspension time per stride greater than most of the faster cantering gaits. Footfalls spread out and more two and one leg support phases appear in the strides as speed is increased. The galloping gaits of fawns average less suspension per stride than those of mature animals.

A change in either front or rear lead will change the type of gallop or canter employed. The rotogallop is maintained by changing both front and rear leads during the same stride, or more commonly by changing the front lead during one stride and the rear lead in the following stride. When making a sharp turn a pronghorn will employ the rotogallop and lead with the inside forefoot.

Occasionally pronghorn will execute a complete cycle of locomotion with only three of the four feet striking the ground during a change in gait. Apparently holding one front leg during the transitional stride of a gait change is often advantageous to the proper reorientation of legs.

When progressing faster than a walk, pronghorn usually employ the canter or gallop. A considerable degree of synchronization of both lead and type of canter or gallop is apparent in running herds.

As a pronghorn increases speed from a walk to a fast gallop certain trends in body movements become apparent: greater swing of limbs with legs striking and leaving the ground at more acute angles, feet lifted higher in relation to body, degree of vertical spine flexion increases and head held lower with increased vertical movement. The implications of these trends as they relate to speed and balance are discussed.

Skeletal proportions indicate that fawns are more specialized cursorially than adult pronghorn. Adaptations for speed at a very early age are of value to pronghorn fawns as flight is one of their chief means of defence.

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Finally to my wife, Elaine, I shall always be grateful for her patient understanding, encouragement and sacrifices without which this study and other graduate work would not have been accomplished.

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INTRODUCTION

The pronghorn antelope, Antilocapra americana (Ord), is the sole living representative of the family Antilocapridae. The characteristics of the animal, therefore, are the characteristics of the genus and also the family. Although the pronghorn is usually, but erroneously, referred to as an "antelope", it is not considered by most authorities to be closely related to the true antelope of the Old World. Simpson (1945) states that the pronghorn evolved during the Pleistocene Epoch and is endemic to North America. He recognizes five subspecies of pronghorn: Antilocapra americana americana (Ord), Antilocapra americana peninsularis Nelson, Antilocapra americana sonoriensis Goldman, Antilocapra americana oregona Bailey and Antilocapra americana mexicana Merriam. A. a. americana is the most widely distributed subspecies in North America and is the only subspecies which occurs in Canada.

The pronghorn antelope is reported by many writers as being the swiftest wild quadruped in North America. Much attention has been given to this fast, agile mammal of the American plains in connection with its very rapid locomotion, but most references refer only to speed and do not attempt an analysis of locomotor behavior. It was the purpose of this study, therefore, to analyze the major types of locomotor activity characteristic of this species and to investigate some of the associated morphological adaptations (basically osteological) that have occurred as a result of evolution in connection with the pronghorn's specific mode of life. An investigation such as this should give some insight into the adaptations incorporated into an animal exhibiting a cursorial mode of locomotion over a relatively flat, hard prairie or semidesert terrain.

Several approaches were utilized in this study to acquire the necessary data for locomotor analysis:

(1) Slow-motion movies were analyzed to identify the various gaits employed by the pronghorn and other selected artiodactyls, and to record the relative positions in space of rapidly moving body structures.

(2) Skeletal material and embalmed animals were studied to give information on anatomical structure and body proportions.

(3) Field observations were conducted to collect information on various aspects of behavior related to locomotion.

To facilitate a more meaningful analysis of the degree of cursorial adaptation present in the pronghorn, comparisons with other artiodactyls of similar body conformation are made insofar as the literature permits. Comparisons are also made between pronghorn of different ages and sexes to determine relative cursorial trends within the species.

REVIEW OF THE LITERATURE

According to historians the Spanish explorers of the sixteenth century were undoubtedly the first Europeans to encounter pronghorn antelope; their accounts, however, were merely passing references. Torquenada (1723, In Yoakum, 1967, p. 58) is credited as author of the first report on the American pronghorn. In this early document a reference is made to a hunt in 1540 in the extreme southwestern part of Mexico where some "verredos" (Mexican word to denote antelope) were killed. The report states that the verredos "not only ran but flew", thus indicating the attention that the remarkable speed of these animals attracted in the first European observers. Warren (1942) quoted Francisco Vasquez Coronado as seeing "stags patched with white" (pronghorn) in 1535 on what are now the Kansas plains. It is quite probable, therefore, that Coronado was the first European to see this animal on its native range. It remained, however, for Lewis and Clark to make this animal known to the scientific world. Lewis and Clark first saw antelope, which they often referred to as "goats", in September, 1804 (Allen, 1842). According to their narratives, they too were impressed with the great speed of the pronghorn: "Of all the animals we had seen, the antelope seems to possess the most wondrous fleetness....... their rapid career seems more like the flight of birds than the movements of a quadruped." Lewis & Clark collected an adult male specimen in 1805. Based upon an examination of this specimen, George Ord described and designated the pronghorn antelope *Antilope americana* in 1815, and later in 1818 bestowed the nomenclature used today, *Antilocapra americana*. However, detailed scientific reports were not available until the mid-nineteenth century when the works of Audubon and Buchman (1851) and Caton (1877) appeared. Although these authors gave disproportionate attention to the formation and structure of the horn, they also gave valuable information on the habits and natural history of the animal.

Seton (1909, 1929) made extensive contributions to our knowledge of pronghorn biology. He devoted attention to pronghorn morphology, taxonomy, history, distribution, migration, population numbers, reproduction, food habits, predators, curiosity, speed, jumping power, etc. Although many facets of these works are not well accepted today (e.g., his statement that the top speed of an antelope was 32 miles per hour), nevertheless they are some of the most frequently cited early references on the pronghorn.

Another early work giving rather general information on pronghorn biology was that of Skinner (1922), which reported that pronghorn were capable of great speed, but did not discuss locomotion further. A less comprehensive report (Grinnell, 1929) mentioned pronghorn locomotion but was mainly concerned with the general status of antelope and attempts at establishing game preserves. Carr (1927), however, was an early worker who devoted an entire short article to the speed of pronghorn. He reported that a herd of several antelope ran seven miles at a rate of about thirty miles an hour.

The works of Einarsen (1948) and Buechner (1950) are probably the most comprehensive studies to date on the pronghorn antelope; they treat many aspects of pronghorn biology, including distribution, structure, ecology, management, and behavior (including some locomotor behavior). Einarsen's monograph contains brief information on the speed, gaits and jumping ability of pronghorn. He concluded that in pronghorn, running is an accomplishment that has nearly reached perfection, but that it is only when hard pressed and under the best of conditions that they can attain high speeds such as 60 mph. Six gaits are recognized and illustrated: two different walking gaits, two trots, a bounding leap and a lope. Buechner (1950) agreed with the top speed suggested by Einarsen (1948), but stated that normal top speed for pronghorn in his region (Trans-Pecos, Texas) was between 35 and 40 mph. He did not discuss gaits.

Many authors, in addition to the few cited above, have included information on various aspects of pronghorn behavior. Wallace (1940), Rouse (1941), Bridge (1942), Kautz (1942), McLean (1944), Rush (1944), Throckmorton (1945), Jewett (1946), Buck (1947), Buechner (1947), Sather and Schildman (1955), Cole (1956), Cole and Wilkins (1958), Hoover, Till and Ogilvie (1959), Popowski (1959), Fichter and Nielsen (1962), Spillett (1964) and others have made reference to some aspects of locomotor behavior. A few of the above works make some mention of the various gaits of pronghorn, but these references are very general and not of an analytical nature.

Only three studies have treated the subject of pronghorn behavior in a relatively comprehensive manner. Gregg (1955) reported on many aspects of pronghorn behavior and devoted a section to gaits. He delineated the gaits of pronghorn antelope as being the walk, trot, bound, lope and gallop. Although Prenzlow et al. (1968) dealt with many behavior patterns of the pronghorn, he did not discuss gaits. Bruns (1969) studies behavioral adaptations of wintering pronghorn and described certain gaits (elegant trotting, stotting or bounding and express galloping) as abnormal running in connection with winter play.

Although many of the early works such as Bailey (1920) and others have dealt with horn development and other morphological structures, information concerning the internal anatomy of the pronghorn is meager. Only five papers deal specifically with the internal anatomy. The earliest of these is a study by Murie (1870), based on the dissection of a male antelope which had died in captivity in London; it described the axial and appendicular skeleton and presented some information on the myology and the hair. Although information concerning the digestive and circulatory systems is limited, the oral and laryngeal regions are well described. Beddard (1909) supplemented the work of Murie by describing certain portions of the circulatory system and appendicular musculature in more detail. He also described the brain in some detail. A more general work (Buck, 1947) treated various aspects of gross anatomy with emphasis on the reproductive system. Lawrence (1951) attempted to aid the archaeological investigators in the Southwest by giving precise descriptions and measurements of some of the post-cranial skeletal elements of deer, pronghorn, sheep and goat with notes on Bos and Bison. The latest work to appear was that of Wenzel (1955), which set forth a fairly detailed description of the internal anatomy of the cephalic, cervical, thoracic, abdominal and sacral regions; most of this work concerned the soft anatomy, with special reference given to the digestive system.

Man has studied animal locomotion since long before the first cave men painted pictures depicting both man and beast. However, it was not until the publication of Borelli's classical work De Motu Animalium (1680) that the study of animal locomotion was placed on a truly scientific basis. Since Borelli's day the study of locomotion has been approached through anatomy, physiology, mechanics and/or motion analysis. The anatomical and mechanical approaches are usually integrated to the point of being difficult to separate. It is also apparent when making a study of the literature relevant to the analysis of locomotion that there is considerable overlap between the motion analysis approach and the other three approaches. Therefore, the categories are somewhat arbitary but nevertheless useful when discussing the relatively large amount of literature dealing with the subject.

In the field of anatomy and mechanics, one of the earliest noteworthy works to appear was a book on the principles of animal mechanics by Haughton (1873). Later, Lull (1904) devoted attention to the adaptations exhibited by mammals toward aquatic, arboreal, fossorial and cursorial habits. Gregory (1912) pursued the problem of adaptations further by reporting on the principles of quadrupedal locomotion in ungulates. His approach was to analyze many skeletal and myological adaptations that had occurred in connection with graviportal and cursorial evolution. This extensive work remains a very useful reference. Still another extensive study on the mechanics of the tetrapod skeleton was made by Gray (1944). He discussed the mechanics of the tetrapod skeleton while considering all of the locomotory structures (muscles and bones) of the vertebrate body as being part of a complete functional unit.

Although photographic records were being used to establish the forces exerted on the ground by the feet of tetrapods, Elftman (1938, 1939) invented an apparatus which, by means of direct measurements, would record the forces exerted on the ground and thus augment the data acquired through photographic means. He used man as his subject. Manter (1938) employed a modified form of this apparatus for studies dealing with the cat, and concluded that the forelimbs produced more retarding action while the hindlimbs contributed more forwarding impulse to the body. Barclay (1946) carried out similar studies on the Amphibia and later (1953) used photography once again in connection with the force apparatus to record the forces exerted on the ground by various mammals.

Several workers have dealt with anatomical structures as they relate to locomotion from a phylogenetic approach. Howell (1937) and Eaton (1944) studied the modification of the shoulder girdle as related to locomotion in mammals. Camp and Smith (1942) presented a lengthy consideration of the phylogeny and function of the digital ligaments in the horse. Schaeffer (1947) reported on the origin and function of the artiodactyl tarsus. A monumental work by Slijper (1946) dealt with the vertebral column and spinal musculature of mammals. Smith and Savage (1955) discussed some locomotor adaptations in mammals by analyzing post-cranial skeletal characters of several different species. Boonstra (1967) made a study of girdles and limbs of early therapsids to demonstrate the possible evolution of the mammalian quadrupedal walking gait.

One of the most extensive analyses of terrestrial locomotion is in a small book by Howell (1944). His investigations considered the muscular system, skeletal characteristics and body portions as well as gaits. Books of a more general nature containing chapters on terrestrial locomotion include Gray (1953), Ottaway (1955) and Slijper (1947). A Sympodium on "Vertebrate Locomotion" by the Zoological Society of London published in 1961 deals with many aspects of locomotion; a number of the contributors are workers who have been mentioned above. An article by Hildebrand (1960) deals predominantly with the anatomical and mechanical aspects of locomotion.

The advent of photography gave great impetus to the study of vertebrate locomotion. Early workers such as Stillman (1882) working with the horse, and Marey (1895) working with various vertebrates played a considerable part in the development of cinematography for locomotion studies. However, the most monumental work making use of photographic techniques for the study of locomotion was that of Edward Muybridge, who published most of his results in 1887 under the title "Animal Locomotion". Muybridge's classic photographs of about 25 species of mammals and several birds during locomotion were obtained by triggering twelve or twenty four still cameras in sequence at rapid intervals. Using these photographs he determined the succession of footfalls (support patterns) and used this as a basis for delineating and describing the gaits of quadrupeds when progressing upon the ground. He concluded that quadrupeds employ eight different regular systems of progression: walk, amble, trot, rack or pace, canter, transverse gallop, lateral gallop and ricochet. Occasional departures from the eight regular systems were considered to be irregular or abnormal.

Subsequent to the work of Muybridge, Paul Magna de la Croix, a French scientist living in Argentina, attempted a comprehensive analysis of the gaits of vertebrates. Although his approach to locomotion was imaginative, it was also highly theoretical. Therefore, his methods have not been followed and his conclusions are often questioned. Two of his many papers (Magna de la Croix, 1928, 1936) are of interest to this study because they discuss the evolution of gaits in quadrupedal animals. Chubb (1929) was another early author to write on the subject of how animals run.

More recently A.B. Howell employed the slow motion movie camera to carry out comprehensive locomotion studies on terrestrial tetrapods. Many of his findings were published in "Speed in Animals", dated 1944. Although many aspects of locomotion are discussed in the book (some are mentioned above) the chapter on gaits adds considerable information to our understanding of locomotion. Howell recognized and named thirteen quadrupedal gaits (three walking gaits, two trots, two paces, two slow gallops or canters, two different fast gallops, a bound and a half-bound) and three types of bipedal progression (walk, run, gallop or ricochet). He found it most logical to divide quadrupedal gaits into symmetrical and asymmetrical groups, according to the rhythm of the feet: the walk, trot and pace were designated as symmetrical gaits because the two feet of a pair (fore or hind) strike the ground at even intervals of time; whereas the various gallops were considered asymmetrical because the feet of a pair strike the ground at uneven intervals of time.

It is apparent from the early works cited above and from the works of Grogan (1951) and Jacobsen (1960) that the horse has received considerable attention in quadrupedal locomotion studies involving cinematography. Other quadrupeds, however, have been studied to a lesser extent. Bartholomew and Caswell (1951) clarified some of the details of bipedal and quadrupedal locomotion in kangaroo rats. Later, Batholomew and Cary (1954) reported on locomotion in pocket mice. Snyder (1949, 1952, 1962) dealt rather extensively with adaptations for bipedal and quadrupedal locomotion in lizards. The galloping gaits of the giraffe were described by Bourdelle (1934), and Dagg (1962) described the role of the neck in giraffe locomotion. Taylor (1970) filled a gap in our knowledge of mammalian locomotion by describing the various gaits of the east African viverrids. Two relatively recent contributions restricted to specific types of quadrupedal gaits were made by Brown (1968), treating walking gaits in general, and Dagg and de Vos (1968) analysing the fast gaits of some pecoran artiodactyls.

Of late, Milton Hildebrand has made extensive use of slow motion pictures to analyze vertebrate locomotion; two of his works (1963, 1964) reported directly on the application of motion pictures for the functional analysis of vertebrate locomotion. Earlier studies (Hildebrand, 1959, 1961) analyzed the asymmetrical, galloping gaits of the cheetah and the horse from a functional standpoint. In these papers (and subsequent ones) he prepared "gait diagrams" which not only included footfall formulas, but also the duration of each pattern of support represented. This was accomplished by studying films frame by frame in a viewer equipped with a frame counter. In a rather general work on walking, running, and jumping gaits Hildebrand (1962) isolated two variables characteristic of symmetrical gaits and plotted them, one against the other on a simple grid. The variable represented on the abscissa was the percentage of stride, in time, that each foot is on the ground; the percentage of stride that the forefoot followed the ipsilateral (same side) hind foot was plotted on the ordinate. Such a graph not only provides information on footfall formulas, but permits new insight into their relationships. Slightly asymmetrical and asymmetrical gaits are handled in a somewhat more complicated manner on the same type of graph. All of Hildebrand's recent locomotion studies (e.g., Hildebrand, 1965, 1966, 1967, and 1968) have dealt with the symmetrical gaits of various tetrapods and have employed this graph as a means of analysis. So far, horses, primates and dogs have been studied in detail.

MATERIALS AND METHODS

The pronghorn antelope utilized in this study is native to southern Alberta and is, therefore, representative of the subspecies occurring in Canada, _Antilocapra americana americana_ (Ord). The analysis of the locomotor gaits and other related information was made by studying 16 mm slow motion movie film frame by frame with a Zeiss-Ikon Moviscop viewer. A two-times magnifying lens was mounted in front of the viewing window to enlarge the image and thus facilitate analysis. This device was used to obtain information leading to the construction of footfall formulas, gait diagrams and graphs as well as the various gaits employed. To facilitate the study of gaits and various body structures during locomotion the film was projected on a solid screen using a 35 mm Graflex filmstrip projector and the sequences that were being studied were traced in silhouette form from the screen. The projector was placed at varying distances from the screen in order to make all tracings of approximately the same size. This procedure was essential for the analysis of various body members and their relative distance from each other and from the ground. All of the pictures utilized in this study were taken by the author with a Pathé Professional Reflex 16 mm movie camera mounted on a modified rifle stock, using black and white Kodak Plus-X Reversal film exposed at 80 frames per second. This rate of exposure was not completely satisfactory for the most rapid gaits of the pronghorn and caused some blurring of the legs at certain phases of the stride. Where the image was blurred, other sequences were studied to elucidate the analysis. A film speed of about 150 frames/second, as suggested by Hildebrand (1964) for running mammals of moderate to large size, was not possible with the camera available for the study.

Although several different lenses were used in filming, a 300 mm f/1.4 Takumar lens with appropriate adapter proved to be the most satisfactory and was used for the majority of the filming. Most film was shot from an angle that would give side-on shots; some sequences, however, were made from directly in front of or behind the moving animal for studying lateral motions of the limbs and body. Over 2000 feet of film were analyzed in studying pronghorn locomotion and 500 feet in connection with the fast gaits of other wild ungulates.

A few of the movie sequences (about 300 feet) dealing with the slower gaits of the pronghorn were taken in large enclosures such as the Alberta Game Farm, Edmonton, Alberta, and Calgary Zoo, Calgary, Alberta. Most of the film (1900 feet) was shot on the open, native grasslands of southern Alberta. Filming during the early spring (April and May) proved to be most satisfactory for the purpose of determining footfall patterns, because the grass of the previous year is matted down and the new spring growth is just beginning, thus giving a less obstructed view of the feet striking and leaving the ground.

Field observations made of various aspects of behavior related to locomotion were facilitated by the use of binoculars and a spotting scope. Field glasses of 7x50 and 8x30 were used for relatively close observations, while the 15x to 60x spotting scope mounted on a tripod was necessary for observing animals from approximately one-half to one mile or more away. Most observations were made from prominent hills which commanded views of large surrounding areas. Caution was taken to observe animals from a great enough distance (usually about one-half mile or more) to ensure that their locomotor behavior was not induced by fright. The McIntyre Ranch, located on the Milk River Ridge

10 miles south of Magrath, Alberta, was the location most frequently used for behavioral observations and for filming. Inasmuch as hunting was not permitted on the ranch, the animals were less "spooky" and therefore easier to approach. Some additional observations were conducted in areas near Aden, Alberta, and Cypress Hills Provincial Park, Alberta.

Six pronghorn skeletons were prepared by bacterial action for the analysis of body proportions. The animals were skinned, eviscerated and most of the flesh removed from the bones. They were placed in a container with enough water to cover the specimens so as to accelerate the decomposition process. After five or six weeks in hot weather, the skeletal material was cleared of any remaining fleshy tissue by a jet of water. The bones were then bleached in a 5% solution of hydrogen peroxide for twenty four hours. Skeletal measurements were made with a vernier caliper to the nearest half of a millimeter for relatively small bones such as phalanges; longer bones were measured with dividers to the nearest millimeter. For the most part measurements express the functional length of the limb segment, i.e., the distance between two centers of articulation or rotation. The skeletons were placed in various age-class and sex groupings to facilitate comparative analysis within each species studied. The specimens were aged by means of mandibular dentition from criteria used by Dow (1952) and Dow and Wright (1962).

During the course of this investigation a mature pronghorn buck was collected and embalmed. Investigations were made of body conformation, extrinsic shoulder and hip musculature and the relative positions of skeletal elements within the body. The animal, which was estimated to be three years old, was collected in August, 1969, in Improvement District Eleven, south of Cypress Hills Provincial Park, Alberta.

The animal was shot in the head by the author which facilitated the embalming process and caused less destruction to the specimen.

Embalming was done by the gravity system. Ten gallons of embalming fluid were administered to the animal. A clear, pliable plastic tube attached to a 14 gauge hypodermic needle (with the sharp end filed off) was used to transfer the embalming fluid into the circulatory system of the animal. Three annular grooves were filed into the tip of the needle to facilitate the tying of the hypodermic needle firmly into the blood vessel. The embalming fluid was administered by way of the left common carotid artery. The animal was held in an upright position, resting on its haunches by means of a rope around its neck suspended from a high support. This arrangement made it possible for the entire body to become embalmed before any loss of fluid through the head wounds was apparent. The pressure necessary to force the embalming fluid into the circulatory system was provided by elevating the embalming fluid reservoir eight feet above the animal. The approximate time required for the distribution and penetration of the embalming fluid to embalm the specimen was seven hours. Approximately one hour of this time was utilized in the embalming of the head. This was accomplished by removing the needle from its posteriorly-directed position in the left common carotid, tying the artery off, and then inserting the needle into the same artery in a cranial direction. During this operation the animal was lowered to the ground. It was found necessary to inject embalming fluid by way of a hypodermic syringe into the hind legs and various parts of the head to complete the process. The embalming solution used was a modification of a formula recommended by Hyman (1942), and consisted of 63 per cent water, 7.5 per cent phenol, 14 per cent ethyl alcohol, 14 per cent glycerin and

1.5 per cent formalin. This solution proved to be very satisfactory, and the specimens remained in very good condition during the course of the study.

An embalmed, 24-hour-old, female antelope fawn collected May 21, 1964, near Brooks, Alberta, was examined for body conformation and skeletal dimensions. These measurements were useful in comparing fawn and adult morphology, and hence body proportions.

Since descriptions of the anatomy of big game animals are limited, the book entitled The Anatomy of the Domestic Animals by Sisson and Grossman (1940) was used as a guide for general comparative purposes. Most of the anatomical terminology used is taken from descriptions of the pronghorn antelope by Murie (1870), Beddard (1909), Lawrence (1951), and Wenzel (1955).

QUADRUPEDAL GAITS IN GENERAL

Locomotion may be described as continuous progression from a state of rest - the act or power of moving from place to place. The locomotory act is a deliberate and controlled change, the manner and duration of which determines the mode of progression employed. It is a vital body function requiring the co-ordinated activity of many body systems or units (Ottaway, 1955). Ideal locomotion requires uniform support of the centre of gravity along with continuous propulsion (Howell, 1944). The development of the various types of locomotor ability must, therefore, be considered as one of the most important facets of animal evolution.

The various manners in which the movements of the four legs of terrestrial quadrupeds accomplish progression are usually referred to as "gaits". Gaits may be divided into many arbitrary categories according to limb sequence (order in which the feet are lifted and advanced), number of feet upon the ground at different times during a cylce of locomotion, time succession of feet striking the ground (rhythm or beat), and the velocity at which the feet strike and leave the ground. Some investigators, therefore, have followed one plan while others have devised their own. However, there is considerable continuity in almost all of the systems as far as the more commonly observed natural gaits such as the walk, trot and gallop are concerned. Regardless of the gait nomenclature used, it is apparent that genetic factors, body structure and conformation, and immediate convenience are in great part responsible for the repertoire of gaits utilized by a particular species of animal.

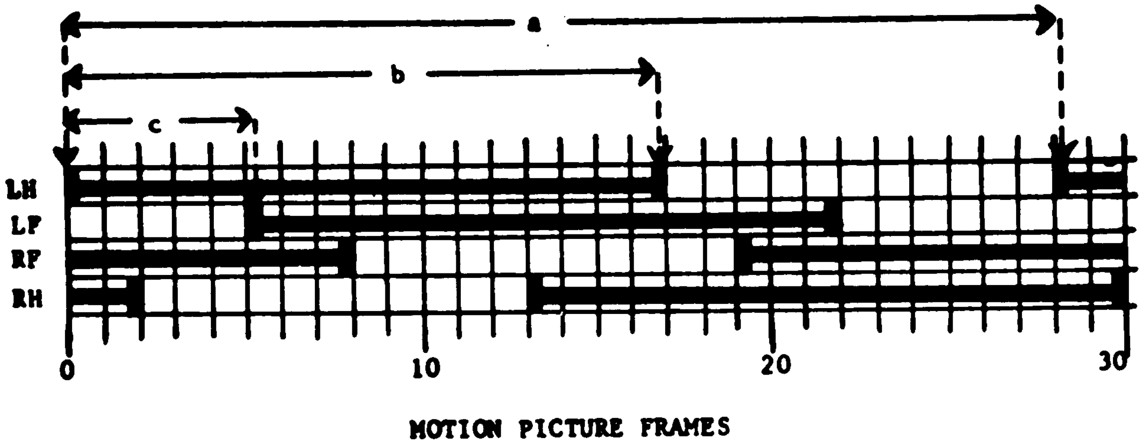
The first comprehensive study of gaits using photographic analysis (Muybridge, 1899), concluded that quadrupeds employ seven different regular gaits: the walk, amble, trot, rack or race, canter, transverse gallop and rotary gallop. Leaping or jumping by the use of all four of the animal's legs was interpreted as an accidental interruption to regular progress. All other methods which were occasionally employed were treated as abnormal and were not named. Howell (1944) distinguished thirteen quadrupedal gaits and also recognized irregular gaits and variations. The diagonal walk, lateral walk, running walk (amble) or single-foot, walking trot, trot, walking pace, pace, transverse gallop, lateral gallop, transverse canter or lope, lateral canter or lope, bound and half-bound were listed as regular gaits employed by quadrupeds. He divided quadrupedal gaits into three main groups, two of them symmetrical and one, asymmetrical in rhythm. In symmetrical gaits the intervals between footfalls are evenly spaced and the support pattern of the feet on the ground is repetitively symmetrical. He further subdivided the symmetrical gaits and classified them as two-time, in which two feet are placed on the ground at the same instant (or nearly so) and four-time, in which each foot is placed on the ground at a different instant from the rest. The trot (diagonal support) and pace (lateral support) were treated as examples of two-time symmetrical gaits while the walk was typical of the four-time. The basic characteristic of the asymmetrical gaits is the uneven spacing of intervals between footfalls. The various types of gallops were cited as asymmetrical gaits, the bound and half-bound were considered as symmetrical renditions of the asymmetrical gallop.

According to Hildebrand (1966), Muybridge and Howell were much too conservative in recognizing only seven or twelve gaits. A difficulty with the terminologies of Muybridge and Howell that contributed to their limited gait nomenclature is that two animals moving according to the same footfall formula, can actually be using visibly different gaits because of differences in the relative durations of the various support patterns (Hildebrand, 1963). Therefore, the audible footfalls and the speed of travel might be strikingly different for two animals employing the same footfall formula. To overcome the shortcomings inherent in the footfall formula approach to gaits, Hildebrand (1963) devised a method of analyzing symmetrical gaits (to a lesser extent asymmetrical) which would permit the convenient comparison of many gaits simultaneously and lead the investigator to general concepts of gait analysis.

By studying his films frame by frame in a viewer equipped with a frame counter, Hildebrand was able to prepare "gait diagrams" which included information on both footfall formulas and the duration of each pattern of support represented (Fig. 1). On graph paper he assigned four adjacent horizontal rows of squares to the feet. Vertical rows represented successive moving picture frames and hence equal intervals of time. A square was "lined in" when its respective foot was in contact with the ground. Although this type of record included information in addition to that found in footfall formula, it still shared with the footfall formula the difficulty of conveniently comparing different gaits. To overcome this difficulty, Hildebrand (1963) isolated two important variables characteristic of symmetrical gaits and plotted them, one against the other on a simple grid (Fig. 2). The variable represented on the abscissa was the percentage of stride, in time, that each foot is on the ground (100 b/a, Fig. 1). For instance, a slowly moving animal may have each foot on the ground 85% of the time while a fast-trotting animal may have each foot on the ground about 22% of the time. This variable is meaningful because it indicates the movements of all four feet during a cycle of a symmetrical gait where the right and left

Figure 1. Gait diagram. Horizontal rows of squares are assigned to the various feet as indicated by the initial letters LH (Left Hind), LF (Left Front), RF (Right Front) and RH (Right Hind). Vertical lines represent successive motion picture frames. Squares are lined in if the respective foot is in contact with the ground. The derivation of the percentage figures (gait formula) that can be plotted to represent graphically the variables of symmetrical gaits are also indicated: 100 b/a is plotted on the abscissa and 100 c/a on the ordinate (after Hildebrand).

Figure 2. Graph of symmetrical gaits (after Hildebrand).


a
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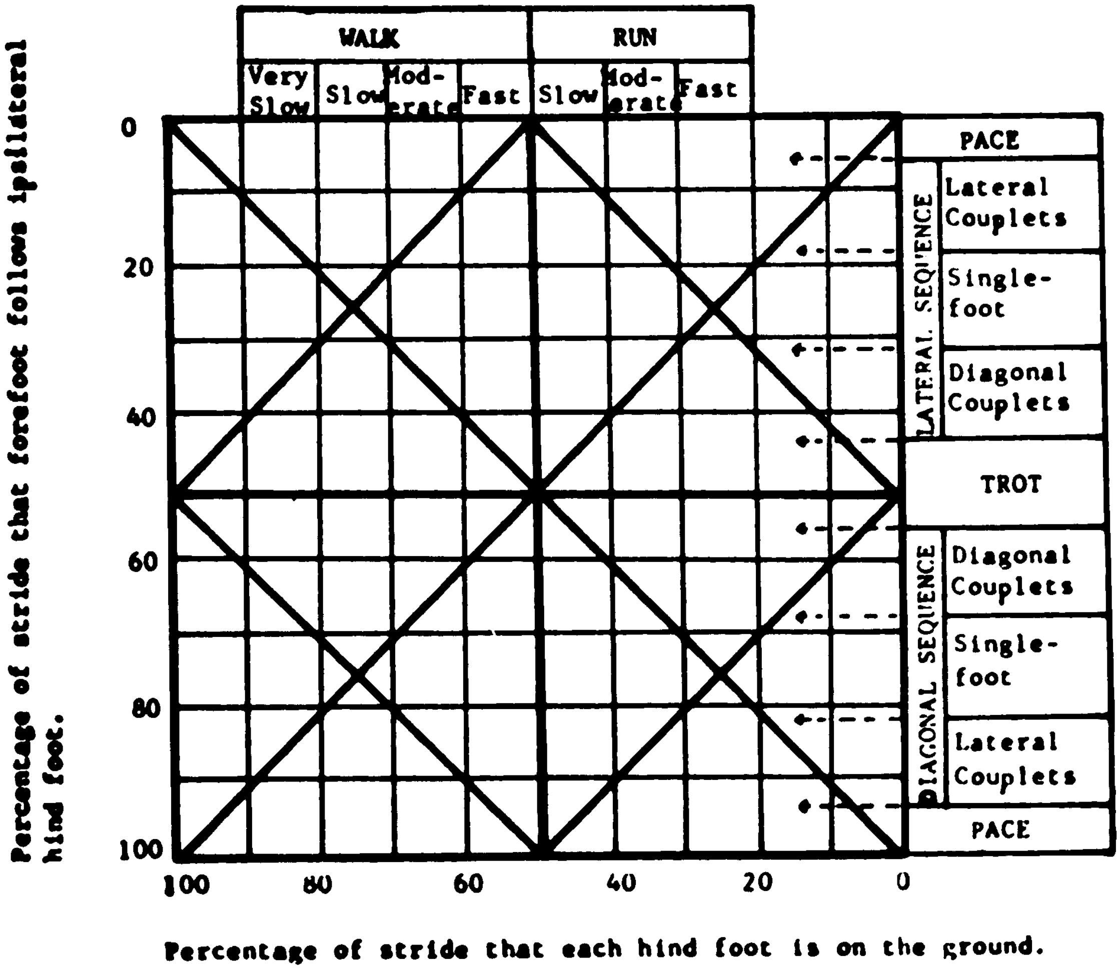
MOTION PICTURE FRAMES


WALK
RUN
Very Slow
Slow
Mod-erate
Fast
Slow
Mod-erate
Fast
PACE
LATERAL SEQUENCE
Lateral Couplets
Single-foot
Diagonal Couplets
TROT
DIAGONAL SEQUENCE
Diagonal Couplets
Single-foot
Lateral Couplets
PACE
0
20
40
60
80
100
100
80
60
40
20
0
Percentage of stride that forefoot follows ipsilateral hind foot.
Percentage of stride that each hind foot is on the ground.

members of a pair have the same intervals of contact with the ground (disregarding trivial idiosyncrasies of individual strides), and the contact of the forefeet is of the same duration (usually) as the contact of the hind feet. For convenience and continuity, Hildebrand (1963, 1965, etc.) arbitrarily chose the stride of the left hind foot to calculate the percentage. In practice, however, the stride of any foot could be used.

If the timing of the footfalls of one foot is known in a symmetrical gait, then the timing of the footfalls of its opposite is also known and the relationship of the fore footfalls to the hind footfalls can be expressed. This variable, plotted on the ordinate of the graph, was expressed by Hildebrand (1963) as the percent of stride interval that the footfall of the forefoot lags behind the strike of the ipsilateral hind foot, or 100 c/a (Fig. 1). Hildebrand explains further that if there is no lag, both feet on the same side of the body move in unison and the animal is pacing. If the lag is 10 to 15%, then the footfall of the hind foot is followed by the footfall of the forefoot on the same side of the body giving a "lateral sequence" gait in which the footfalls of the lateral feet come in couplets (1,2--3, 4) and are more closely spaced than the footfalls of diagonal feet. He refers to this sequence of footfalls as a lateral sequence, lateral couplets gait and indicates that many long-legged ungulates and carnivores walk in this way. If the lag of each forefoot behind the ipsilateral hind foot is 25% of the stride, then the feet strike singly at even intervals of time, 1-2-3-4, and the gait is a lateral sequence single-foot characteristic of the horse and most large ungulates. If the lag is 35 to 40%, the lateral sequence is retained but the diagonal footfalls are more closely spaced than the laterals and we have a lateral sequence, diagonal couplets gait (4, 1--2,3) used by small mammals. When the lag is 50%, diagonal feet move in unison, giving a trotting gait. And if the lag is more than 50%, the next forefoot to strike after a given hind foot is the contralateral or diagonal rather than the ipsilateral, and we move into the diagonal sequence family of gaits.

Thus, all symmetrical gaits can be expressed by two percentage figures referred to as a "gait formula" by Hildebrand (1966). The figures are plotted on the graph so that hundreds of gait formulas can be compared simultaneously. On the abscissa of the graph, Hildebrand proposes seven intervals of 10% each, extending from 20 to 90%, and terms these (from left to right): very slow, slow, moderate, and fast walking gaits; slow, moderate, and fast running gaits. No terminology is given for the extreme left of the graph (90 to 100%) because no gaits were found that had each foot on the ground nearly 100% of the time. Likewise, no plots fall at the extreme right of the graph (0 to 20%) because no animals using symmetrical gaits were found to have their feet on the ground less than 18 or 20% of the time. On the ordinate, he uses eight intervals of 12 1/2% termed (from top to bottom): pace, lateral sequence lateral couplets gaits, lateral sequence single-foot, lateral sequence diagonal couplets gait, trot, diagonal sequence diagonal couplets gait, and diagonal sequence single-foot. He found no animal employing the diagonal sequence lateral couplets gait. By combining the terminologies expressing variation along the two axes of the graph, Hildebrand establishes gait names which he believes to be descriptive and unambiguous, e.g., a gait formula of 55-18 would be a fast, lateral sequence, lateral couplets walk characteristic of the cheetah.

Hildebrand (1963) analyzed many different gaits and found that if the graph is ruled into sixteen triangles in the form of an overlay (Fig. 2, heavy lines) all plots falling within one triangle represent gaits having the same footfall formula, and each triangle has a different formula. He also found that there is another and different formula at every intersection of lines and along every line between intersections. It follows, then, that forty-four footfall formulas are theoretically possible when dealing with symmetrical gaits. Hildebrand (1963) asserts that the formulas along the diagonal lines and at the intersections include the so-called irregular and abnormal gaits of Muybridge (1899) and Howell (1944). He classifies such gaits as "transitional" rather than abnormal.

Slightly asymmetrical gaits, i.e., gaits in which the anterior contacts are not of exactly the same duration as the posterior contacts, are analyzed on the same grid or graph as the symmetrical gaits by Hildebrand (1966). To determine the footfall formulas corresponding to plots representing such gaits, he draws in different and more complicated overlays (diagonal lines etc.); a separate one for each relative anterior-to-posterior contact (80%, 90%, etc.) Only the duration of hind foot contacts are plotted on the abscissa.

Hildebrand (1966) reports that although the graph system of naming symmetrical and slightly asymmetrical gaits has 164 theoretically possible footfall formulas (and hence names), the fifteen orders of mammals and a less complete representation of amphibians and reptiles studied, actually used about 118 different formulas. However, only 28 of the 118 formulas were thought to be significant (frequently used).

Asymmetrical gaits have also been analysed by Hildebrand (1963) on a graph similar to the one used for symmetrical gaits. On the abscissa he plots the proportion of total duration of a stride during which one or both hind feet are on the ground. Then considering both front and hind pair of feet, he establishes "midtime" which is the point in time which is midway between the striking of the first foot of a given pair and the moment when the last foot of the same pair leaves the ground. He then expresses the lag of the midtime of the forefeet behind the midtime of the hind feet as a percentage of the duration of stride and plots this on the ordinate. He reports that the resulting graph is not as useful as the one used for symmetrical gait analysis.

Work with trained horses (Grogan, 1951) has demonstrated that in addition to the more natural gaits such as the walk, trot, pace (when bred to use the gait), and various gallops, a goodly number of gaits can be acquired. Literature concerning these so-called man-made gaits is confusing because of the overlapping and differences of nomenclature used. Grogan lists five acquired gaits: slow gait and rack (called the pace, amble, broken amble, running walk, fox trot, broken trot, etc. by various authors), running walk and the pace. The acquired gaits of horses are not for the most part natural gaits employed by wild ungulates. Therefore, they will not be discussed in this study. It should be pointed out, however, that the pace (legs of animal moving in lateral pairs simultaneously) is a natural gait of the camel, the giraffe, an occasional dog, and possibly of a few other animals (Muybridge, 1899). Hildebrand (1966) does not include the giraffe in his list of animals that employ the pace as a natural gait. This can probably be explained by the fact that Bourdelle (1934) described the "ambling walk" of the giraffe as legs moving on either side of the animal almost together and not alternately as in most ungulates. This gait, then, would not be considered as a true pace by Hildebrand, but as a lateral sequence, lateral couplets gait. Hildebrand (1966) points out that the pace is limited to long-legged, cursorial animals having good balance and little straddle of the limbs, thus allowing for a long smooth stride without interference between fore and hind limbs.

A few terms used to explain various aspects of locomotion need to be defined before undertaking an analysis of pronghorn gaits: A "stride" (cycle) is one completed action of all four feet; a "step" is the complete movement of one foot; a "stride interval" is the duration of a stride; the "swing" of any limb is the completed advancement or retardation of a single limb; and a "phase" is any particular point or instant of motion during a stride.

SYMMETRICAL GAITS OF PRONGHORN

There appears to be little discrepancy among workers reporting on the symmetrical gaits of pronghorn. However, there is some confusion in the terminology used to describe the various types of walking and trotting gaits. Einarsen (1948) depicts two walking and two trotting gaits by way of illustrations: the sedate walk, the pompous alarmed walk, the leisurely trot and the elegant trot. Bruns (1969) referred to an elegant trot while Gregg (1955) was more explicit and briefly described a slow walk, a normal walk and a trot. Howell (1944) delineates the symmetrical gaits of the pronghorn as consisting of the walk and a rather slow trot which is executed with unusual spirit and action. Some writers (e.g., McLean, 1944 and Throckmorton, 1945) have commented on the stiff, jerky and somewhat awkward appearance of the walking gait of pronghorn. Others have brought attention to the fact that both the walk and the trot can be a rather fast mode of covering distances. It is obvious from the literature, however, that studies involving symmetrical gaits have dealt only with nomenclature and have not approached the subject from an analytical standpoint.

The terminology used in naming the symmetrical gaits of pronghorn antelope is taken from Muybridge (1899) and Howell (1944), with Hildebrand's gait nomenclature being incorporated as a method of further analysis.

<u>Very Slow Diagonal Walk (Crawl)</u>

The walk is the slowest gait employed by the pronghorn. Of the various types of walks employed, the very slow diagonal walk or crawl is the slowest means of progression. From the viewpoint of support and balance it is also the most stable of all the gaits, having no fewer than three feet on the ground at any time during a complete cycle of locomotion. It is possible, therefore, for the body to stop at any instant during a stride without causing the animal to lose balance. The crawl is a four-time symmetrical gait having eight important phases, one for each of the four footfalls, and one for each period that a foot is suspended. These movements may be best conveyed by a system of notations (diagram) consisting of symbols designating the support patterns of the legs during a complete cycle of locomotion. Such stylized diagrams are usually referred to as "footfall formulas". If the left hind foot is arbitrarily chosen as the foot to initiate the locomotor cycle (Fig. 3), then it will always be followed by the left front foot. The next leg to move is the right hind and it is followed by the right front. The three-point support is shifted, with the help of an intermediate four-point support, first laterally (Fig. 3-B), then diagonally (Fig. 3-D), then to the other lateral (Fig. 3-F) and to the other diagonal (Fig. 3-H), completing the cycle of eight different phases. The support formula (number of feet on the ground at different phases of locomotor cycle) for the sequence of legs is 4-3-4-3-4-3-4-3. Based on the sequence of footfalls, Howell (1944) refers to this type of walking gait as being transverse or diagonal. He arrived at this terminology in a rather arbitrary manner based upon the observation that the second footfall is diagonal to the first footfall when the left front foot is chosen to initiate the locomotor cycle (e.g., LF-RR-RF-LR). Hildebrand (1963), however, refers to such a gait where the hind foot is followed by the footfall of the ipsilateral forefoot as being a lateral sequence gait. He points out that such a sequence is superior for avoiding interference between fore and hind feet, and that all of the various walks employed by the vast majority of ungulates are of this type.

Although the very slow walk is considered to be a symmetrical gait, it is frequently executed in an asymmetrical manner. When progress is extremely slow, the advancement of individual legs may be at uneven intervals of time. This results in a gait with variation in the duration of the three-point support phases even though the actual time interval for the advancement of each of the four feet remains relatively constant.

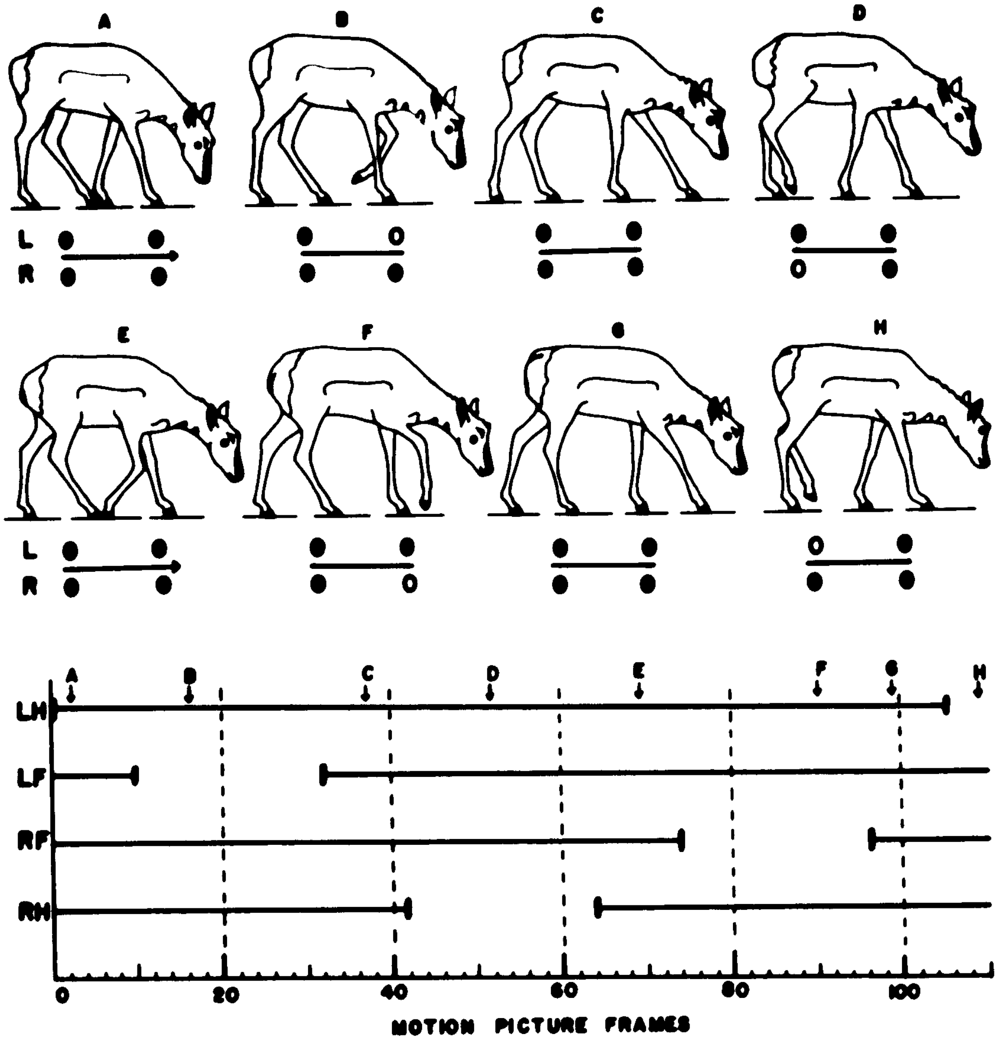
Pronghorn employ the very slow walk most frequently during feeding activities and when approaching an object that has elicited curiosity. The gait is also used for moving short distances when engaging in various social activities. During this very slow walk the progress is slow because each foot advances only a few inches and a complete stride requires more than a second to be executed. It is not necessary, therefore, to have the hind feet pass lateral to the forefeet as in the case of some fast tempo walks, because the hind feet do not strike the ground in close proximity to their respective ipsilateral forefeet.

Slow Diagonal Walk

Like the crawl, the slow walk is a combined diagonal- and lateral-support gait with the support alternating between diagonal and lateral limbs but at a faster tempo (Fig. 4). The footfalls are all separate and support is by never fewer than two feet, two diagonals being substituted for two of the four-foot supports incorporated in the very slow walk. Accordingly, the support formula for the slow diagonal walk is 4-3-2-3-4-3-2-3. Therefore, this gait is only slightly less stable than the very slow walk and is employed when progression slightly faster

Figure 3. Pronghorn employing a very slow diagonal walk (crawl). The support patterns of the feet (footfall formula) are represented below the pronghorn silhouettes by circles which are black when the respective foot is on the ground. The gait diagram below (compare Fig. 1) indicates the periods of contact of the feet with the ground; time scale is in motion picture frames at 80 frames per second. Initial letters on the left margin of the figure refer to various feet: LH (Left Hind), LF (Left Front), RF (Right Front), RH (Right Hind), L (Left) and R (Right). Pronghorn silhouettes A-H are comparable to stride phases A-H of the gait diagram below.

Figure 4. Gait diagram (compare Fig. 1) of a pronghorn employing a slow diagonal walk. The footfall formula (feet represented by circles which are black when respective foot is on ground) for the eight phases of the gait is indicated above the graph.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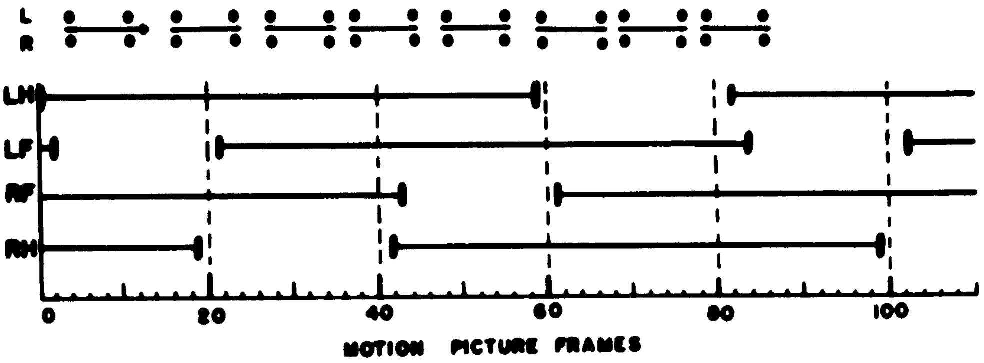
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MOTION PICTURE FRAMES

than a crawl is warranted. Strides are completed in about one second, with a distance of approximately 31 to 33 inches (79 to 84 cm.) being covered during each stride.

Fast Diagonal Walk

Although "fast" is a relative term and many gait variations occur between the slow and so-called fast walks (e.g., moderate walks etc.), it is convenient to classify walking gaits in this manner and then indicate various types of transitional support sequences encountered. In many instances, however, the slow walk merges so insensibly into a faster tempo that it is difficult, and somewhat meaningless, to account for all of the intermediate footfall sequences.

The most frequently employed fast walk of the pronghorn (Fig. 5) differs from the slow walk in that the two remaining four-point supports of the slow walk are abandoned and two lateral two-point supports are substituted (Fig. 5 - D and H). This footfall sequence is brought about by an increase in the rate of walking which necessitates each hind foot being lifted off the ground before the contralateral forefoot reaches the ground. Thus the eight phases of each cycle of locomotion are composed of four three-point and four two-point support periods (3-2-3-2-3-2-3-2), the three-point supports alternating between the two-point diagonal and lateral supports. The relative instability of two additional two-point supports appears to be compensated for by increased body momentum due to increased speed, and by each two-point support being followed by a three-point support during which any loss of equilibrium may be corrected.

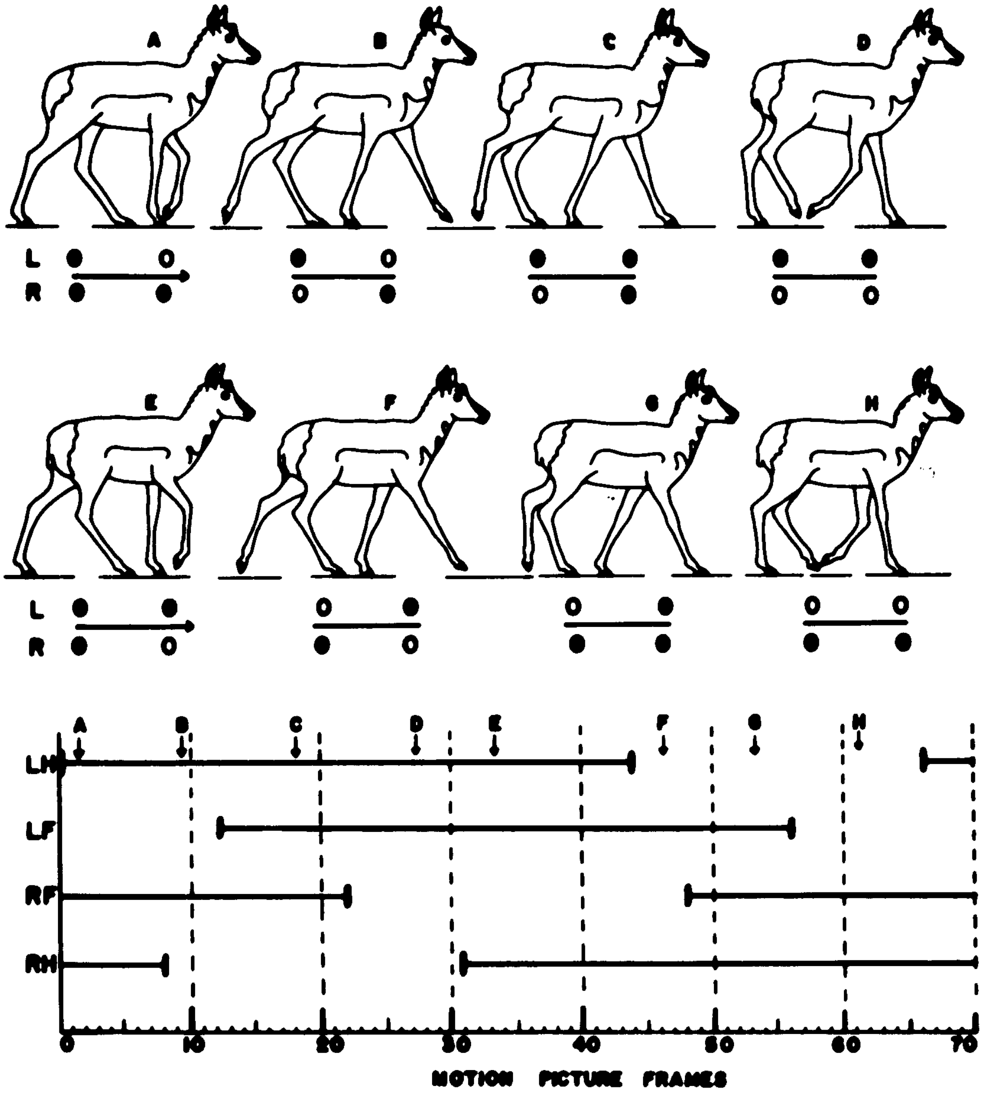
When the pronghorn is walking at a moderate speed, each front foot leaves the ground just before the ipsilateral hind foot strikes the ground. Therefore, the imprint of the hind foot almost coincides with that of the forefoot. In faster walks, however, the imprint of the hind foot is slightly in front of, and lateral to, the imprint of the ipsilateral front foot. Straddling of the forelimbs by hindlimbs is necessary to prevent interference of lateral legs, while a degree of overstride by hind feet is necessary in order to increase length of stride and hence speed. During a fast walk a pronghorn will move about 38 to 41 inches (97 to 104 cm.) with each completed stride; the duration of stride being approximately .80 second.

Some of the more commonly used support sequences encountered in the various walking gaits of pronghorn are illustrated after the manner of Hildebrand (1965) in Fig. 6. It will be noted in Fig. 6-B (a moderately fast walk) each hind foot is lifted at the same instant contact is made with the contralateral forefoot, and each front foot is lifted at the same instant the ipsilateral hind foot contacts the ground. This results in a shortened support pattern with a support formula of 3-3-3-3. The support pattern illustrated in Fig. 6-C is also somewhat shortened due to synchronization of lifting and placing feet. The fast walk (Fig. 6-A), the slow walk (Fig. 6-D) and the crawl (Fig. 6-E) are illustrated for comparative purposes. Individual idiosyncrasies are not reported.

Gait formulas calculated from gait diagrams and plotted on Hildebrand's symmetrical gait graph (Fig. 7) indicate that the pronghorn employs the very slow, slow, and moderate lateral-sequence, single-foot walks. According to Hildebrand (1966) the lateral sequence, single-foot provides continuity of support and is selected as the walking gait by most large ungulates.

Figure 5. Footfall formula and gait diagram (compare Fig. 3) of a pronghorn employing a fast diagonal walk. One complete stride is illustrated.

Figure 6. Five support sequences that might be used by a pronghorn when walking. The initials L, R, F and H stand for left, right, fore and hind feet. Dark circles indicate feet in contact with the ground; open circles, suspended feet. Within each diagram, a vertical column of four circles shows a particular pattern of support. Each sequence starts with the footfall of the LH foot.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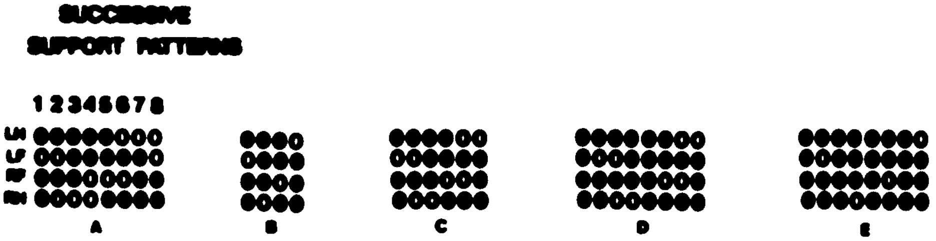
MOTION PICTURE FRAMES


SUCCESSIVE
SUPPORT PATTERNS
1 2 3 4 5 6 7 8
LH
LF
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A
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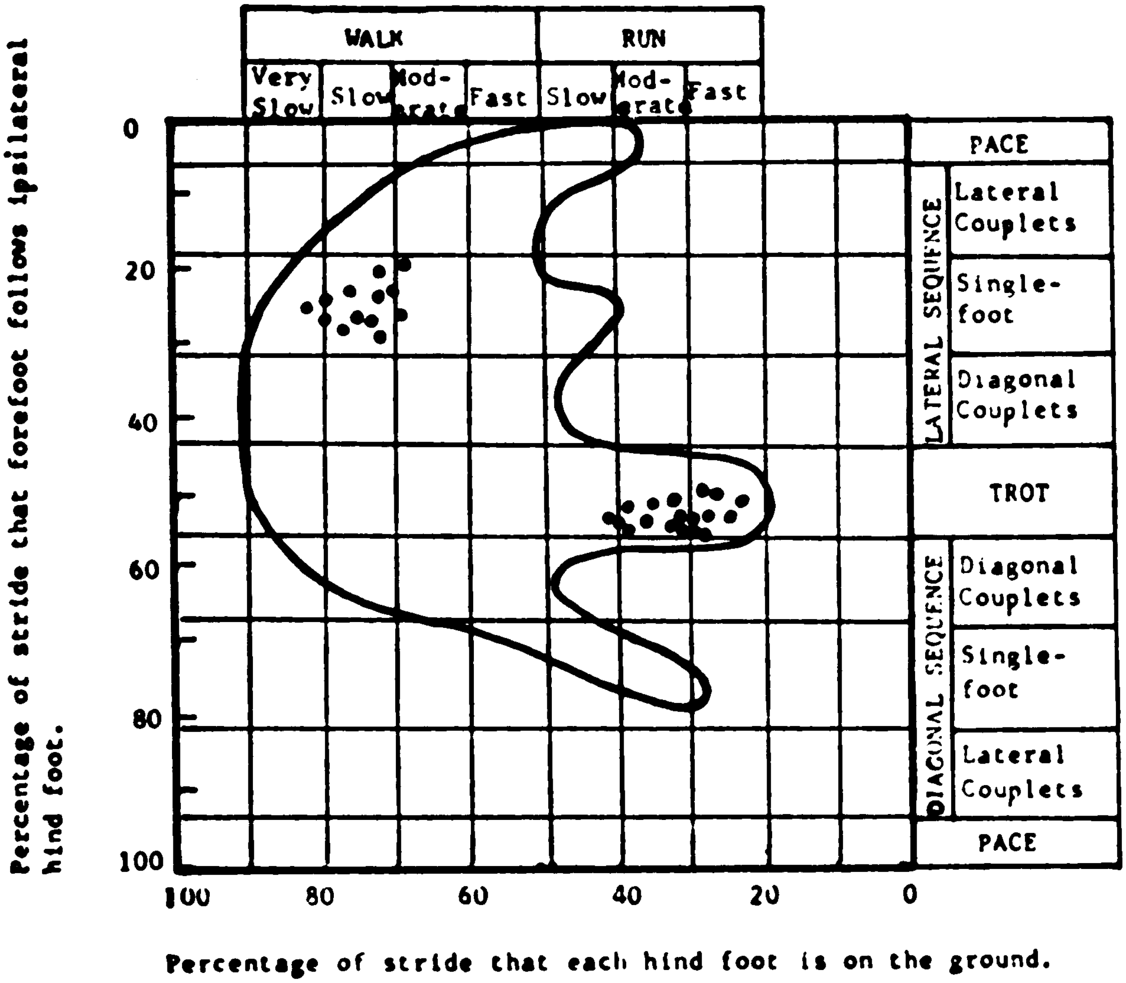
E

Figure 7. Symmetrical gait graph showing the distribution of some of the gait formulas for the symmetrical gaits of pronghorn. All of Hildebrand's plots (gait formulas) for the gaits of wild quadrupeds (833 formulas for animals belonging to 158 genera) fall within the area of the graph outlined by a heavy line.


WALK
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Very Slow
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Lateral Couplets
Single-foot
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TROT
DIAGONAL SEQUENCE
Diagonal Couplets
Single-foot
Lateral Couplets
PACE
0
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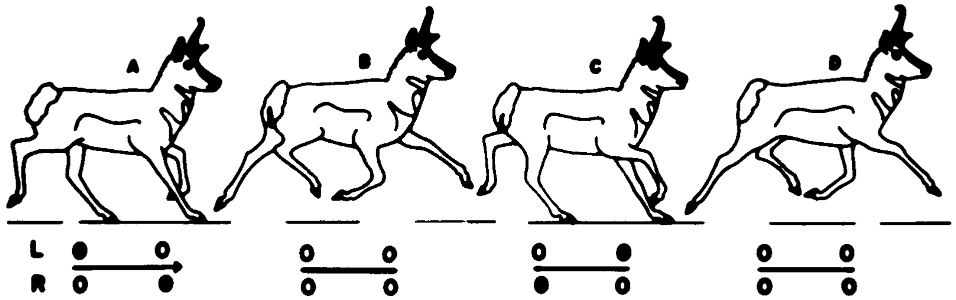
80
60
40
20
0
Percentage of stride that forefoot follows ipsilateral hind foot.
Percentage of stride that each hind foot is on the ground.

Trot

The pronghorn employs the so-called "true trot" (Howell, 1944) or "running trot" (Hildebrand, 1965) as its gait of medium speed. In this two-time symmetrical gait, support is furnished by alternation of diagonal pairs of limbs moving in unison, or at least approaching synchronization. It is a sure-footed gait providing good balance because the line of support passes approximately under the animal's center of mass. If the diagonal pairs strike and leave the ground in exact unison (Fig. 8), then the support formula is shortened to four different phases, 2-0-2-0. The body, then, is unsupported twice during each cycle of locomotion (Fig. 8-B and D). This completely synchronized trot is slightly slower in tempo than the more frequently employed footfall sequence of the running trot, and appears to be limited to occasional strides mingled with the more normally executed trotting sequences. The gait occurs most frequently when the terrain is flat and relatively smooth, thus facilitating the exact placement of the feet. More commonly, however, the symmetrical rendition of the trot is accomplished by either the hind foot striking the ground slightly in advance of the contralateral forefoot and leaving the ground slightly in advance of same (Fig. 9-A), or by the front foot of a pair contacting and leaving the ground prior to the contralateral hind foot (Fig. 9-B). Although in both instances the duration of contact is the same for both feet of a diagonal pair and the trot retains its symmetry, the gait does not consist of synchronized diagonal support. Both of the above footfall sequences are used only occasionally by pronghorn, the sequence in which the front feet contact the ground first is the least employed of the two. The support formula is the same for both footfall sequences: 1-2-1-0-1-2-1-0.

Figure 8. Footfall formula and gait diagram (compare Fig. 3) of a pronghorn employing a symmetrical and synchronized rendition of the trot.

Figure 9. Gait diagrams (compare Fig. 1) of some of the sequences of footfalls employed by trotting pronghorn.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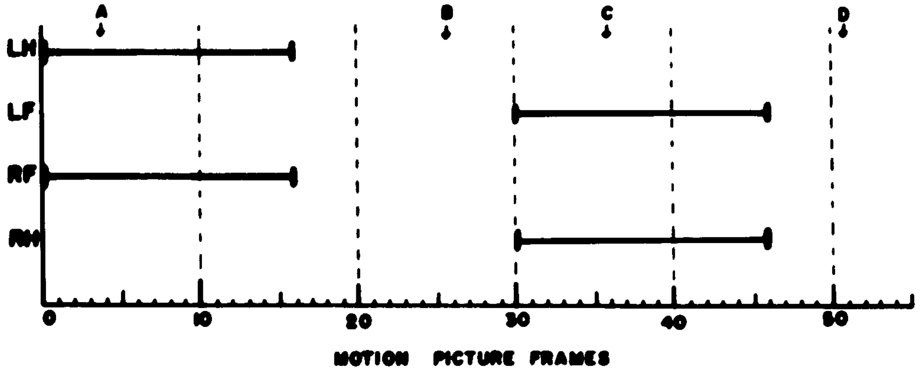
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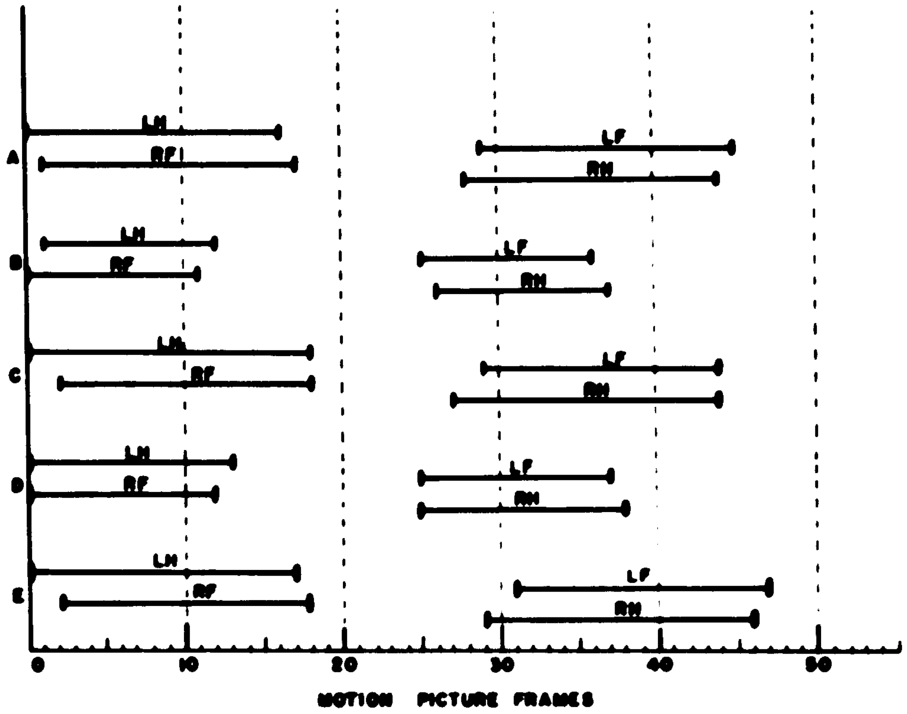
MOTION PICTURE FRAMES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MOTION PICTURE FRAMES

Inasmuch as the front legs of pronghorn antelope are somewhat shorter than the hind legs (see section dealing with skeletal proportions), a full stride of the hind legs cannot be matched by the front legs when the animal is trotting at high speed. Therefore, the most frequently employed trotting sequences are slightly asymmetrical, i.e. the hind feet are in contact with the ground for a longer period of time (6 to 11%) than the front feet. Of these support sequences, two appear to predominate: one in which the hind foot of a diagonal pair strikes the ground first and then both feet leave the ground at precisely the same instant (Fig. 9-C) and alternately, when both members of a diagonal pair contact the ground simultaneously but the front leg leaves slightly in advance of the hind leg (Fig. 9-D). Occasionally the hind foot of a diagonal pair will contact the ground prior to the contralateral forefoot and leave in advance of it (Fig. 9-E) but will be in contact with the ground for a slightly longer period of time. On rare occasions a trotting pronghorn may execute a stride in such a manner that the front foot of a diagonal pair will strike the ground subsequent to the contralateral hind foot and leave in advance of it. It is also possible for a trot to be of such a slow tempo that there are no periods of suspension in the gait whatsoever. This rather anomalous footfall sequence appears to occur only when a pronghorn is going from a slow trot to a walk or vice versa, and is, therefore, probably transitional in nature.

During most of the trotting sequences described above, the hind foot that is being brought forward (flexed) passes lateral to the ipsilateral forefoot during a period of suspension. This is necessary to prevent interference of ipsilateral feet. The straddling maneuver of the hind legs causes slight lateral hip movement which undoubtedly adds somewhat to the length of stride and results in a slight increase in speed.

The spacing of footfalls (total length of stride) and the duration of stride (time required to execute a stride) vary with the speed of the trot and the individual animal performing the gait. Measurements taken from the foot impacts of several trotting pronghorn indicate that the length of stride varies from about seven to nine feet (2.1 to 2.7 m.) and the duration of the various stride lengths from .57 to .68 second. As the rate of stride increases (less time required for each stride) the length of stride also increases, resulting in a greater rate of speed.

When gait formulas are calculated and plotted on Hildebrand's symmetrical gait graph (Fig. 7), it can be seen that the pronghorn employs the slow, moderate and fast running trot. Several of the plots fall near or on the line separating the trot from the diagonal sequence, diagonal couplets gait. It is also apparent from the graph that as the trot gets faster, the periods of support shorten and the periods of suspension lengthen. Therefore, as the rate of stride increases, the animal is suspended without support for a greater interval of time during each stride.

The trotting gait is frequently executed in a very elegant manner with considerable leg action: head held high, chin pulled back, mane raised, rosette (rump-patch) raised and considerable flexion between epipodial and metapodial leg elements. Although it is difficult in most instances to determine the eliciting factor of the elegant rendition of the trot, a pronghorn that has been alarmed will usually employ this type of trot. The trotting gait in general, including the elegant trot, does not demonstrate excessive vertical body movement and is, therefore, a relatively smooth gait.

ASYMMETRICAL GAITS OF PRONGHORN

As was the case with symmetrical gaits, the literature dealing with the asymmetrical gaits of pronghorn is also fragmentary, superficial and general in nature. There appears to be unanimous opinion, however, among all workers in ascribing the term "gallop" to the pronghorn's most rapid gait. Howell (1944) was more specific and referred to the pronghorn gallop as being a lateral or rotogallop. A galloping gait at a slow tempo is referred to as a lope (Einarsen, 1948 and Gregg, 1955) or canter (Howell, 1944).

Transverse (Diagonal) Canter or Lope

The canter or lope is for the most part a slow gallop but because of the exigencies of equilibrium at slow galloping speeds, support looms larger in the picture. In the transverse or diagonal canter the fore and hind feet use the same lead; i.e., the second hind footfall (leading hind foot) and the second front footfall (leading front foot) are unilateral. If a pronghorn initiates a stride with the right hind foot striking the ground (Fig. 10-A), then the next foot to contact the ground is the left hind (Fig. 10-B) followed by the right front (Fig. 10-D) and then by the left front (Fig. 10-E). The left front foot (leading foot), and to a lesser extent the right front foot (lagging foot), give a powerful upward thrust to the body resulting in a period of suspension with the legs gathered together (Fig. 10-H) in preparation for the next stride. The pronghorn's body appears to go through a rocking or see-saw type action when employing this gait.

The speed at which the canter is executed has a great deal to do with the footfall sequence used. In a slow canter the second rear and first front footfalls may coincide, making a three-time canter instead of the typical four-time canter (Fig. 12-A), or the first front footfall may precede the second hind footfall (Fig. 12-B). The latter is referred to as an "atypical" canter by Howell (1944). In both of the aforementioned slow canters, as well as in the more normally executed slow canter (Fig. 12-C) the leading front foot strikes the ground before the lagging hind foot is lifted, thus resulting in a four-point support phase during the stride. The support formulas for these three slow canters are 1-3-4-3-1-0 for the three-time canter and 1-2-3-4-3-2-1-0 for the two four-time canters. The typical formula for the moderate canter (Fig. 12-D) is 1-2-3-2-3-2-1-0, the formula for the fast canter (Fig. 10) being 1-2-1-2-1-2-1-0.

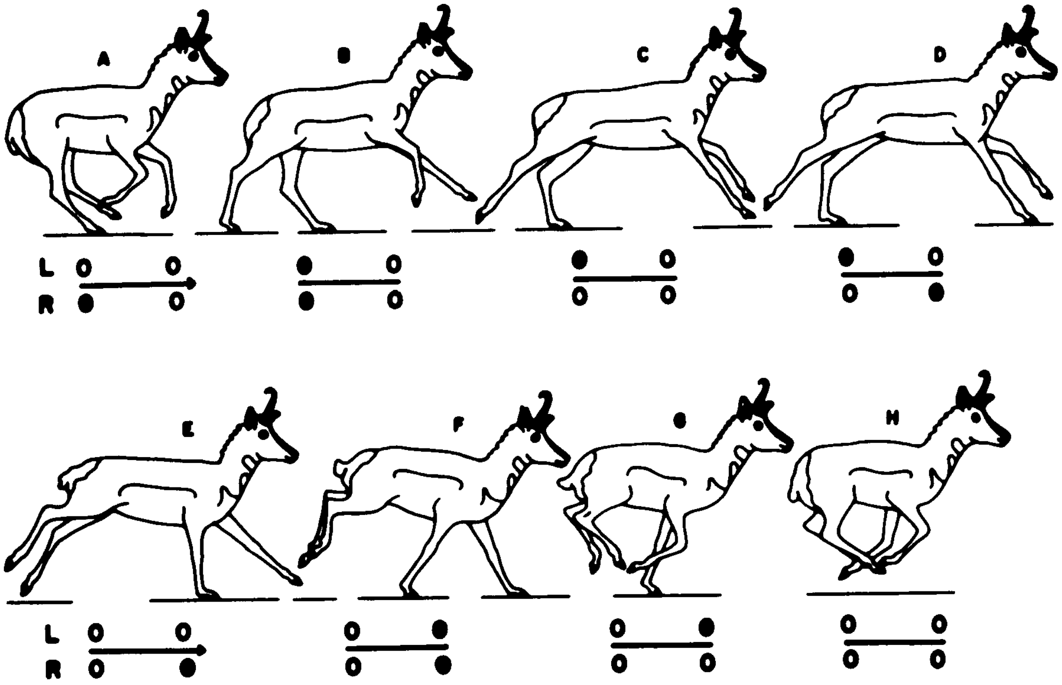
The length and duration of stride vary considerably with the speed of the canter and with the individual animal performing the gait. The length of stride varies from about eight feet (2.4 m.) in the slow canter to 14 feet (4.2 m.) in the fast canter, while the duration of stride varies from .31 to .45 second. Although the visual method of evaluating speed is somewhat arbitrary, it appears that in all cases the rate of stride increases as the length of stride increases, thus resulting in a greater rate of speed. Compared to the time interval of a trotting stride (.60 to .68 second), it can be seen that the increased rate of stride in the canter accounts for at least some of the greater speed of the canter.

Lateral (Rotary) Canter or Lope

This gait is essentially the same as the transverse canter except for the sequence of footfalls (Fig. 11). In the lateral or rotary

Figure 10. Footfall formula and gait diagram (compare Fig. 3) of a pronghorn employing a transverse (diagonal) canter or lope.

Figure 11. Gait diagram (compare Fig. 1) of a pronghorn employing a lateral (rotary) canter or lope. The footfall formula (feet represented by circles which are black when respective foot is on ground) for the eight phases of the gait is indicated above the graph.



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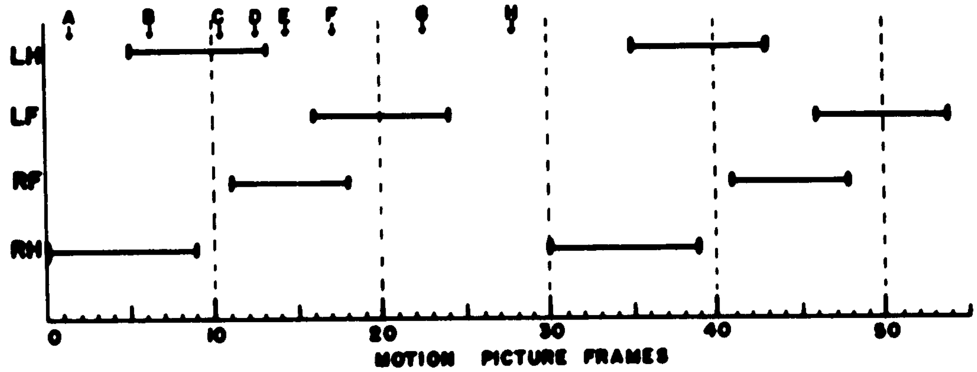

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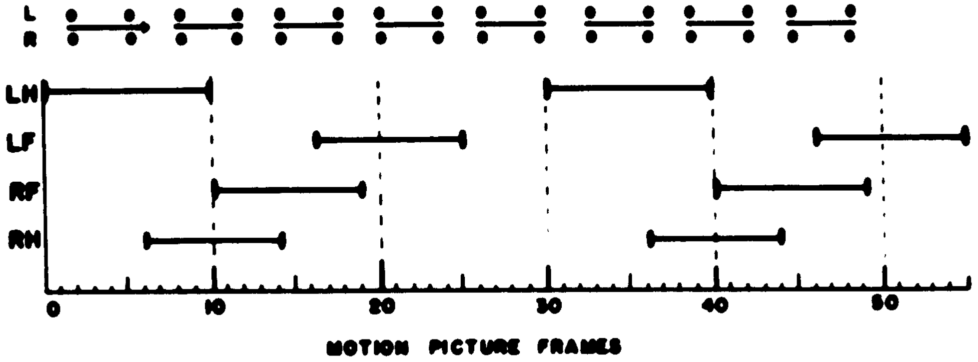

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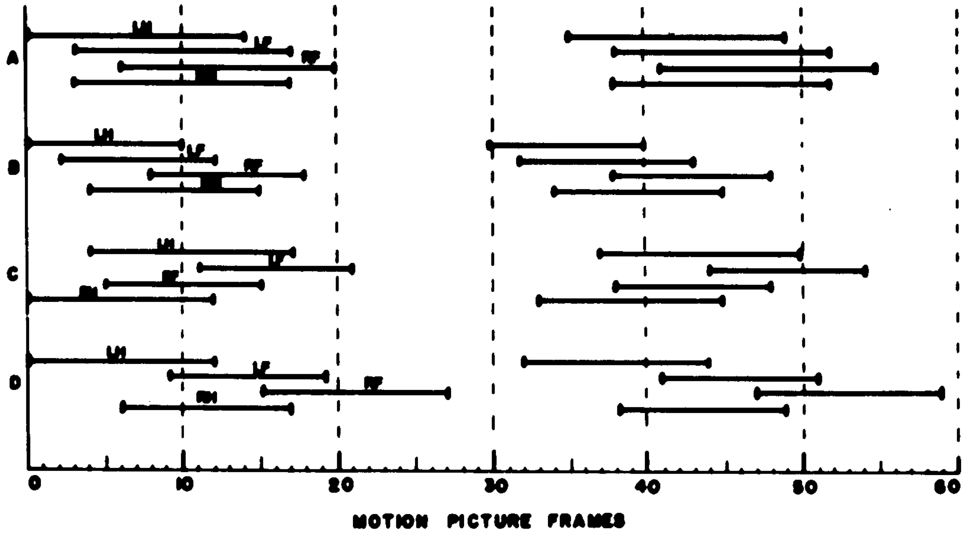
Figure 12. Gait diagrams of some of the footfall sequences used by pronghorn when employing the transverse canter or lope.

Figure 13. Footfall formula and gait diagram of a pronghorn employing a lateral (rotary) gallop.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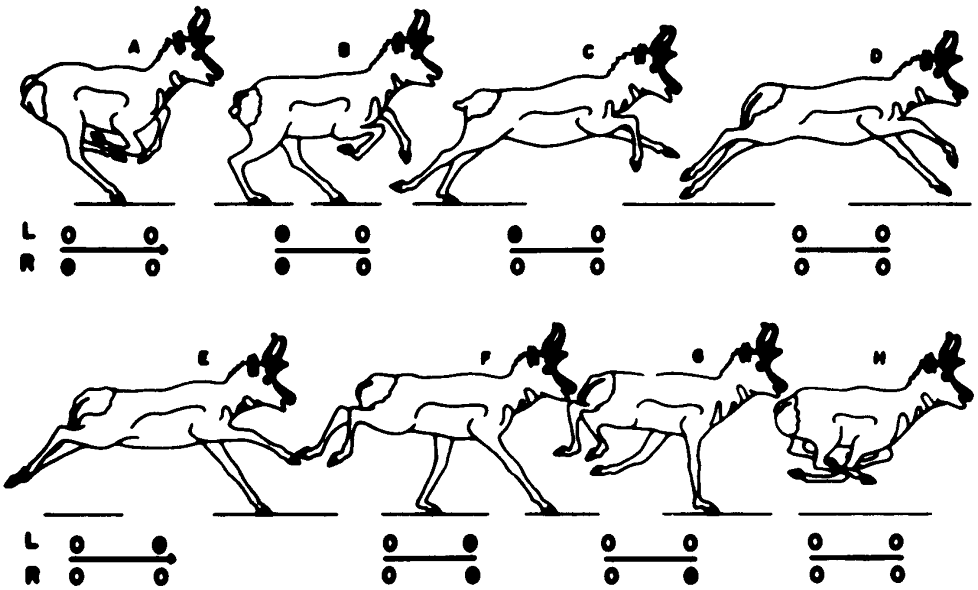
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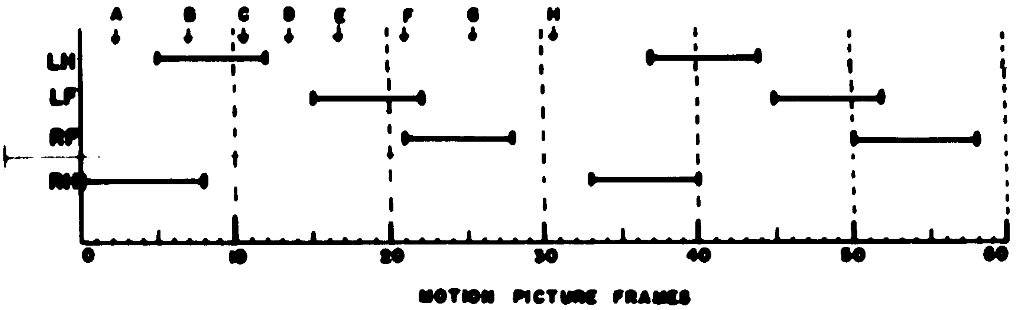
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canter the fore and hind feet use opposite leads. Therefore, the footfalls succeed each other in a rotary manner, e.g., LH, RH, RF and LF. Straddling of the leading front foot by the lagging hind foot (ipsilateral foot) during the suspension phase of the stride is more pronounced in this sequence of footfalls than it is in the transverse canter. According to the literature this type of canter or "gallop" is the only one employed by pronghorn. Data from this study, however, show this to be false. Although the rotary canter may be employed more frequently (but only slightly), the transverse canter is a regularly used footfall sequence. This is particularly true for the slow and moderate canters.

As in the transverse canter, there are several different footfall sequences utilized by pronghorn when employing the rotary canter. The support formulas reported for the transverse canter are essentially the same as those found in the rotary canter. Therefore, these footfall sequences will not be elaborated upon. However, one stride of a very slow canter that had no period of suspension was encountered in a film sequence. Inasmuch as the stride was executed during the transition from a slow canter to a walk, it can probably be viewed as being transitional in nature and not a frequently employed footfall sequence. This type of stride is probably rare but also encountered in the transverse canter.

Lateral (Rotary) Gallop

The lateral, rotary, or rotogallop is employed by the pronghorn as its most rapid gait. Typically, at very fast speeds, there are two periods of suspension during a stride: an extension phase where all four feet are extended just prior to the contact of the lagging forefoot (Fig. 13-D) and a flexion phase where all four feet are gathered under the body (Fig. 13-H). Accordingly, the support formula is 1-2-1-0-1-2-1-0. The durations of the flexed and extended suspension phases vary with the speed, terrain, individual animal etc. In the majority of cases the flexed suspension is usually of greater duration. However, the two suspension period may be of equal duration or, occasionally, the extended suspension period may exceed the flexed one. It also appears that the total suspension time per stride increases, while the total contact time decreases. Therefore, with increased speed the animal is suspended for a greater percentage of time during each stride.

The rocking action characteristic of the canter disappears in the gallop and the animal's back remains low and parallel to the ground. The head is held low, ears laid back and mouth open. The horizontal extent of the leaps or strides is increased to 17 feet (5.2 m.) or more, but the duration of each stride (about .34 to .41 second) remains within the limits reported for the canter. It can be seen, therefore, that although speed is a product of rate and length of stride, the increased stride length accounts for most of the increase in speed. The rotary sequence appears to be the only sequence employed by pronghorn when progressing at very rapid speeds. Perhaps this sequence of footfalls provides subtle benefits to rate of speed, balance, muscle function, etc.

Transverse (Diagonal) Gallop

Transition from a canter to a gallop is gradual. Therefore, it is difficult to discuss canters and gallops without being somewhat arbitrary. If a slow gallop (fast canter) is considered as a true gallop, then this gait (having the same footfall sequence as a transverse canter) is employed by pronghorn. If, on the other hand, only the very fast gallops with two periods of suspension are considered true gallops, then, according to the film viewed in this study the pronghorn employs the rotogallop exclusively.

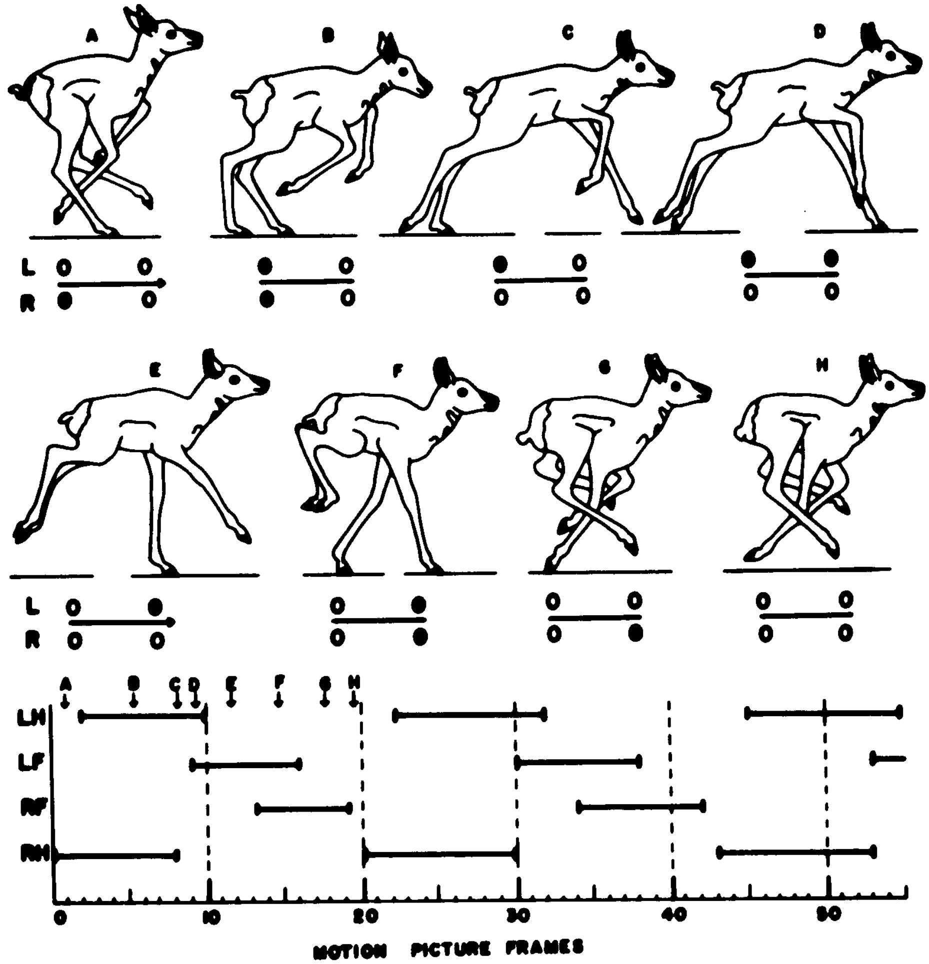
"Gallop" of Fawns

A newly born fawn exhibits a very limited repertoire of gaits. Studies of fourteen different fawns moving from one hiding place to another indicate that fawns are only capable of executing a few feeble steps of a slow walk and a rather awkward boundlike gallop. The most commonly observed fast gait was found to be a normal rotary canter with one very short period of flexed suspension (Fig. 14). However, many strides consisted of a normal rotary canter sequence without any period of suspension whatsoever (Fig. 15-A). Hence, the running fawn always had at least one foot on the ground at all times. This unusual footfall sequence was found to be common among fawns but was only observed on one occasion in a mature animal. A few fawns exhibited a true fast rotogallop sequence (Fig. 15-B) but the two periods of suspension were very short and usually of about equal duration. The transverse arrangement of footfalls was not encountered in the film sequences of several different running fawns. No symmetrical gaits were employed by any fawns studied until they were approximately ten days to two weeks of age and running with their mothers.

The apparent awkwardness with which fawns employ fast gaits could be due in part to the lanky body conformation (legs long in proportion to body), lack of muscular and nervous coordination, and the rough terrain (high grass hummocks etc.) they must traverse in the fawning areas. Perhaps the rotary fashion of footfalls, which necessitates a great deal of straddling to prevent lateral leg interference, is also partially

Figure 14. Footfall formula and gait diagram of a pronghorn fawn employing a rotary canter or gallop.

Figure 15. Gait diagrams of two footfall sequences frequently used by pronghorn fawns when employing the rotary canter or gallop.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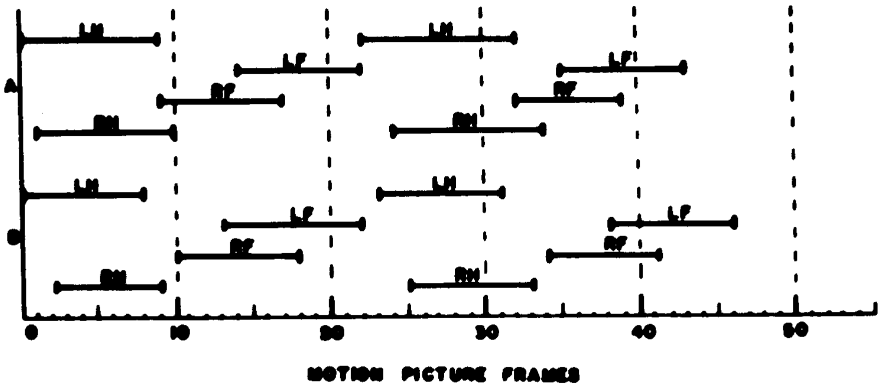
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responsible for making the gait appear awkward. In any event, the straddling of the front legs by the hind legs of a galloping fawn (Fig. 16-C and D) is considerably pronounced and exaggerated in comparison to the straddling action of a mature animal (Fig. 16-G and H).

Bound

The true bound is a symmetrical rendition of the asymmetrical gallop (Fig. 17-A). In this gait an animal leaps from both hind legs together and lands upon both front feet together (Howell, 1944). The advantage, and hence purpose, of this gait would appear to be in the synchronized action of the powerful hind legs facilitating a propulsive force to the mass of the body. Although pronghorn were not found to use this method for quick starts or gaining speed rapidly, one doe was observed to use it when bounding up a hill of considerable grade. Only one stride, however was truly symmetrical, the remainder exhibited disparity in the synchronization of leaping hind feet and landing forefeet.

Half-bound

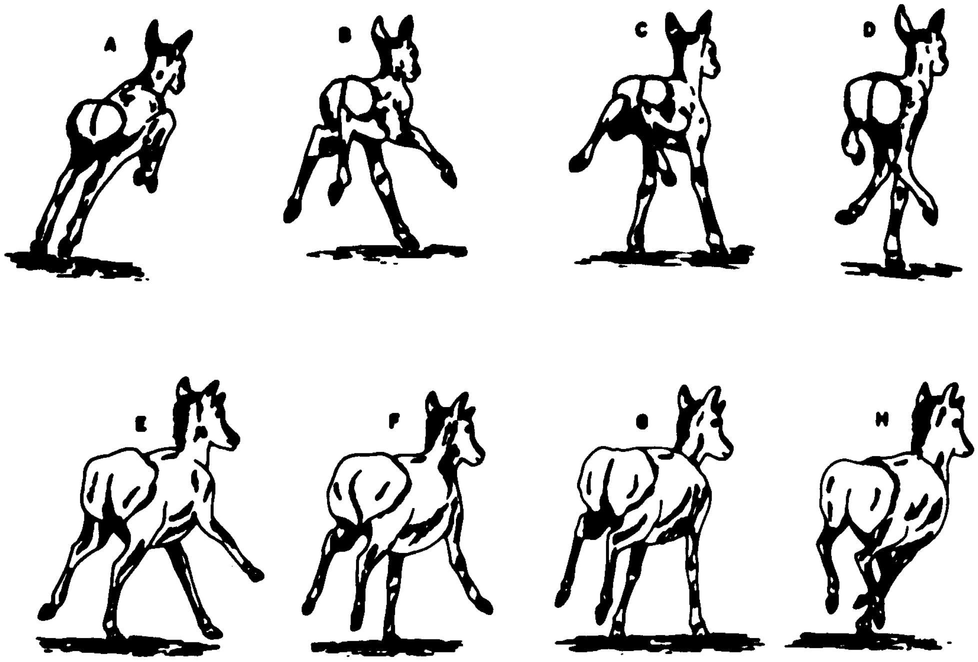
Howell (1944) describes the half-bound as a gait whereby an animal springs from both hind feet at once and lands first on one front foot and then on the other (Fig. 17-B). One stride of the doe cited above was of this type.

Bounding "Gallop" or Leap

Although Howell (1944) does not name this unique "gallop", he treats it as a gait peculiar to the mule deer. In it all four feet leave the ground in unison, this being followed by a relatively long period of suspension with front and hind legs hanging parallel to each other, and

Figure 16. A comparison of body and leg movements (particularly the straddling of front legs by hind legs) of a galloping fawn (A-D) and an adult pronghorn (E-H).

Figure 17. Gait diagrams of pronghorn employing the bound (A), half-bound (B) and bounding gallop (C). The footfall formula (feet represented by circles which are black when respective foot is on ground) for each gait is indicated above the gait diagram.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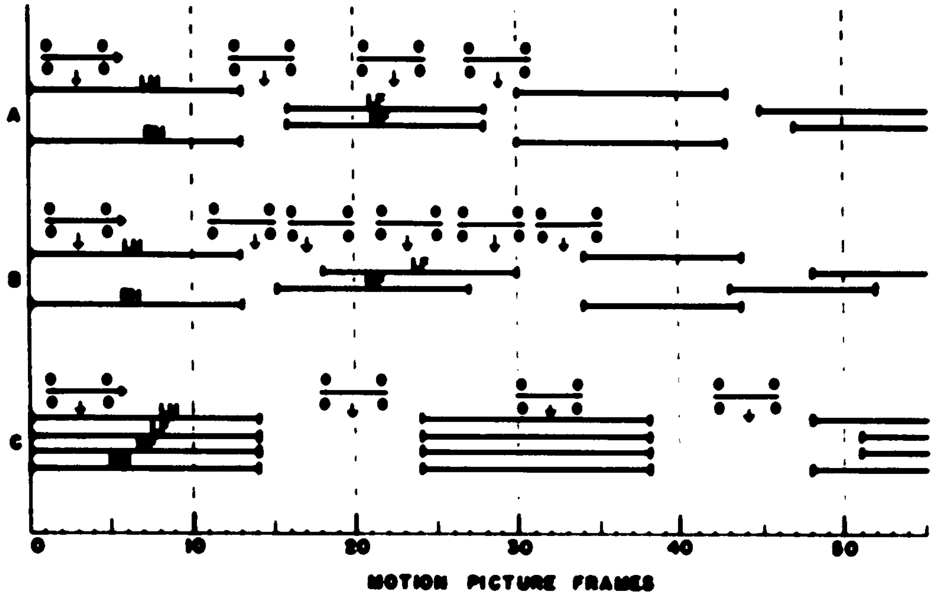
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then all four feet contact the ground in unison. Einarsen (1948) refers to this gait, when employed by pronghorn, as the "sudden bounding leap". According to my data this gait is most commonly used by pronghorn to initiate a rapid start from a standing position. Here again the powerful musculature of the hind legs work in unison to overcome body inertia (Fig. 17-C). In most instances, however, the true form of this gait was rarely seen. Usually the symmetry of the gait was broken by the front feet striking the ground at different intervals of time, followed by a gradual separation of the hind footfalls until a true gallop sequence was accomplished.

Stotting

Stotting consists of a stiff-legged stomping action in which the animal bounds high into the air and lands on all four feet simultaneously. Although the footfall formula is identical to the bounding gallop or leap, there is usually no (or little) horizontal movement accomplished. Couey (1950) states that stotting appears to be a warning gesture and that it has been observed in bighorn, mule deer and elk. In African gazelles stotting (prelljumping) is used to increase speed or to express excitement (Walther, 1968). Bruns (1969) recognized the gait in pronghorn antelope as a form of winter play activity. During the course of this study pronghorn were observed stotting most frequently during the mating season. Stotting was usually accomplished in a very elegant manner with head held high, mane raised and rosette raised.

GENERAL GAIT ANALYSIS

Support Intervals of Fast Gaits

To obtain a better insight into the support phases of the feet during strides of various fast gaits, it is convenient to calculate the percentage of a stride spent on various combinations of supporting legs. This has been done for the trot and bounding gallop (Table 1), and for the canters and gallops of both mature pronghorn and fawns (Tables 3 and 4). These values tabulate what some individual animals have done, and thereby give some indication and generalizations about what pronghorn usually do when employing various gaits.

From Table 1 it is evident that pronghorn spend most of each trotting stride on diagonal supporting legs. One hind or front leg may, however, give complete support to the body for short periods of time during a stride, the hind leg giving longer intervals of support, particularly at fast speeds. As the speed of the trot increases the total period of suspension also increases, while the total diagonal support phase decreases. Therefore, at a fast trot the body is suspended for a greater portion of the stride than at a slow trot.

Although the pure rendition of the bounding gallop is rarely employed by pronghorn, when it is (Table 1) the period of suspension is usually slightly more than half of the total stride duration. More commonly, however, the hind feet are on the ground for a greater portion of the stride than are the front feet. It is also relatively common for one leg (front or hind) to give sole support to the body momentarily. These latter sequences usually grade into slow canters and are, therefore, difficult to classify and evaluate.

The accurate tabulation of the time intervals of the various

Table 1. Average percentage time of stride spent on combinations of supporting legs for the trot and bounding gallop of mature pronghorn

Combinations of supporting legs, not in the order in which they are used.	Moderate Trot	Fast Trot	Bounding Gallop
Lateral legs on ground	0	0	0
Diagonal legs on ground	62	48	0
Four legs on ground	0	0	46
One hind leg on ground	4	6	0
One front leg on ground	1	1	0
Total suspension	33	45	54
No. of strides averaged	20	20	2

support combinations of an "average" canter or gallop is difficult because of the many variations encountered in these gaits, the idiosyncrasies of individual animals employing the gaits, and because of the problem of determining relative speeds. However, a few trends appear to be significant, especially those between the moderate canter and the fast gallop (Table 2). As speed increases both front and hind footfalls are spaced further apart; the feet of a pair being on the ground together for a shorter period of time. With increased speed the support of the leading hind foot and forefoot is reduced. At all speeds, however, the leading forefoot is on the ground proportionately longer than the leading hind foot. The flexed suspension phase is reduced throughout the canters as speed increases. With the addition of an extended suspension phase, the gallop acquires more suspension time per stride than the faster canters. The flexed suspension phase remains proportionately longer, however, than the extension phase. The three- and four-foot support phases are eventually lost as speed increases. The two-leg support is low in the boundlike and slow canters (legs striking the ground in close proximity to one another), rises sharply in the moderate and fast canters and then tapers off as more one-leg support phases appear in the gallop.

The slow canter is often boundlike in nature and executed with considerable variation in footfall formula. Such variation in the execution of a gait makes it difficult to compare the support combinations of the gait with other gaits. However, the support combinations that are relatively constant (flexed suspension, four-leg support, three-leg support and two-leg support) fit into the general support trends outlined above

Table 2. Average percentage time of stride spent on combinations of supporting legs for the gallop and various canters of mature pronghorn.

Combinations of supporting legs, not in the order in which they are used.	Slow Canter	Moderate Canter	Fast Canter	Gallop
First hind leg on ground only	11	17	14	15
Both hind legs on ground	24	20	17	13
Lead hind leg on ground only	12	17	13	11
Extended suspension	0	0	0	9
First foreleg on ground only	15	17	18	16
Both forelegs on ground	17	14	9	6
Lead foreleg on ground only	17	22	19	16
Flexed suspension	35	19	16	14
Two legs on ground	9	30	33	20
Three legs on ground	25	14	0	0
Four legs on ground	6	0	0	0
No. of strides averaged	20	20	10	10

for the other canters and the gallop.

Support trends of the galloping gaits of fawns are similar to those of the adults but not as pronounced (Table 3). One noticeable exception to the support trends reported for the cantering gaits of adult animals is the increase in the flexed suspension phase of the canter of fawns as speed is increased (there is a decrease in the suspension phase of the canter in adult animals as speed is increased). Table 3 also indicates that fawns have both hind legs on the ground together for a greater portion of the stride, as are both of the front legs, than do adult animals employing the same gait. A large percentage of the fawn's stride is spent on two legs, a very small percentage on three legs and no four-leg support is present. The footfalls of fawns are spread out over the stride in such a manner that they eliminate (slow canter) or at least restrict (moderate canter and gallop) the suspension phases. Therefore, a galloping fawn has at least one leg supporting the body all of the time, or practically all of the time.

Leads

During a slow canter the lagging hind foot and forefoot are usually on the ground about 92 percent as long as their leading counterparts. However, it is not uncommon for the two front feet to be on the ground for the same length of time. With increased speed the disparity between the contacts of the front feet is increased and the lagging forefoot is only on the ground approximately 83 percent as long as the leading one. The hindfeet, however, reverse the trend at higher speeds and the leading hindfoot is usually on the ground about the same length of time as, or 85 percent as long as the lagging hindfoot. This latter trend is continued in the fast canter and the various gallops.

Table 3. Average percentage time of stride spent on combinations of supporting legs for the running gaits of fawns.

Combinations of supporting legs, not in the order in which they are used.	Slow Canter	Moderate Canter	Gallop
First hind leg on ground only	7	9	9
Both hind legs on ground	34	30	26
Lead hind leg on ground only	9	4	4
Extended suspension	0	0	4
First foreleg on ground only	23	17	13
Both forelegs on ground	14	22	17
Lead foreleg on ground only	23	22	22
Flexed suspension	0	4	4
Two legs on ground	55	52	43
Three legs on ground	5	4	0
Four legs on ground	0	0	0
No. of strides averaged	10	10	10

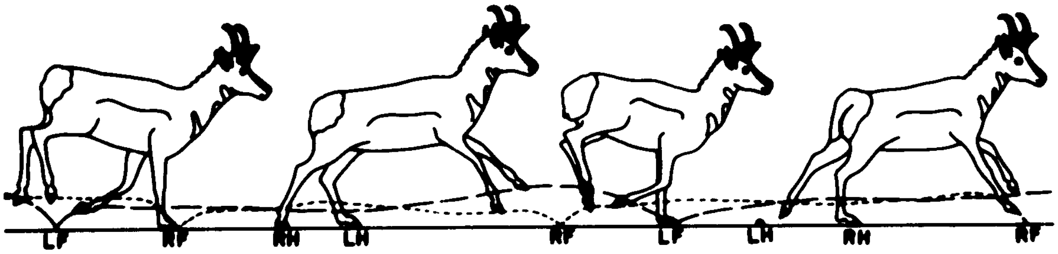
Perhaps the reason for the leading hindfoot and forefoot being on the ground longer than their lagging counterparts in the slow canter is because the leading feet not only have a larger support function, but also give a more powerful thrust, with a certain amount of "follow through", before leaving the ground. At faster speeds the leading hind foot apparently spends a smaller proportion of its energy in merely keeping the body from falling and uses more of its energy in executing a quick powerful propulsive thrust.

Film tracings of the paths followed by the leading and lagging feet of both front and rear pairs of feet indicate that individual strides often vary as much as, or more than, do leading and lagging feet. Therefore, it is difficult to determine whether the feet of a pair are doing different things spatially or just utilizing energy in different ways. In any event, due to the difference in duration of support between leading and lagging feet and the disparity in resulting stresses, leads are changed periodically. Howell (1944), Grogan (1951), Hildebrand (1959) and Jacobsen (1960) suggest that one function of lead change is to equalize the work of the leg muscles in order to postpone fatigue. It is also evident, however, that leads are changed in anticipation of turns or gait changes, or in order to maintain balance while traversing rough terrain. The actual lead changes are accomplished during the period (or periods) of suspension when the feet are off the ground and the legs can be reoriented before striking the ground. Figure 18 shows four positions of a cantering pronghorn changing front lead (top), and four positions of a galloping pronghorn changing rear lead (bottom). Trajectories followed by the feet are in correct spatial relationship.

Front and rear leads usually change at about the same

Figure 18. Four positions of a cantering pronghorn changing front lead (above), and four positions of a galloping pronghorn changing rear lead (below). Trajectories followed by the feet are in correct spatial relationship, long dashes for left feet and short dashes for right feet. Positions of footfalls are indicated below ground line by the initial letters LH, LF, RH and RF.

Figure 19. Gait diagram of a cantering pronghorn executing a sharp turn. Pronghorn silhouettes A-D are comparable to stride phases A-D of the gait diagram below.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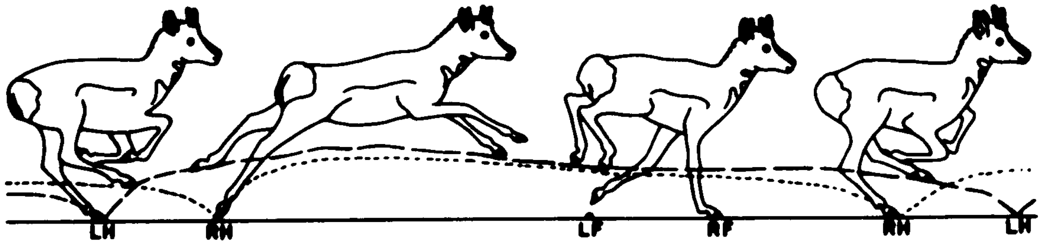
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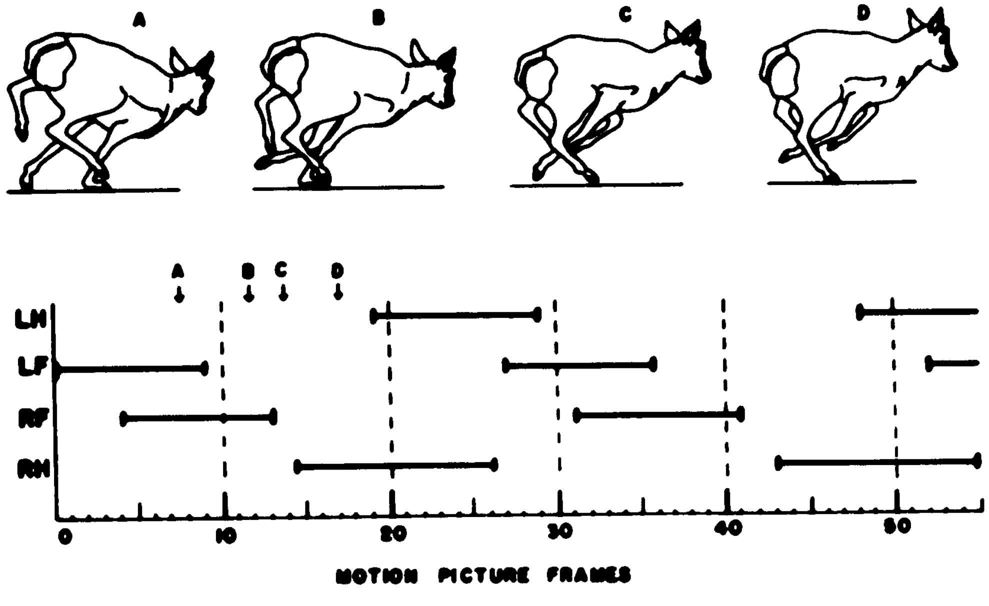
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frequency. However, at slow speeds the front lead appears to be changed more frequently. Lead changes in general (both front and rear) usually occur most frequently during the fast galloping gaits when the legs are under considerable stress. However, some animals were observed to change leads very frequently while employing a slow canter. This latter phenomenon appeared to have little to do with the fatigue factor involved in lead changes.

A phenomenon that has not been mentioned in the literature (perhaps it has not been applicable to any of the animals studied thus far), but which is very much in evidence in pronghorn locomotion, is the changing of front and rear leads independently. If a pronghorn is employing a rotary canter or gallop and changes the front or hind lead (not both), then the footfall sequence changes to that of a transverse canter or gallop. The pronghorn must change both front and hind leads simultaneously in order to maintain the same type of canter or gallop. Film sequences analyzed in this study indicate that pronghorn change leads frequently and often independently. Therefore, it is relatively common for a cantering pronghorn to change footfall sequences (and hence type of canter) every few strides and occasionally every other stride.

In order to maintain the rotogallop (the exclusive gait at fast speeds) a pronghorn must change front and rear leads simultaneously. This, however, is seldom the case. More commonly, the front lead is changed during one stride and the rear lead in the following stride. This, of course, results in a stride between front and rear lead changes with the footfall sequence of a transverse gallop. It is apparent, therefore, that although the rotogallop is maintained at fast speeds, a few transverse gallop strides are mingled with it. This order of lead change was the only one encountered in pronghorn employing the rotogallop. It was not uncommon for a pronghorn to change leads every five or six strides during a rotogallop.

Turning

When making a sharp turn during a canter or gallop a pronghorn will lead with the inside forefoot (Fig. 19). The obvious advantage of this lead is to place the body in a stable trajectory path during the period of flexed suspension. The inside leg is usually the first hind leg to touch the ground in order to keep the body in a proper attitude for executing the turn. It follows, then, that for sharp turns a rotary gallop or canter is preferred, regardless of the considerable amount of straddling and overstride of the inside legs that is necessary (Fig. 19-C). The pasterns of the inside legs (particularly the front) are flexed to a considerable degree so as to shorten the inside legs and make proper placement of the outside feet possible (Fig. 19, A and B). Leads are frequently changed a few strides in advance of a turn.

Hildebrand (1959) reports that a galloping cheetah (rotogallop) can turn more sharply by leading with the inside forefoot. The horse also leads with the inside foreleg while executing a turn (Grogan, 1951 and Jacobsen, 1960). The horse employs a transverse gallop and would, therefore, lead into the turn with a different hind foot than the pronghorn.

Change of Gait

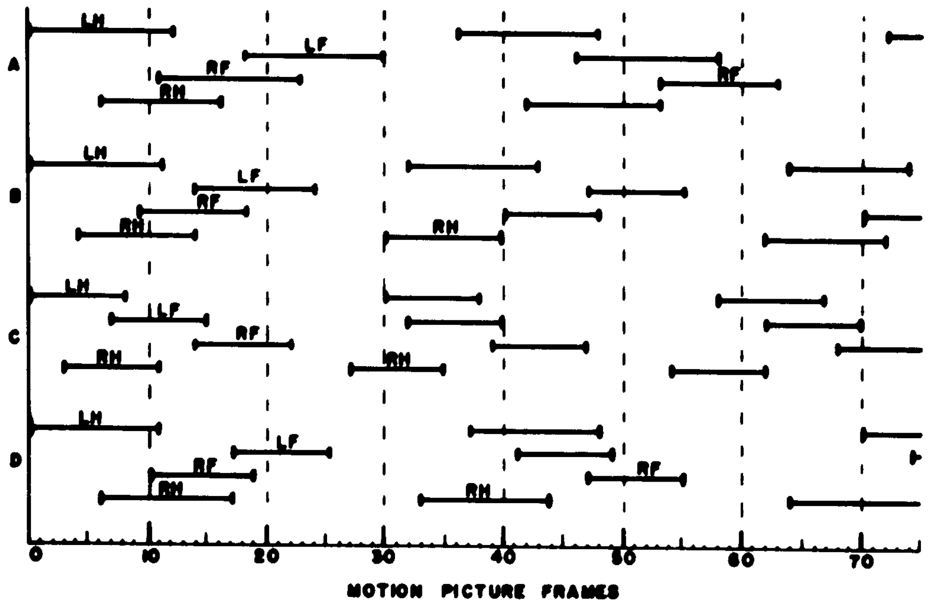
Changes from one gait to another are made very smoothly in pronghorn. It is possible for different animals to change gaits in different ways, and for the same animal to change gaits in different ways at different times. Therefore, the footfall sequences that can be used in changing from one gait to another are numerous and variable. It is not the purpose of this study to examine the many possible ways in which gait changes can be accomplished by pronghorn, but rather to indicate a few of the more interesting ones encountered.

The section dealing with "Leads" has already indicated how asymmetrical gaits (canters and gallops) can be changed by a mere change in front or hind lead. When a pronghorn is employing a rotocanter, a change of front lead (Fig. 20-A) or rear lead (Fig. 20-B) will result in the footfall sequence of a transverse canter. Likewise, a transverse canter can be changed to a rotary canter by changing either the rear lead (Fig. 20-C) or front lead. However, when both leads are changed during the same stride (simultaneously), the gallop or canter remains the same and no gait change occurs (Fig. 20-D).

In several film sequences of galloping and cantering pronghorn, complete cycles of locomotion were observed in which only three of the four feet would strike the ground. Although these three-legged strides were rare, they were observed in both bucks and does and on several different occasions. Figure 21 depicts a mature cantering buck employing (or approaching) a three-legged stride by holding the left front leg (Fig. 21-D) in an extended position until the right front leg pushes the body into a period of suspension (Fig. 21-F). The left front leg (fourth leg of stride) strikes the ground, gives total support to the body for a time, and then pushes the body into another period of suspension (Fig. 21-H). The foregoing sequence of footfalls can be viewed as being either one three-legged stride and one one-legged stride

Figure 20. Gait diagrams of pronghorn changing the type of canter or gallop employed by changing front or rear leads.

Figure 21. Footfall formula and gait diagram of a pronghorn executing an atypical cantering stride in which there is a period of suspension between the striking of the two front feet.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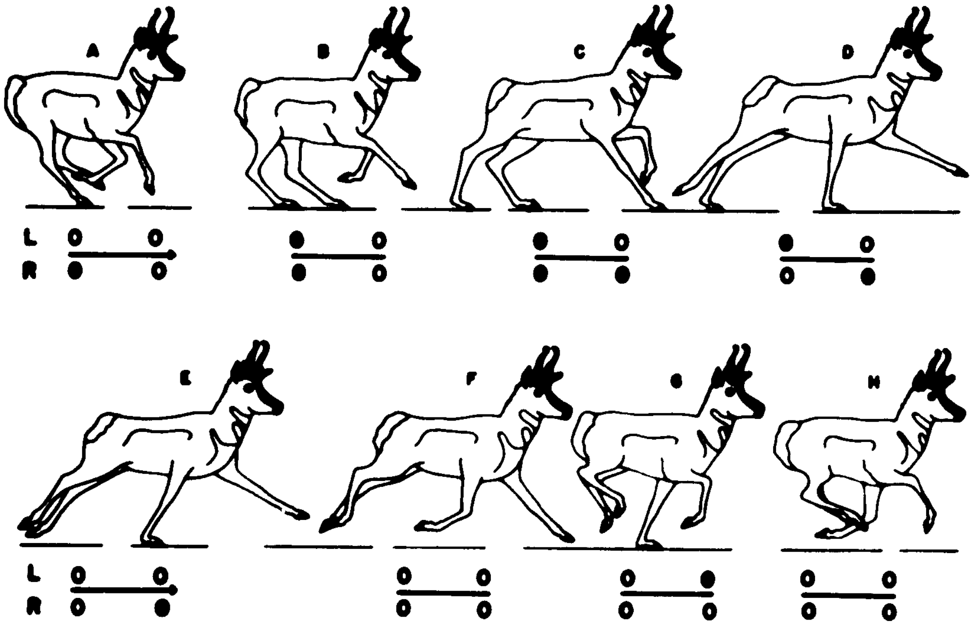
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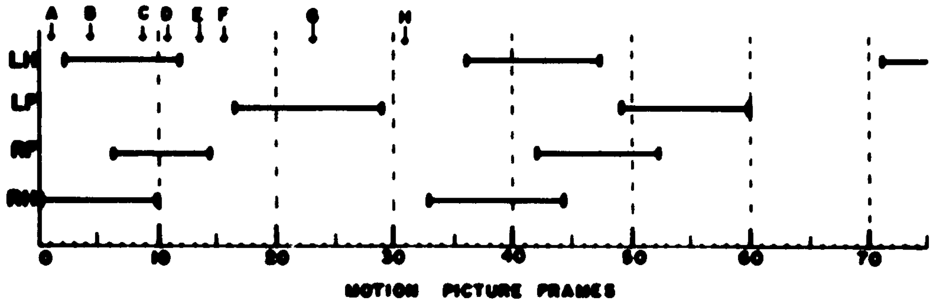
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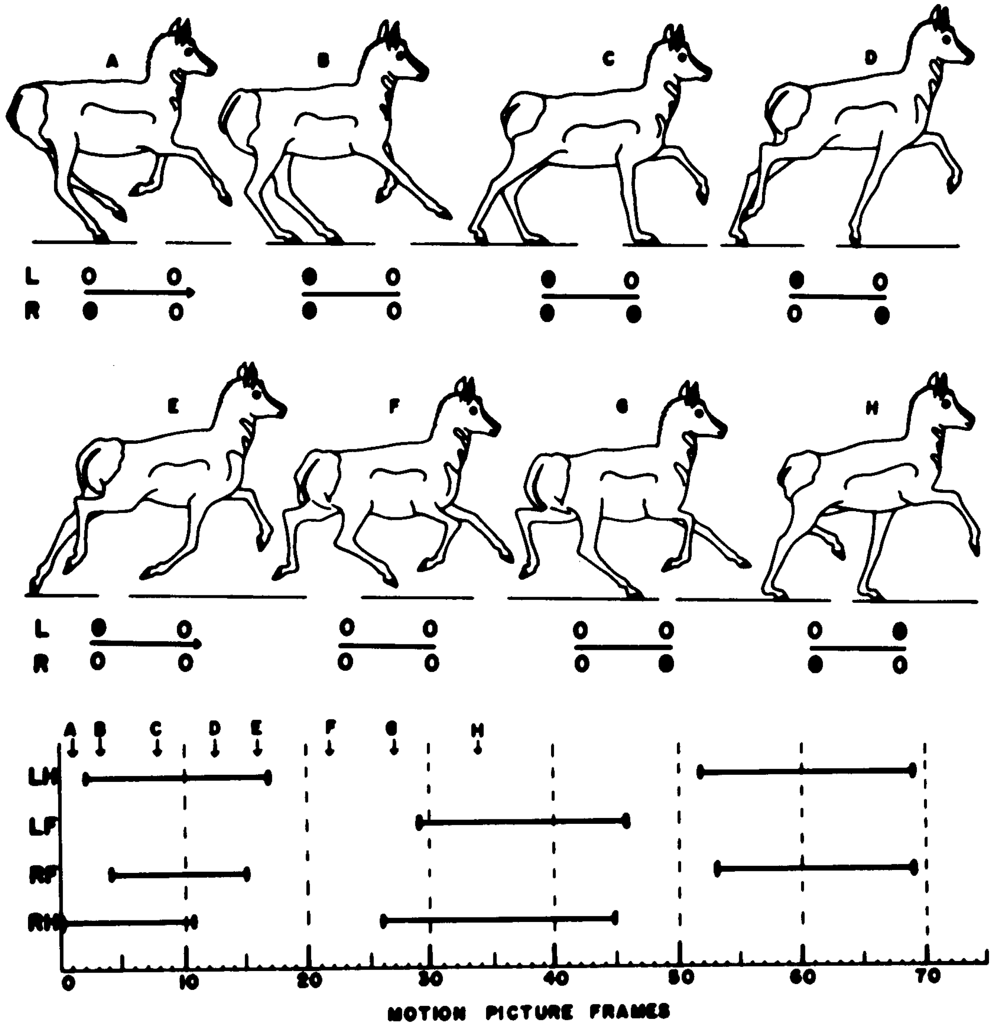
or as an atypical stride in which there is a period of suspension between the striking of the two front feet. The terrain being traversed by the pronghorn was relatively smooth, therefore, it would probably not be necessary for the animal to make leg adjustments in order to assure proper foot placement. Inasmuch as the buck changed gaits from a slow canter to a trot a few strides later, perhaps a more plausible explanation for the atypical footfall sequence might be that a gait change was anticipated and then not executed at that time. A stride consisting of only three feet striking the ground followed by a period of suspension was observed as a transitional stride between a transverse canter and a trot (Fig. 22) and between a bounding gallop and a trot (Fig. 23-A). In both instances the foreleg being held during the transitional three-legged stride was the foreleg involved in the first trotting stride. The leg was apparently being held so that proper alignment of diagonal pairs could be accomplished and a trotting stride executed. A three-legged stride was also encountered as a transitional stride between a transverse canter and a rotary canter (Fig. 24). In this case the foreleg that was being held came down before the leading hind leg, thus resulting in an atypical, slow rotocanter.

One of the most frequently observed gait changes occured between the trot and canter. Figure 23-B is an example of how one pronghorn went from a trot to a rotary canter, while Figure 25 illustrates a pronghorn going from a transverse canter to a trot without holding one foreleg during the transitional stride. It should be noted that in both cases the canter is being employed at such a slow tempo that it is atypical: lagging forefoot strikes ground before leading hind foot.

Changes from a walking gait to a trotting gait (and vice versa)

Figure 22. Footfall formula and gait diagram of a pronghorn changing gaits (transverse canter to trot) with a transitional stride consisting of only three feet striking the ground.

Figure 23. Gait diagrams of pronghorn changing gaits: A, bounding gallop to trot with three-legged transitional stride; B, trot to rotary canter.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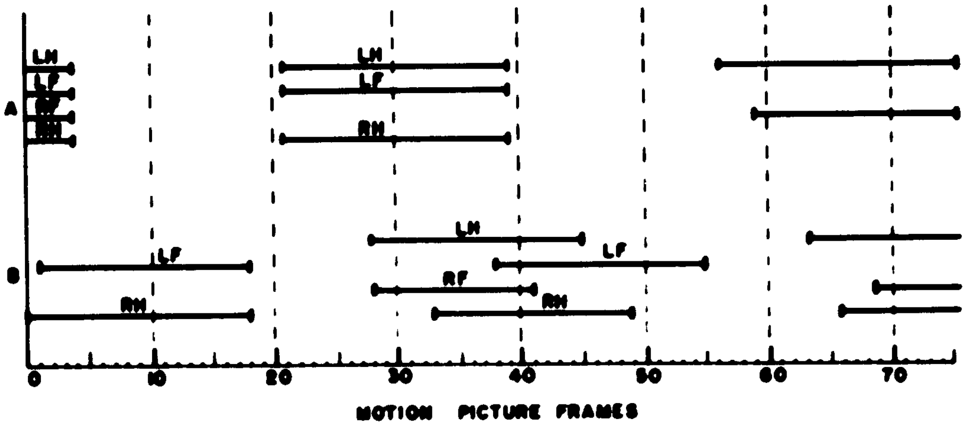
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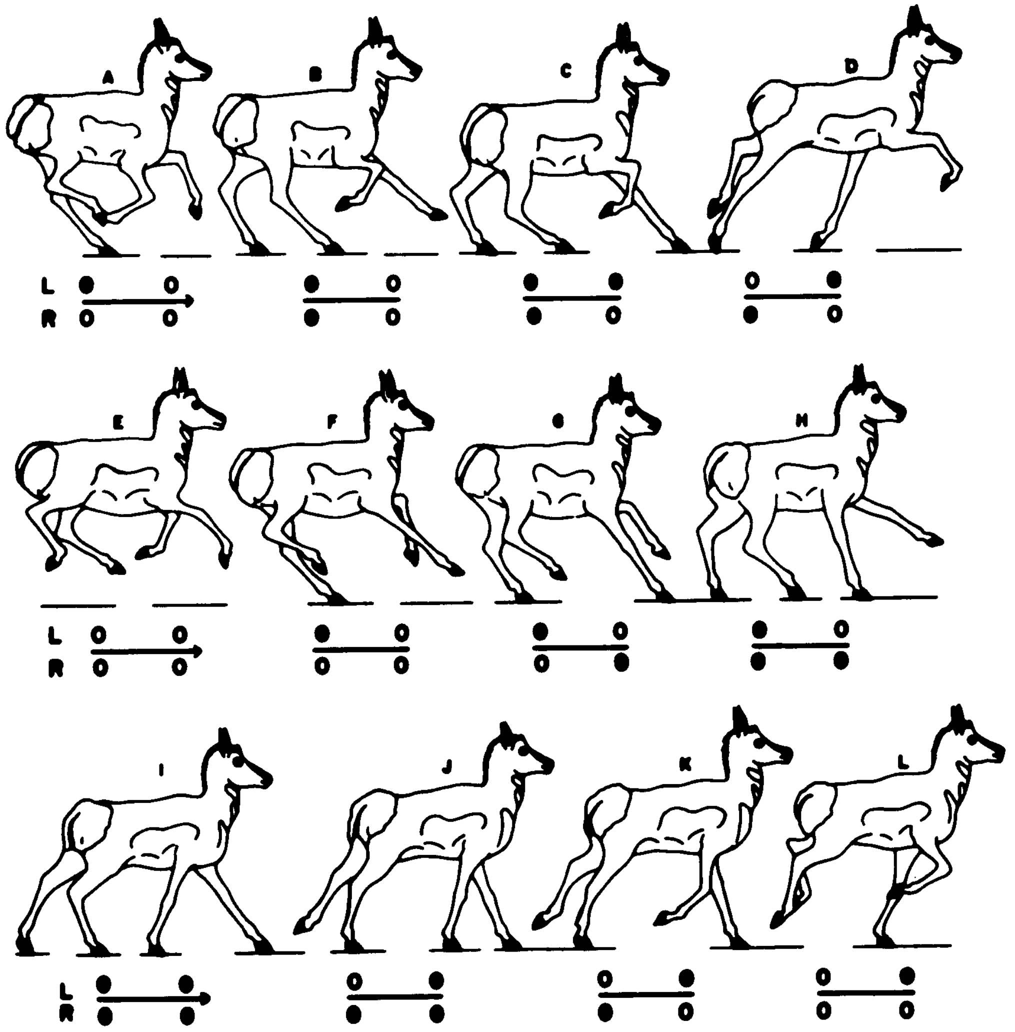
Figure 24. Footfall formula and gait diagram of a pronghorn going from a transverse canter to a rotary canter with a transitional stride consisting of only three feet striking the ground.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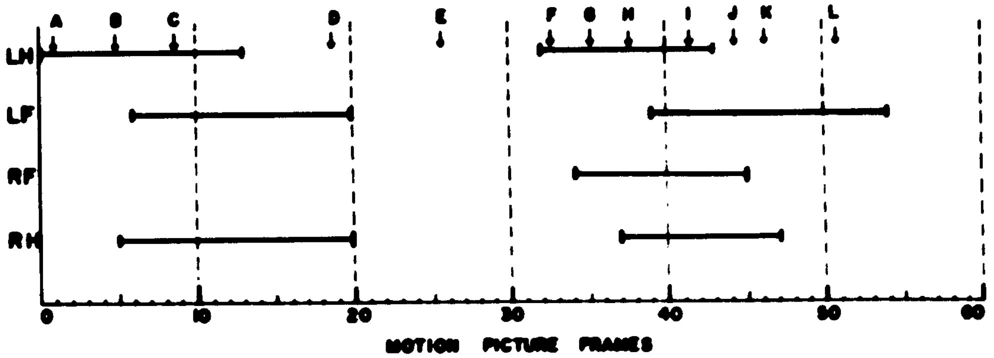
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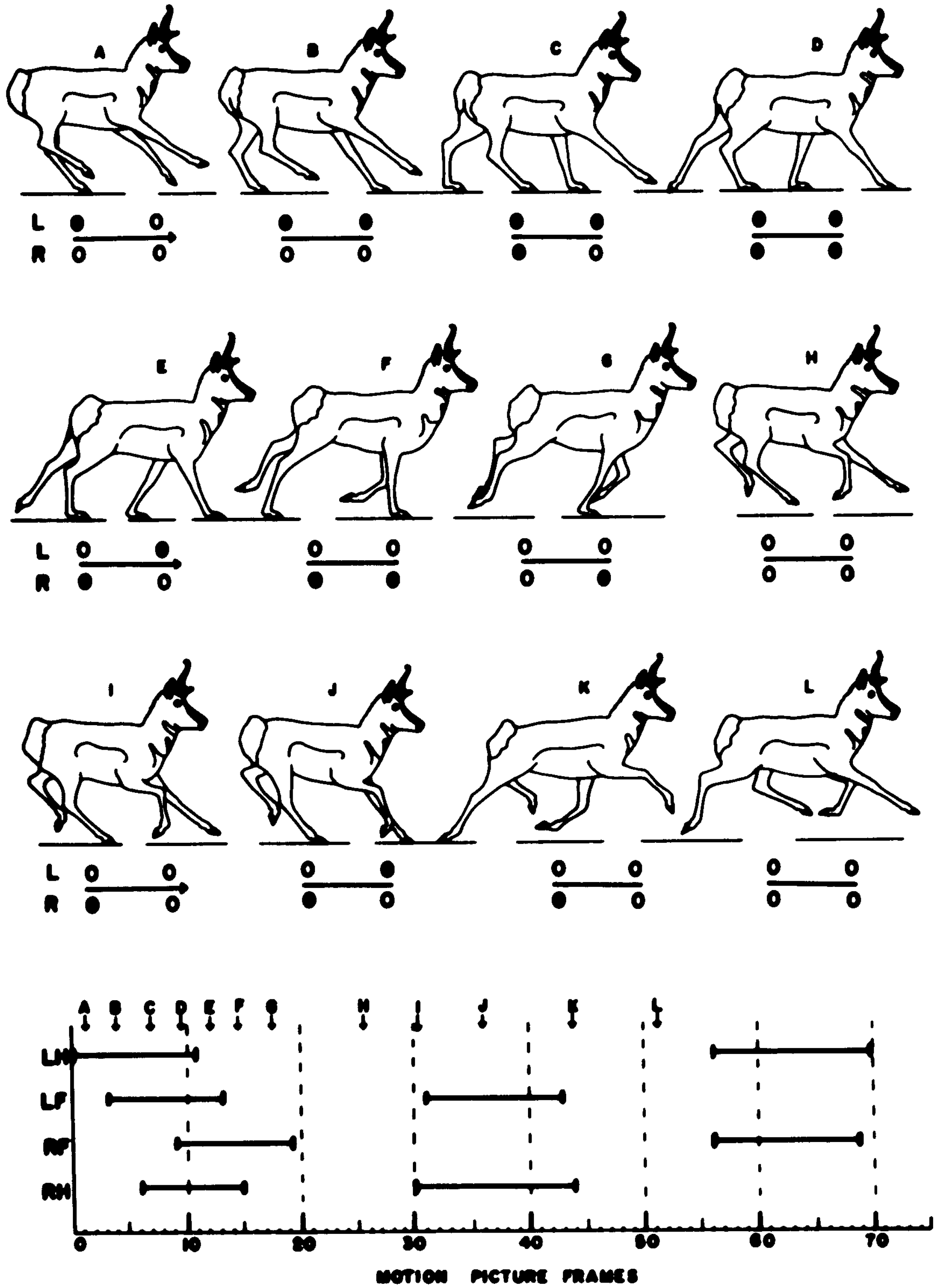
Figure 25. Footfall formula and gait diagram of a pronghorn going from a transverse canter to a trot.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are extremely variable in pronghorn and usually occur over several strides. Therefore, it is difficult to generalize about these changes except to say that the footfall pattern is gradually arranged to accommodate the new gait. A series of photographs depicting a horse going from a walk to a trot (Muybridge, 1899) is similar to one of the sequences observed in pronghorn. However, his photographs of a horse going from a trot to a gallop are not representative of any of the pronghorn gait changes analyzed in this study.

Synchronization of Gait and Lead

Howell (1944) asserted that gregarious animals, especially wild ones, exhibit a group synchronization in gaits to the extent that often every individual of a closely bunched herd will be leading with the same foot. Pronghorn, being both gregarious and social, not only exhibit a considerable degree of synchronization in lead (forefoot) but also in the type of canter or gallop employed (Table 4). Of the 22 herds of running pronghorn analyzed, 13 of the herds were closely bunched and nine were strung out. The closely bunched herds demonstrated an average of 97 percent synchronization of gait and 92 percent synchronization of lead. The nine herds that were strung out exhibited an average of 79 percent synchronization of gait and 70 percent synchronizaation of lead. All 22 herds combined gave a 90 percent gait and 83 percent lead synchronization. Therefore, it is apparent that closely bunched herds exhibit a greater tendency toward both synchronization of gait and lead, and that the synchronization of gait is greater in both types of herds than is the synchronization of lead. It should be noted at this point that individual animals in a herd change lead periodically and

Table 4. Synchronization of gait and lead (forefoot) in pronghorn.

No. in herd	Closely bunched	No. transverse canter or gallop	No. rotary canter or gallop	No. left front lead	No. right front lead
4	yes	4	0	1	3
2	yes	0	2	0	2
4		1	3	2	2
4	yes	1	3	4	0
10		2	8	9	1
3	yes	3	0	2	1
5		2	3	3	2
4		2	2	2	2
5	yes	1	4	4	1
6		0	6	5	1
5	yes	0	5	0	5
4		2	2	0	4
3	yes	3	0	3	0
4	yes	4	0	3	1
4	yes	4	0	4	0
10		0	10	9	1
2	yes	0	2	2	0
4		0	4	2	2
3	yes	0	3	3	0
4	yes	0	4	4	0
7		0	7	4	3
2	yes	0	2	2	0

that this change of lead is synchronized throughout the herd within a few strides. Therefore, it becomes difficult (and somewhat arbitrary) in some cases to determine the degree of synchronization of lead at any one given time in a herd structure. It should also be pointed out that there does not appear to be any correlation between the leading foot (left or right) and the type of gallop or canter being employed.

Utilization of Fast Gaits

Results of observations of pronghorn spontaneously employing gaits faster than a walk are tabulated in Table 5. Although more observations might substantiate the frequencies of gaits more accurately, it is apparent from the data presented that pronghorn "prefer" the asymmetrical canter or gallop when progressing faster than a walk. As the trot is basically used to initiate and/or complete a burst of locomotion, it is employed much less frequently than is the canter or gallop. Usually an animal (adult or juvenile) will go directly into a gallop from a standing position but use the trot sequence to finish the locomotor activity. However, many bursts of locomotion are initiated with a few trotting strides. Occasionally an animal will go a short distance employing the trot exclusively.

Trotting was not observed in fawns until they were about two weeks old and running with their mothers. Fawns appear to acquire the ability or propensity to employ the trot at approximately the same frequency as adults when they are from three to six weeks of age. Gregg (1955) noted that young fawns ten days old are capable of executing all pronghorn gaits.

Table 5. Frequency of fast gait utilization in pronghorn for various sexes and age classes.

Age class and sex	No. of observations	% Trot	% Gallop and/or canter
Mature males	80	14	86
Mature females	80	16	84
Mature animals	160	15	85
New born fawns	14	0	100
Three week old fawns	50	8	92
Six week old fawns	50	13	87

Table 6. Methods used by pronghorn in traversing barbed wire fences (measurements in inches).

Age class and sex	No. of strands	Approximate distance between strands	Fence height	Height of bottom strand	Method of traversing fence
Mature female	4	10	49	19	Crawled under
Mature male	4	11	50	17	" "
Mature female	4	11	51	18	" "
Mature male	2	14	38	24	" "
Mature male	4	10	53	23	" "
Fawn	4	11	50	17	" "
Mature male	4	9	41	15	Jumped
Mature male	4	9	34	8	Jumped

Jumping

During the course of this study eight pronghorn were observed traversing barbed wire fences (Table 6). From the data collected it would appear that pronghorn will usually crawl under a fence rather than jump over it if the bottom wire is at least 17 inches (43 cm.) from the ground, notwithstanding the fact that the fence may only be 38 inches (97 cm.) high. When crawling under a low fence wire a pronghorn will drop to its knees, push forward with the hind legs until the front legs are bent back and the chest is on the ground. The back is arched downward to avoid rubbing the wire, and the hind legs are extended out back until recovery is made on the other side of the wire. This crawling procedure can be accomplished at very rapid speeds when the animals are being pressed.

The two instances of jumping were somewhat atypical in that the animals were being moderately pressed and the bottom strand of wire was unusually close to the ground. Several animals were observed to approach fences of moderate height (about 38 inches) with bottom strands close to the ground (less than 17 inches) and walk down them rather than attempting to jump over, or crawl under them. Inasmuch as pronghorn are native to the flat prairie and semidesert terrain and have little need for jumping vertical barriers, it is not surprising that most of them appear to be reluctant to make vertical jumps, and do so only rarely. However, broad jumps of 20 to 25 feet (6.1 to 7.6 m.) to cross horizontal obstacles are relatively common.

Although no pronghorn were observed during this study to cross a fence by going between strands of wire, such observations have been reported by Howell (1944), Throckmorton (1945) and others. According to them, this method of traversing a wire fence can also be accomplished at a very rapid speed.

Speed

Accurate records of the speeds at which pronghorn employ their various gaits were not obtainable. An approximation of speed was arrived at for each gait by utilizing motion picture tracings and taking into account the speed of exposure and the distance travelled in each stride relative to the length of the pronghorn's body in the picture, and then equating this to the actual length of a pronghorn's body. This method proved helpful in determining relative speed but was not accurate enough to be used for the purpose of indicating absolute speed. Therefore, the literature will be relied upon for this information.

Although the literature to date does not give relative speeds for the various pronghorn gaits, many references have been made to the maximum speed a pronghorn can obtain. Both Einarsen (1948) and Belden (In Howell, 1944) concluded that pronghorn can reach speeds of up to 60 miles per hour for relatively short distances. A speed of 53 miles per hour was recorded by McLean (1944) for two bucks over a distance of one-half mile. Speeds in the neighborhood of 40-50 miles per hour have been reported by Cottam and Williams (1943), Chapman (1948), Bridge (1942), Jaegar (1961) and others. Carr (1927) reported pacing a pronghorn with an automobile at 30 miles per hour for seven miles. One or two day old fawns can reach speeds of up to 20 miles per hour (Ormond, 1958), while older fawns have been observed maintaining an average speed of 36 miles per hour for 27 miles (Howell, 1944). According to the references cited above, it would appear that speeds of up to 60 miles per hour can be reached on occasion by exceptional individuals under the best of conditions and that they can only maintain such speeds for short distances. Pronghorn can, however, maintain speeds of 30-40 miles per hour for several miles (Hildebrand, 1959).

During the study several pronghorn were paced by automobile. The fastest speed recorded was 45 miles per hour. It became apparent during these occasions that does and young adult animals were fleeter afoot than were older animals, especially older bucks.

FUNCTIONAL ANALYSIS OF BODY STRUCTURES DURING LOCOMOTION

In this section the actual movements of the body and various body members are analyzed for the gaits of pronghorn. A series of tracings was used to facilitate the analysis of each gait. Several strides from several different animals were analyzed for each gait to make the data more representative of the species. It is admitted, however, that individual idiosyncrasies may have been encountered and that the data are probably only indicative of some of the trends in body movements during the various gaits.

Role of the Legs

Although the legs are basically responsible for locomotion in quadrupeds and have, therefore, been discussed in previous sections, the actual movements and trajectories of the legs during locomotion are the concern of this section. Figure 26-A, B, C and D demonstrates the method used to calculate leg angles (the series of silhouette tracings is of a buck employing a fast gallop). Some difficulty was encountered in determining the exact instant (motion picture frame) a foot would strike or leave the ground. This difficulty, along with the problem of separating some gaits (e.g., slow canter from moderate canter), and the individuality of animals, are some of the reasons for the rather wide range of leg angles encountered for each gait. Nonetheless, if the angles at which the legs strike and leave the ground are calculated for different gaits (Table 7) it is apparent that as speed increases the average strike-departure angles become more acute, resulting in the pronghorn getting lower to the ground with each leg moving through a greater arc while in contact with the ground. This gives each leg a

Figure 26. A composite figure demonstrating the methods used to determine movements of body members during locomotion. A-D, leg-ground angles (fast gallop); leg-ground angles for upper and lower foreleg elements during a walk (E), trot (F), canter (G) and gallop (H); I-P, paths followed by the feet in relation to approximate limb pivots at shoulder and hip for the walk, trot, canter and gallop, respectively; paths followed by the leading (solid line) and lagging (short dashes) feet of a pair in relation to approximate limb pivots at shoulder and hip by the front feet during a slow canter (Q), moderate canter (R), fast canter (S), and by the hind feet during a slow canter (T); U and V, flexion of spine (short dashes) as indicated by chest-buttock length (solid line); W and X, neck-back angles.

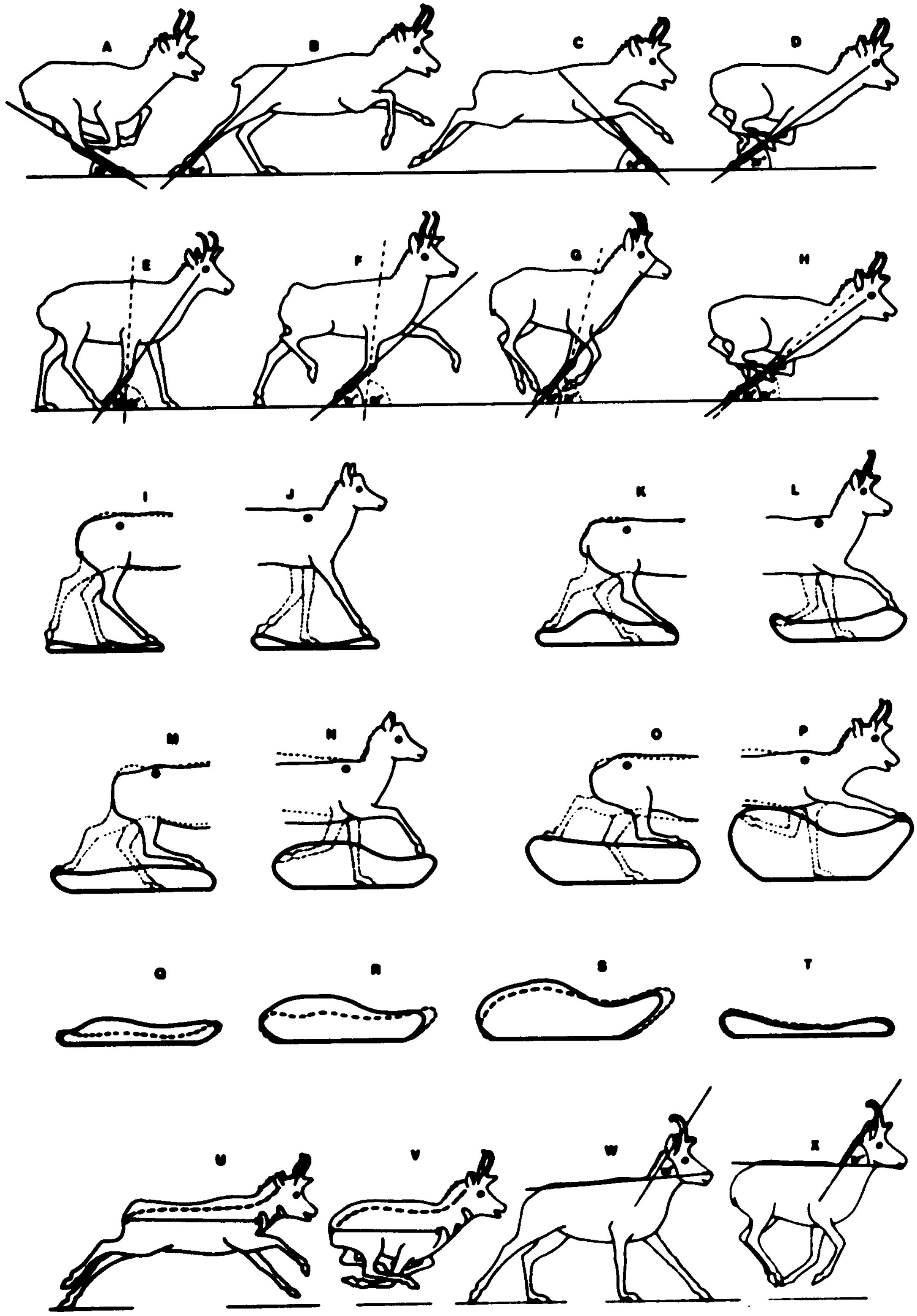
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Table 7. Angles of the legs striking and leaving the ground for various gaits of pronghorn (angle in degrees).

Gait	Hind leg averages (Ranges in parentheses)		Front leg averages (Ranges in parentheses)	
	Angle of strike	Angle of departure	Angle of strike	Angle of departure
Slow walk	58(55-61)	73(71-75)	63(61-64)	48(46-50)
Fast walk	53(50-59)	70(68-73)	64(60-68)	46(42-49)
Trot	51(44-53)	63(61-70)	55(49-58)	49(44-54)
Slow canter	48(44-52)	57(52-61)	54(51-60)	48(44-53)
Moderate canter	46(40-56)	55(47-62)	56(40-62)	49(45-53)
Fast canter	38(32-44)	44(40-52)	49(43-56)	38(34-41)
Fast gallop	36(31-44)	41(40-50)	40(31-60)	36(31-48)

better opportunity for exerting a propulsive force (pulling and pushing) on the moving body.

The trend towards more acute strike-departure angles is best demonstrated in the hind legs. The strike-departure angles of the front legs remain relatively constant for the trot, slow canter and moderate canter, and then become progressively more acute in the faster gaits (Table 7). The angles of departure of the front legs were the most difficult angles to measure accurately because of the way in which the lower leg (metapodial) flexed upon the upper leg (propodial and epipodial) as the tip of the hoof was leaving the ground (solid line, Fig. 26, E-H). Therefore, measurements were taken of the angle that each upper leg element made with the ground at the time of lower leg departure (dotted line, Fig. 26, E-H). The average angles were: normal walk, 87°; trot, 82°; moderate canter, 74°; and gallop, 42°. This set of measurements is probably more indicative of actual foreleg movement during the various gaits, and the resulting trend in departure angles is more in line with the other leg parameters reported.

Tracings of the paths followed by the front and rear hooves in relation to approximate limb pivots at shoulder (anterodorsal border of scapula) and hip (crest of ilium), demonstrate that the legs are flexed and extended more (areas scribed by trajectory paths of hooves larger) as speed is increased from a walk to a fast gallop (Fig. 26, I-P). Aside from the trend of greater vertical magnitude of trajectory paths as speed is increased, other noteworthy data can be deduced from such tracings. The paths followed by each hind foot during the walk (Fig. 26-I) exhibits three crests and two troughs, the crests being during the lifting of the leg from the ground, mid-point of swing, and just prior to the hoof striking the ground. The path of the hind foot during the trot (Fig. 26-K) is similar to that found in the walk except that the mid-swing crest is considerably higher than the other two crests. The foot, therefore, is raised to its highest point when the leg passes under the hip. The mid-swing crest is lacking in the canters and gallops. In the canter (Fig. 26-M) the hind foot reaches its maximum height in the flexed position as the leg is preparing to strike the ground. The pattern is reversed in the gallop (Fig. 26-O) and maximum foot height is reached shortly after the foot leaves the ground (extended phase of leg).

The trajectory paths followed by the front feet for the walk (Fig. 26-J) and trot (Fig. 26-L) are similar. During the canter (Fig. 26-N) and gallop (Fig. 26-P) the front legs reach their highest point during the flexed phase of the limb swing. The front legs remain extended until contact is made with the ground (true of other fast gaits as well).

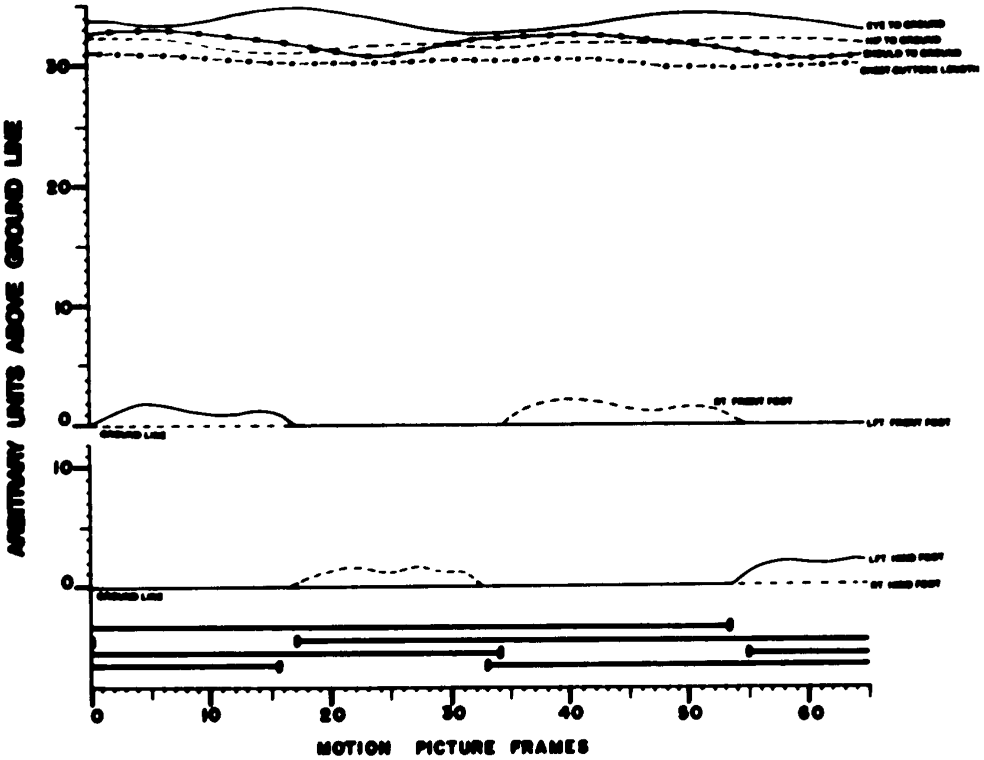
Although there is considerable variation in the paths followed by leading and lagging feet of a pair, the film sequences analyzed indicate that in the majority of cases the leading feet (front and rear) usually scribe a trajectory path that is the same as, or larger than, the lagging feet (Fig. 26, Q-T). More data are needed in this area before a conclusive statement can be made. The problem is complicated by the fact that running pronghorn are constantly making adjustments for terrain, slight turns, gait and lead changes, etc.

The trajectory paths discussed above are traced in relation to approximate limb pivots at the shoulder and hip and are, therefore, indicative of, but not equal to, the actual spatial relationship of the hooves above the ground during the various gaits. While the tracings give a record of leg movements with reference to the body, Figures 27-32 give the trajectories of the feet, shoulder, hip, head, etc., in correct spatial relationship to the ground with reference to the action of the feet (gait diagram). The two types of records are very similar as far as foot trajectory is concerned except for the gaits that are executed with excessive spring and bounce (e.g., in the bounding gallop the legs are not flexed a great deal during the suspension period but the hooves are off the ground a considerable distance). Also, the feet of a young animal that has considerable spring in its galloping strides will be lifted higher off the ground (Fig. 32) than will the feet of an older animal (Fig. 31) travelling at approximately the same speed. However, the trajectory paths of the hooves in reference to the body (shoulder and hip) may be greater in the older animal (Fig. 26-S) than in the younger (Fig. 26-R). The disparity in paths followed by leading and lagging feet with reference to distance above the ground is illustrated for one example of each type of gait in Figures 27-32.

The movements of the shoulders and hips are closely associated with the action of the feet. When a pronghorn is walking the withers are closest to the ground during the two phases of the stride when both front feet are on the ground together and farthest away from the ground when a front foot is raised (shoulder-to-ground curve, Fig. 27). The movement of the hind quarters during the walk is similar but related to the lifting and placing of the hind feet (hip-to-ground curve, Fig. 27). During a trotting stride the withers and hind quarters rise and fall twice in unison, rising to their highest points during the suspension phases and to their lowest points during the diagonal support phases

Figure 27. Relation of body movement to action of the feet (gait diagram) of a pronghorn during a little less than one stride of a slow walk. Motion is from left to right. Letters R, L, H and F mean right, left, hind and front, respectively. Curves indicate, by distance above the ground line, variations in foot to ground, shoulder to ground, hip to ground and eye to ground height, and chest-buttock length. All distances above ground line are arbitrary but in proportion to actual distances.

Figure 28. Relation of body movement to action of the feet (gait diagram) of a pronghorn during a little more than one stride of a trot (compare Fig. 15).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HIP TO GROUND
SHOULD TO GROUND
CHEST BUTTOCKS LENGTH
RT FRONT FOOT
LFT FRONT FOOT
GROUND LINE
LFT HIND FOOT
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GROUND LINE
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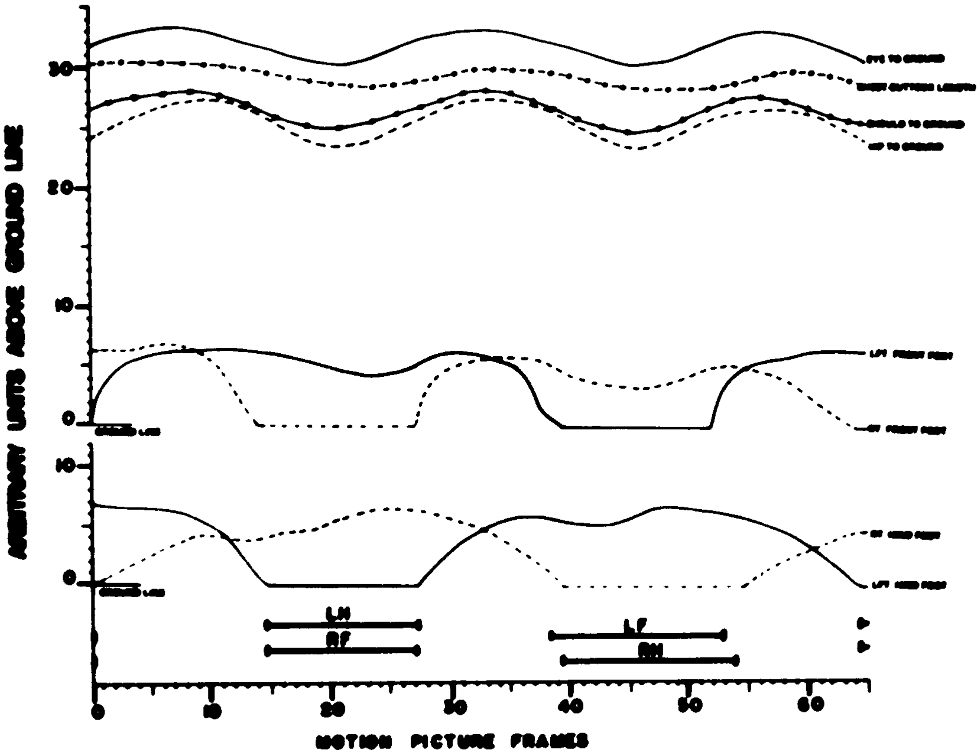
ARBITRARY UNITS ABOVE GROUND LINE
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RT FRONT FOOT
GROUND LINE
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LFT HIND FOOT
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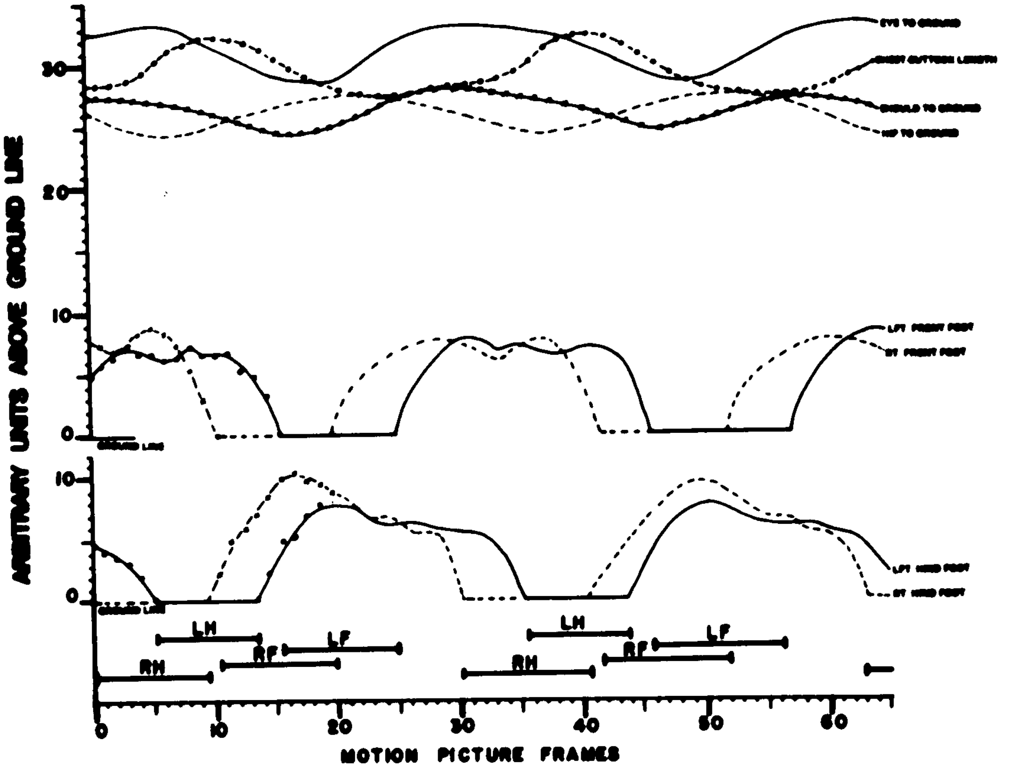
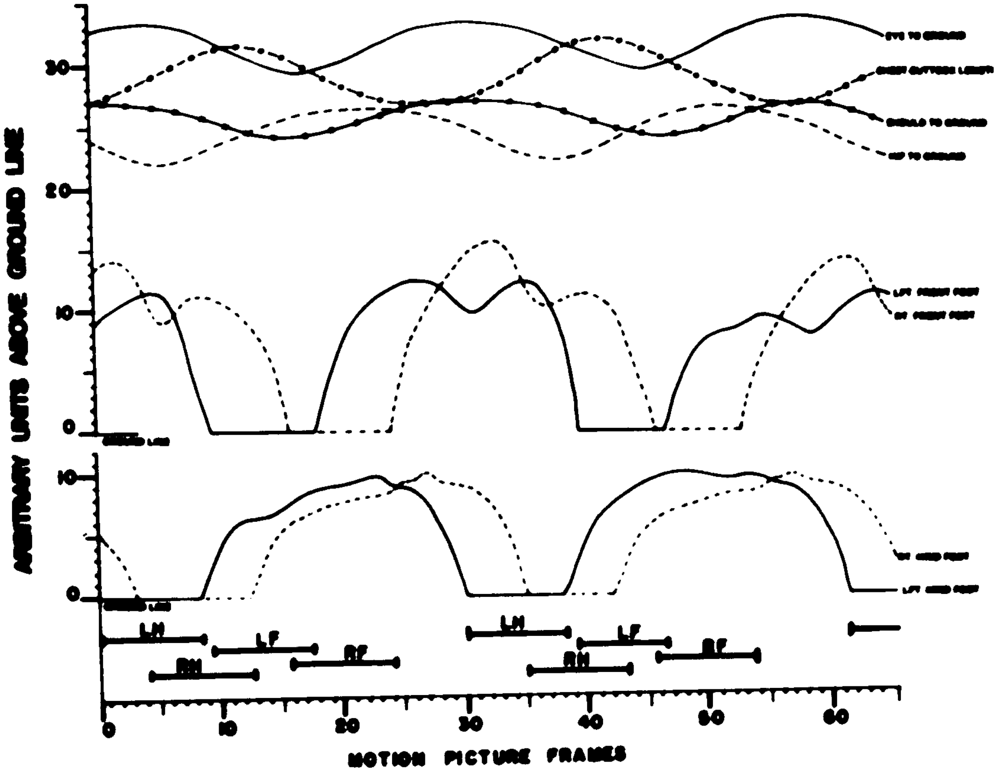
MOTION PICTURE FRAMES

Figure 29. Relation of body movement to action of the feet (gait diagram) of a pronghorn during two strides of a slow canter (compare Fig. 15).

Figure 30. Relation of body movement to action of the feet (gait diagram) of a pronghorn during two strides of a moderate canter (compare Fig. 15).



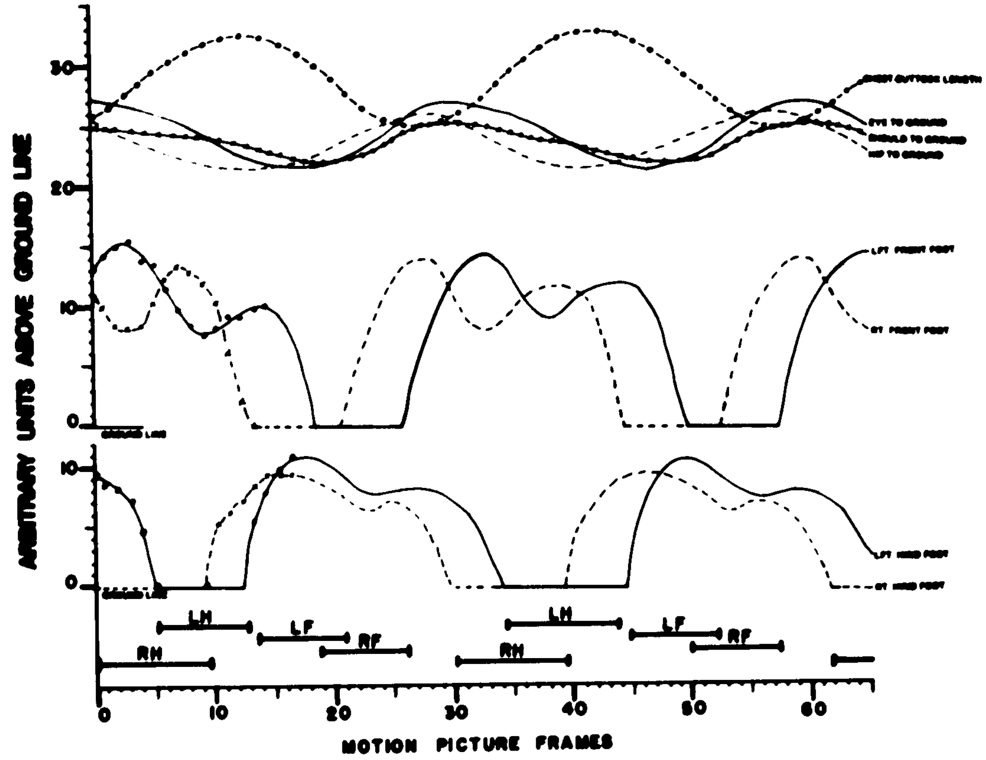
ARBITRARY UNITS ABOVE GROUND LINE
30
20
10
0
10
0
EYE TO GROUND
CHEST BUTTOCK LENGTH
SHOULD TO GROUND
HIP TO GROUND
LFT FRONT FOOT
RT FRONT FOOT
GROUND LINE
LFT HIND FOOT
RT HIND FOOT
GROUND LINE
LH
LF
RF
RH
LH
LF
RF
RH
0
10
20
30
40
50
60
MOTION PICTURE FRAMES

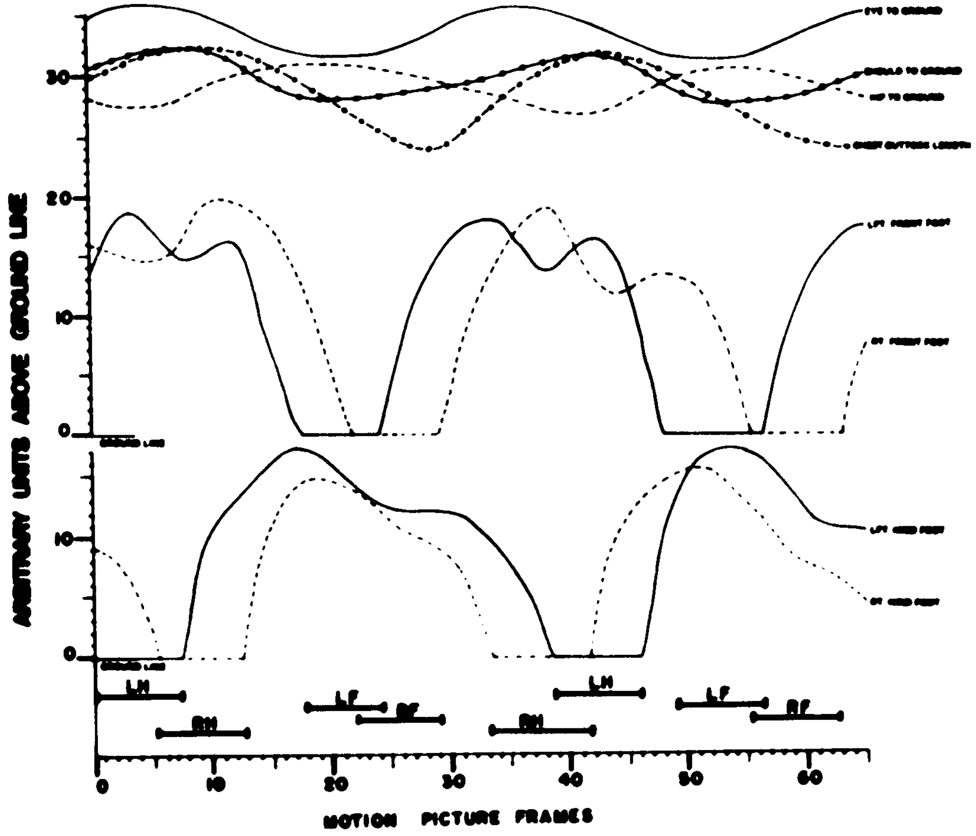


ARBITRARY UNITS ABOVE GROUND LINE
30
20
10
0
10
0
EYE TO GROUND
CHEST BUTTOCK LENGTH
SHOULD TO GROUND
HIP TO GROUND
LFT FRONT FOOT
RT FRONT FOOT
GROUND LINE
RT HIND FOOT
LFT HIND FOOT
GROUND LINE
LH
LF
RF
RH
LH
LF
RF
RH
0
10
20
30
40
50
60
MOTION PICTURE FRAMES

Figure 31. Relation of body movement to action of the feet (gait diagram) of a mature pronghorn during two strides of a fast gallop (compare Fig. 15).

Figure 32. Relation of body movement to action of the feet (gait diagram) of a juvenile pronghorn during two strides of a fast gallop (compare Fig. 15).


ARBITRARY UNITS ABOVE GROUND LINE
30
20
10
0
10
0
CHEST BUTTOCK LENGTH
EYE TO GROUND
SHOULD TO GROUND
HIP TO GROUND
LFT FRONT FOOT
RT FRONT FOOT
LFT HIND FOOT
RT HIND FOOT
GROUND LINE
GROUND LINE
LH
LF
RF
RH
RH
LH
LF
RF
0
10
20
30
40
50
60
MOTION PICTURE FRAMES


ARBITRARY UNITS ABOVE GROUND LINE
30
20
10
0
10
0
EYE TO GROUND
SHOULD TO GROUND
HIP TO GROUND
CHEST BUTTOCK LENGTH
LFT FRONT FOOT
RT FRONT FOOT
LFT HIND FOOT
RT HIND FOOT
GROUND LINE
GROUND LINE
LH
RH
LF
RF
RH
LH
LF
RF
0
10
20
30
40
50
60
MOTION PICTURE FRAMES

(Fig. 28). The shoulders maintain a slightly higher "shoulder-to-ground height" throughout the stride. In the canters and gallop the hind quarters are closest to the ground when the hind feet are on the ground but the withers, in contrast, begin to rise when the lagging forefoot strikes the ground and continues to rise until the leading forefoot is lifted (Figs. 29-32). The hip-to-ground curve is usually lower in amplitude than the shoulder-to-ground curve but the difference between maximal and minimalvalues is about the same for both curves. In the canters and gallops the shoulder- and hip-to-ground curves decrease in amplitude and in amplitude difference between maximal and minimal values as speed is increased (Figs. 29-32). Therefore, it is apparent that as speed is increased from a canter to a gallop, the pronghorn's body levels out somewhat (less vertical movement) and remains closer to the ground.

Role of the Back

As is the case with most artiodactyls, the back of the pronghorn is held fairly rigid during locomotion. Most vertical spine flexion during locomotion is restricted to the posterior lumbar region near its juncture with the sacrum. As speed increases the degree of spine flexion also increases and a larger stride is accomplished. Most of the increase in stride length is due to the hindquarters being drawn toward the forequarters just prior to and during the period of flexed suspension, resulting in the hind feet straddling the forefeet and striking the ground with a considerable degree of overstride (Fig. 26-V). However, while the hind feet are on the ground the body is extended and the spinal column straightened (Fig. 26-U). This action, along with the rotating elongate scapula, increases the extension of the forefoot and also adds to the total length of stride.

The chest-buttock length is indicative of the degree of spinal flexure and hence speed. At a fast gallop (Fig. 26-U and V) the chest-buttock length during the flexed position is approximately 79 to 80 percent of its length in the extended position (approximated from tracings of photographs) compared to an average of 90 percent and 98 percent for the canter and trot respectively. The walking gaits demonstrated very little or no apparent spinal flexure. When the chest-buttock length is related to the footfall patterns of various gaits (Figs. 27-32), certain trends become apparent. During a trotting stride the chest-buttock length is greatest during the periods of suspension when contralateral legs (one front and one hind) are extended and least during the diagonal support phases (Fig. 28). In the canters the greatest chest-buttock length occurs about the time of the striking of the lagging forefoot; the shortest length during the period of flexed suspension (Figs. 29 and 30). Figures 31 and 32 indicate that during a stride of a fast gallop the chest-buttock length is greatest during the period of extended suspension and least just prior to and/or during the flexed suspension phase.

Role of the Neck

The angles made by the back of the neck (mane excluded) and a line projected forward from the small of the back (Fig. 26-W and X) during the execution of various gaits are given in Table 8. From the angles measured it can be generalized that in the gaits faster than a walk the average maximal and minimal neck-back angles are greater (head held more erect) in the trot and slow to moderate canters than in the fast canter and gallop, but that the average difference between maximal and minimal values is greater for the fast canter and gallop than for the slower canters and the trot. Therefore, the head has more movement in the vertical plane at fast speeds. The greater vertical head movement in the case of the gallop over the fast canter is due not only to smaller minimal neck-back angles but also to larger maximal angles as well. The slow canter is frequently employed in a boundlike manner (neck held almost at right angle to back during this type of gait) resulting in the average neck-back angles being greater than would normally be the case for a slow cantering gait. Therefore, the average neck-back angles of the slow canter are abnormally high in comparison to other gaits (Table 8). However, the average angle difference in slow canters is in line with the trend towards greater vertical head movement with increased speed.

Neck-back angles are extremely variable in slow walks, but appear to be more stable in the fast walk (Table 8). The neck is usually held more erect in the fast walk than in the slower walks; the difference between maximal and minimal neck-back angles being about the same for both gaits. The various walks display more vertical head movement than the trot, but less than the asymmetrical gaits.

Figure 33 is a graph resulting from the tracings of a walking pronghorn drawn in sequence. Frames (time) is plotted against neck-back angles. During the walking stride the neck completes two cycles (two crests and two troughs on the graph). When a hind foot is raised the curve reaches its highest level and the neck-back angle is at its maximum. When a front foot is being lifted the curve reaches the lowest level and the neck-back angle is at a minimum (neck reaches

Table 8. Average neck-back angles (in degrees) for various pronghorn gaits (ranges in parentheses).

Gait	Maximum angles	Minimum angles	Amplitude difference between averages
Slow walk	42	25	17
Fast walk	60(54-68)	44(34-55)	16
Trot	68(66-86)	55(54-74)	13
Slow canter*	83(80-85)	63(60-65)	20
Moderate canter	62(54-68)	38(31-45)	24
Fast canter	54(50-68)	23(18-40)	31
Fast gallop	58(55-65)	20(18-25)	38

* Many of the slow canters are boundlike, hence average neck-back angles are greater than would otherwise be the case.

farthest forward). The neck, therefore, moves backward as each hind leg is being moved and swings forward in time with the movement of each foreleg.

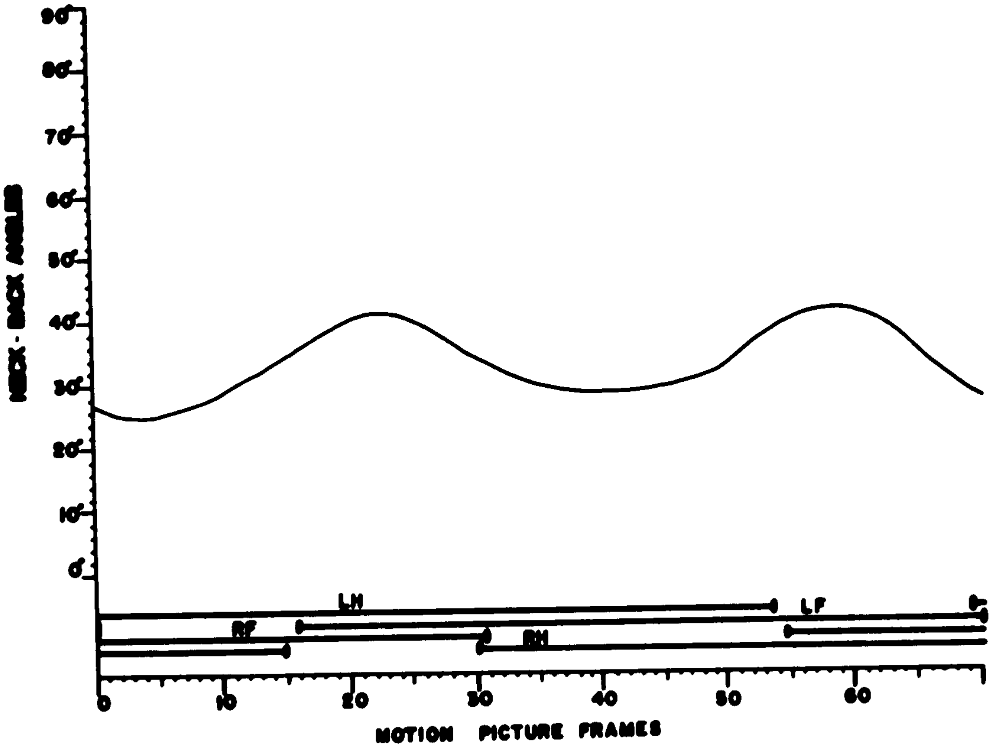
Like the walk, the neck completes two cycles during the stride of a trot. The two crests of the curve for the trotting gait (Fig. 34) occur when diagonal pairs of feet strike the ground. While each diagonal pair is on the ground the curve descends (neck moves forward) reaching its lowest point just prior to a period of suspension.

In the canters and gallops the neck moves backward and forward once for each complete stride. Due to the leaping nature of the strides associated with these gaits, the movement of the neck, and hence center of gravity, is probably more important for maintaining balance and facilitating forward and backward momentum than in the symmetrical gaits. During the moderate canter (Fig. 36) and gallop (Fig. 37) the neck-back angle is at its minimum value when the hind legs are on the ground and the front legs are extended. The neck is pressed back and reaches its maximum angle just prior to or during the beginning of the flexed suspension phase of the stride, thus shifting the center of gravity back and enabling the pronghorn to keep its balance. The neck is then stretched forward again and the center of gravity is moved slightly anterior to help speed up forward momentum as the power stroke of the hind legs is being executed. The neck movements of a pronghorn employing a slow, boundlike canter are almost opposite to the canter described above (Fig. 35). In the bounding canter the neck-back angle is highest when all four feet are on the ground, and lowest just prior to or during the period of flexed suspension. In this rendition of the canter the center of gravity is shifted to the rear (neck pressed back) to facilitate balance at the time when the feet strike the ground after a rather extensive period of suspension. Figure 38 compares the neck-back angle curve of this atypical canter with curves of the other gaits discussed above. Such a graph facilitates the comparison of gaits with reference to time instead of footfall patterns.

Curves plotted from the movements of the head during locomotion (eye-to-ground curve, Figs. 27-32) are closely correlated with the neck-back angle curves (Figs. 33-37) for corresponding gaits. Therefore, in all gaits analyzed the neck moves in relation to the back in such a way that the head is highest when the neck-back angles are greatest.

Figure 33. Relation of neck-back angles to the periods of contact of the feet with the ground (gait diagram) during a stride of a slow walk. Motion is from left to right. Letters R, L, H and F mean right, left, hind and front respectively.

Figure 34. Relation of neck-back angles to the periods of contact of the feet with the ground (gait diagram) during a little more than one trotting stride (compare Fig. 33).


NECK - BACK ANGLES
90°
80°
70°
60°
50°
40°
30°
20°
10°
0°
LH
LF
RF
RH
0
10
20
30
40
50
60
MOTION PICTURE FRAMES

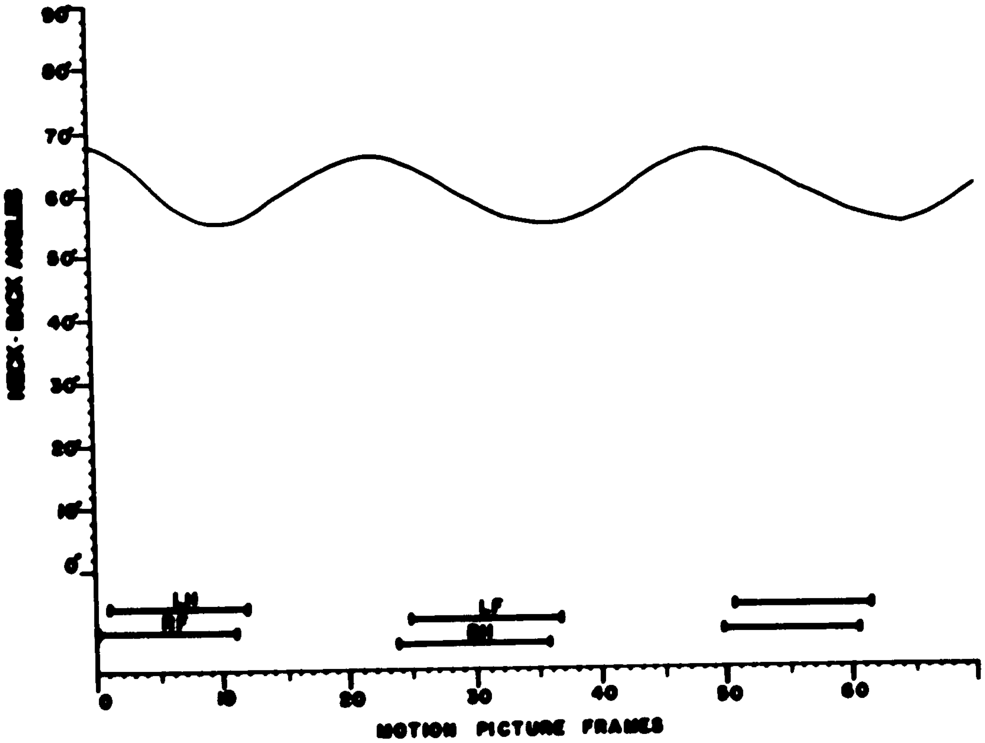
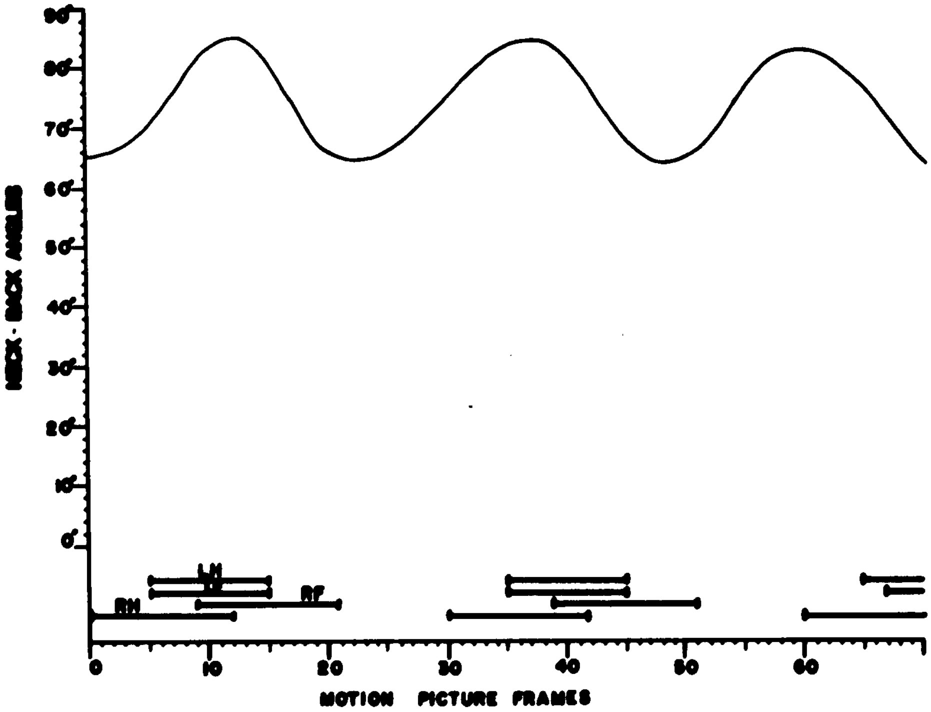

NECK - BACK ANGLES
90°
80°
70°
60°
50°
40°
30°
20°
10°
0°
LH
RF
LF
RH
0
10
20
30
40
50
60
MOTION PICTURE FRAMES

Figure 35. Relation of neck-back angles to the periods of contact of the feet with the ground (gait diagram) during a little more than two strides of a boundlike canter (compare Fig. 33).

Figure 36. Relation of neck-back angles to the periods of contact of the feet with the ground (gait diagram) during a little more than two strides of a moderate canter (compare Fig. 33).


90°
80°
70°
60°
50°
40°
30°
20°
10°
0°
NECK - BACK ANGLES
LM
LF
RF
RH
0
10
20
30
40
50
60
MOTION PICTURE FRAMES

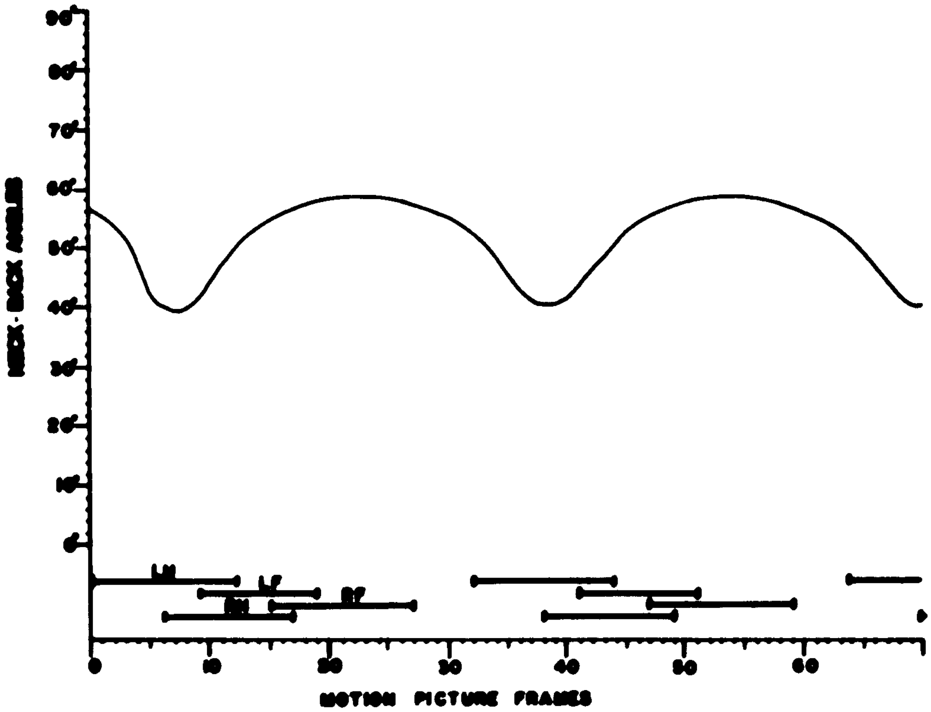
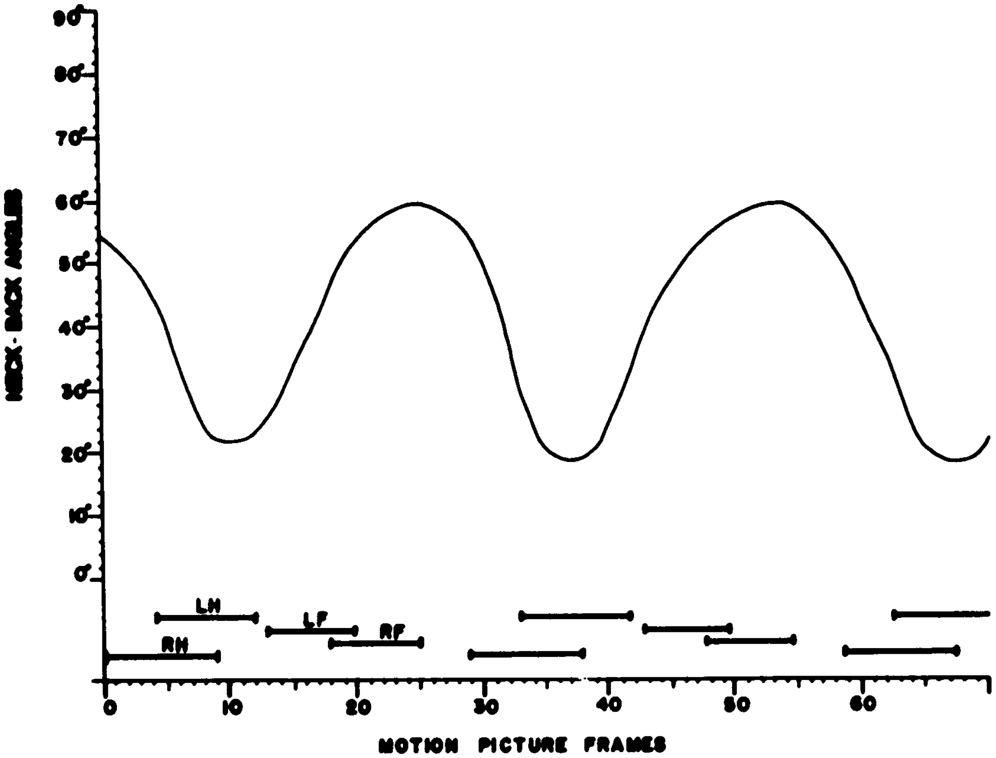
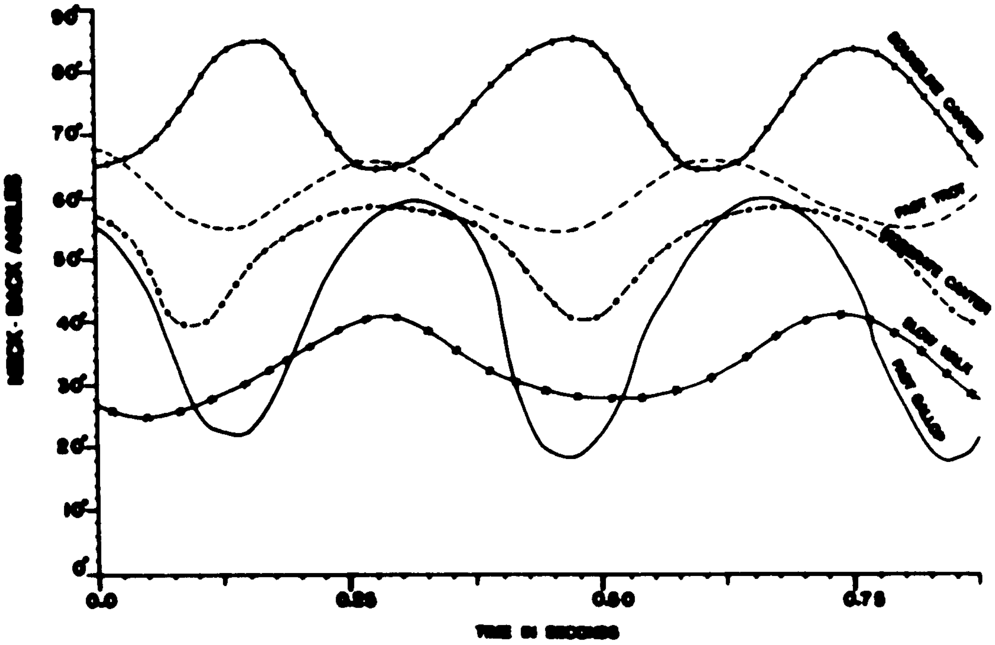

90°
80°
70°
60°
50°
40°
30°
20°
10°
0°
NECK - BACK ANGLES
LM
LF
RF
RH
0
10
20
30
40
50
60
MOTION PICTURE FRAMES

Figure 37. Relation of neck-back angles to the periods of contact of the feet with the ground (gait diagram) during a little more than two strides of a fast gallop (compare Fig. 33).

Figure 38. A comparison of neck-back angles in relation to time in seconds for various gaits. The curve for each gait starts when a hind foot strikes the ground initiating a stride.


90°
80°
70°
60°
50°
40°
30°
20°
10°
0°
NECK - BACK ANGLES
LH
LF
RF
RH
0
10
20
30
40
50
60
MOTION PICTURE FRAMES


90°
80°
70°
60°
50°
40°
30°
20°
10°
0°
NECK - BACK ANGLES
CANTER
FAST TROT
CANTER
SLOW WALK
FAST GALLOP
0.0
0.25
0.50
0.75
TIME IN SECONDS

CURSORIAL ADAPTATIONS: SKELETAL PROPORTIONS

The skeleton of the pronghorn exhibits the basic cursorial adaptations that are found in most other ungulates of similar body conformation. Gregory (1912), Gray (1944), Howell (1944) and Smith and Savage (1955) discussed some of the skeletal modifications of cursorial ungulates, the more important ones were thought to be: a relatively rigid spine to minimize stresses resulting from body movements during locomotion, unguligrade foot posture to increase the functional length of limbs and hence increase length of stride, propodial limb elements relatively short and stout with distal bones slender and elongate to reduce the moment of inertia during the swing of the limbs, coalesced third and fourth metacarpals and metatarsals into single cannon bones that resist bending better than two bones of the same total cross-sectional area, loss of clavicle for free movement of the scapula, high narrow scapula for added functional length of forelimb, and ilium lengthened in relation to the ischium and pubis for better arrangement of muscles in order to impart a more rapid movement to the leg. Flerov (1962) asserts that the distal parts of limbs have evolved in connection with the type of substrate that must be traversed. He points out that dew-claws are well developed in ruminants that inhabit soft substrates (marshes, tundra, etc.) or localities with abundant snow, but reduced or absent in inhabitants of dry regions with hard ground. The pronghorn antelope, with its lack of dew-claws, is a good example of an animal adapted to a relatively hard dry substrate (giraffes, okapis and camels also lack dew-claws). Pronghorn avoid soft mud and make every effort to keep on dry and solid ground. Although the pronghorn's hooves are relatively large, perhaps the lack of dew-claws hampers them in mud (McLean, 1944).

On several occasions during this study pronghorn were observed to avoid deep snow and run on the wind swept ridges. They would, however, cross deep snow in ravines to get from one range area to another.

To gain greater insight into the cursorial adaptations of the pronghorn, and to understand more completely the reasons for body structures moving as they do during locomotion, it is necessary to study skeletal proportions. Bone measurements used to calculate ratios express the functional length of the skeletal element, i.e., the distance between two centers of articulation. To facilitate an intraspecific as well as interspecific comparison, various ages and sexes of pronghorn have been analyzed. Inasmuch as the number of specimens available for study was limited, the analysis contains the following limitations:

(1) A complex statistical analysis could not be made.

(2) There is a danger that individual specimens represent extremes and thereby invalidate conclusions.

(3) The degree of sexual dimorphism is difficult to determine.

(4) Only trends in skeletal proportions (and hence cursorial adaptation) can justifiably be indicated.

Differences in length between right and left members of a pair of limb bones were found to be inconsequential, and were exceeded by individual variations among pronghorn. Therefore, to standardize measurements only right limb bones have been tabulated in Tables 9 and 10.

Previous workers dealing with body proportions have not included the phalanges as a significant part of the functional length of a limb. Although it is true that phalangeal length is small when compared to other leg elements, nonetheless, it is a functional unit of the leg and should be considered. In particular the first and second phalanges (lateral and medial) should be considered because they add to the functional length of a limb when the animal is standing. The distal phalanx, however, is placed horizontally on the ground and the keratinized hoof surrounding it is more indicative of length than the actual phalanx. Therefore, only the first and second phalanges have been included in Tables 9 and 10. It is apparent from Table 10 that the first phalanx contributes more to digit length than the second and that the first phalanges of the manus are slightly longer than those of the pes. The second phalanges are about equal in length for both manus and pes. The lateral digit (first and second phalanges) was slightly longer than the medial digit in both manus and pes for all seven pronghorn examined. The disparity in length of digit appears to be due to a slight reduction in length of either or both of the medial phalangeal elements. In the case of the hind foot, perhaps the longer lateral digit facilitates a more uniform contact with the ground when it passes lateral to the front foot during straddling.

In order to make measurements of skeletal structures more meaningful, various elements of the skeleton can be expressed as fractions (ratios) of some part (or parts) adopted as a standard. When limb segments are expressed as percent of total limb length (Table 11) it can be seen that in both the front and the hind leg of pronghorn the humerus and radius become proportionately longer and the metacarpus and phalanges proportionately shorter as the pronghorn matures from a fawn to an adult. Therefore, the distal leg elements are proportionately longer in fawns than in adults. Inasmuch as an increase in the length

Table 9. Length, in millimeters, of pronghorn limb bones for various sexes and ages.

Sex	Age	Humerus	Radius	Olecranon	Metacarpal	Lateral digit (Manus)	Medial digit (Manus)	Scapula	Femur	Tibia	Metatarsal	Lateral digit (Pes)	Medial digit (Pes)	Calcaneum
♂	5½ yrs.	181	205	50	213	76.5	75	191	230	273	222	75	74.5	52
♂	4 yrs.	176	204	49	211	77	76	185	225	269	224	75.5	74.5	52
♂	3½ yrs.	183	204	50	208	80	79.5	182	228	269	218	80	79.5	52.5
♀	2 yrs.	180	200	48	205	80.5	78.5	185	220	267	216	79.5	78.5	50.5
♀	8 mos.	164	192	44	200	80.5	80	163	210	254	210	80.5	80	51
♂	44 days	139	157	32	179	69	68.5	123	173	209	181	69	68	42
♀	24 hrs.	99	112	20.5	149	51	50.5	79	116	146	149	49.5	49	26.5

Table 10. Length, in millimeters, of pronghorn phalanges for various sexes and ages.

		Manus				Pes			
Sex	Age	First lateral phalanx	First medial phalanx	Second lateral phalanx	Second medial phalanx	First lateral phalanx	First medial phalanx	Second lateral phalanx	Scond medial phalanx
♂	5½ yrs.	52	51.5	30	30	51	50	30	30
♂	4 yrs.	52	51	30.5	30	51	50	30	30
♂	3½ yrs.	53.5	53	32	32	52.5	52.5	32.5	32
♀	2 yrs.	53.5	53	32	31.5	52	52	32	32
♀	8 mos.	54	53.5	31.5	31	53	52.5	33	33
♂	44 days	47.5	47	27	26.5	46.5	46	28.5	28
♀	24 hrs.	33	33	20.5	20	32	31.5	20	20

Table 11. Limb segments of pronghorn expressed as per cent of total limb length.

		Front leg				Hind leg			
Sex	Age	Humerus	Radius	Metacarpus	Phalanges	Femur	Tibia	Metatarsus	Phalanges
♂	5½ yrs.	26.8	30.3	31.5	11.4	28.8	34.0	27.8	9.4
♂	4 yrs.	26.4	30.5	31.6	11.5	28.3	33.9	28.2	9.6
♂	3½ yrs.	27.1	30.2	30.8	11.9	28.7	33.8	27.4	10.1
♀	2 yrs.	27.0	30.1	30.7	12.2	28.1	34.1	27.6	10.2
♀	8 mos.	25.7	30.1	31.5	12.7	27.8	33.6	27.8	10.8
♂	44 days	25.6	28.9	32.8	12.7	27.4	33.1	28.6	10.9
♀	24 hrs.	24.1	27.3	36.3	12.5	25.2	31.6	32.3	10.9

of metapodials and decrease in the relative length of propodials indicates cursorial specialization (Howell, 1944), fawns show a greater degree of cursorial adaptation than adults. Pronghorn fawns also have considerably longer legs in relation to spine length than adult animals (Table 12). Howell (1944) asserts that the disproportionately long legs of some newborn ungulates is also a cursorial adaptation. Table 12 indicates that the greater proportional leg length in fawns is a result of all leg elements being longer in proportion to spine length, but that the metapodial elements and phalanges of both legs contribute proportionately more to the relatively longer limb length.

Long legs in relation to body size make it possible for the relatively small fawns to execute relatively long strides. This supposed advantage for speed is negated by the lack of muscular and/or nervous coordination (apparent awkwardness) of fawns at an early age. At this early age, however, they remain hidden most of the time and locomotion is not an important factor for survival. When fawns are approximately two weeks old and running with the herd they can keep up with the adult animals, indicating that they are using their disproportionately long legs to good advantage.

Following Howell (1944) and Gregory (1912) the following skeletal indices (ratios multiplied by 100) were employed to analyze the body proportions of pronghorn:

FRONT LIMB INDICES

Humeroradial Index = $\frac{\text{Radius}}{\text{Humerus}} \times 100$

Humerometacarpal Index = $\frac{\text{Metacarpus}}{\text{Humerus}} \times 100$

Table 12. Comparative skeletal proportions of pronghorn with spinal column length (atlas to sacrum) equated to 100, and skeletal elements indicated in proportion.

Skeletal element(s)	Sex and Age			
	24 hr. doe	8 month doe	2 yr. doe	3½ yr. buck
Cervical vertebrae (Neck)	35.9	37.2	35.0	35.8
Thoracolumbar Vertebrae (Back)	64.1	62.8	65.0	64.2
Humerus	28.2	20.9	20.8	21.2
Radius	31.9	24.4	23.8	23.6
Metacarpal	42.5	25.4	24.2	24.0
Phalanges (Carpus)	14.5	10.2	9.4	9.2
Front leg	117.1	80.9	78.2	78.0
Femur	33.0	26.7	26.4	26.4
Tibia	41.6	32.3	31.8	31.1
Metatarsal	42.5	26.7	26.4	25.2
Phalanges (Tarsus)	14.2	10.2	9.4	9.2
Hind leg	131.3	95.9	94.0	91.9

$$\text{Humeral Index} = \frac{\text{Humerus}}{\text{Humerus + Radius + Metacarpal}} \times 100$$

$$\text{*Radial Index} = \frac{\text{Radius}}{\text{Humerus + Radius + Metacarpal}} \times 100$$

$$\text{Metacarpal Index} = \frac{\text{Metacarpal}}{\text{Humerus + Radius + Metacarpal}} \times 100$$

$$\text{*Phalangeal Index} = \frac{\text{First and Second Lateral Phalanges}}{\text{Humerus + Radius + Metacarpal + Phalanges}} \times 100$$

$$\text{*Humerophalangeal Index} = \frac{\text{Humerus}}{\text{First and Second Lateral Phalanges}} \times 100$$

$$\text{*Scapular Index} = \frac{\text{Scapula}}{\text{Total Leg Length}} \times 100$$

$$\text{*Olecranon Index} = \frac{\text{Olecranon}}{\text{Radius + Metacarpal + Phalanges}} \times 100$$

HIND LIMB INDICES

$$\text{Femorotibial Index} = \frac{\text{Tibia}}{\text{Femur}} \times 100$$

$$\text{Femorometatarsal Index} = \frac{\text{Metatarsal}}{\text{Femur}} \times 100$$

$$\text{Femoral Index} = \frac{\text{Femur}}{\text{Femur + Tibia + Metatarsal}} \times 100$$

$$\text{*Tibial Index} = \frac{\text{Tibia}}{\text{Femur + Tibia + Metatarsal}} \times 100$$

$$\text{Metatarsal Index} = \frac{\text{Metatarsal}}{\text{Femur + Tibia + Metatarsal}} \times 100$$

$$\text{*Phalangeal Index} = \frac{\text{First and Second Lateral Phalanges}}{\text{Femur + Tibia + Metatarsal + Phalanges}} \times 100$$

$$\text{*Femorophalangeal Index} = \frac{\text{Femur}}{\text{First and Second Lateral Phalanges}} \times 100$$

$$\text{Calcaneum Index} = \frac{\text{Calcaneum}}{\text{Metatarsal + Phalanges}} \times 100$$

INTERMEMBRAL INDICES

$$\text{Femorohumeral Index} = \frac{\text{Humerus}}{\text{Femur}} \times 100$$

$$\text{Tibioradial Index} = \frac{\text{Radius}}{\text{Tibia}} \times 100$$

$$\text{*Metapodial Index} = \frac{\text{Metacarpal}}{\text{Metatarsal}} \times 100$$

$$\text{*Intermembral Phalangeal Index} = \frac{\text{Phalanges (Carpus)}}{\text{Phalanges (Tarsus)}} \times 100$$

$$\text{Propodial-Epipodial Index} = \frac{\text{Humerus} + \text{Radius}}{\text{Femur} + \text{Tibia}} \times 100$$

$$\text{Propodial-Epipodial-Metapodial Index} = \frac{\text{Humerus} + \text{Radius} + \text{Metacarpus}}{\text{Femur} + \text{Tibia} + \text{Metatarsus}}$$

$$\text{*Leg Index} = \frac{\text{Total Front Leg Length}}{\text{Total Hind Leg Length}} \times 100$$

*Indices devised by the author

Although the calculations from all of the indices outlined above are informative, much of the data merely corroborates the trends that have already been indicated by previous ratio analyses. However, a few indices (Table 13) indicate trends in cursorial adaptation that are not apparent in the ratio methods previously used. According to the leg index the front and hind legs of pronghorn are about of equal length, the legs of fawns being closer to the same length than those of adults. As long hind legs are indicative of saltatorial or jumping gaits, and legs of about equal length are adapted cursorially (Howell, 1944) fawns appear to be relatively more adapted for speed than their parents. Howell (1944) also points out that a high metapodial index (metacarpals and metatarsals of about equal length) indicate cursorial adaptation. Fawns have a slightly higher metapodial index than adults. The jumping ability of pronghorn (according to metapodial and leg indices) probably increases with maturity. This hypothesis is given more weight when olecranon and calcaneum indices are considered. The ratios of both indices are greater in adults than in fawns and juveniles, indicating

Table 13. Skeletal proportions of pronghorn as indicated by a few selected indices.

Sex	Age	Metapodial Index	Leg Index	Intermembral Phalangeal Index	Scapular Index	Olecranon Index	Calcaneum Index
♂	5½ yrs.	96	85	102	28	10	18
♂	4 yrs.	94	84	102	28	10	17
♂	3½ yrs.	95	85	101	27	10	18
♀	2 yrs.	95	85	101	28	10	17
♀	8 mos.	95	84	100	26	9	18
♂	44 days	99	86	100	23	8	17
♀	24 hrs.	100	89	102	19	7	14

greater lever arms for muscle attachment and therefore greater jumping ability. Smith and Savage (1955) report that a proportionately large olecranon allows the triceps to impart a slow but powerful movement to the lower leg. They also infer that within certain limits jumping ability increases as the moment arm of the gastrocnemius muscle (indicative of length of calcaneum) becomes larger. The mule deer is an ungulate similar in body conformation to the pronghorn but adapted for saltatorial or jumping gaits instead of smooth galloping gaits. Olecranon, calcaneum, metapodial and leg ratios calculated from the skeletons of three mule deer indicate that jumping ability is in fact correlated with high olecranon and calcaneum ratios and low metapodial and leg ratios (Table D). It is also interesting to note that the mule deer has a proportionately shorter scapula than the pronghorn, indicating less cursorial specialization. Unlike the pronghorn with front digits slightly longer than the hind ones, the mule deer has longer digits on the hind legs adding length to the rear limb and increasing the jumping ability of the animal.

The scapula is proportionately smaller in fawns and juveniles than in adults (Table 13), indicating that the increase in leg length (and hence stride) due to increased scapular length is correlated with maturity. The lack of scapular length in fawns is partly offset by their proportionately longer front legs.

DISCUSSION

Pronghorn Gaits

Although the pronghorn, like most quadrupeds, employs the diagonal walk, Gray (1944) asserted that walking quadrupeds can theoretically advance their four feet in six different sequences: (1) RH (right hind), RF (right front), LH (left hind) and LF (left front). (2) RH, LF, LH and RF. (3) RH, LH, RF and LF. (4) RH, LH, LF and RF. (5) RH, RF, LF and LH. (6) RH, LF, RF and LH. Sequence 1 in which the front foot begins advancing only after the ipsilateral hind foot has done so, appears to be the one that evolution has favored and is the sequence used by the vast majority of quadrupeds. Brown (1968), discussing Gray's six sequences, stated that only in sequence 1 do the feet form the best triangles - the bases of tripods - to support and balance the animal properly. He pointed out that in the five other sequences the feet form triangles that are small and do not lie under the center of gravity and that an increase in speed would bring problems of balance and risk of one foot interfering with another. Gray (1953) maintained that sequence 1 is the only order of stepping which conforms to the requirement that no foot should ever be lifted unless the center of gravity of the body lies over the triangle marked by the other three. Sequence 2, referred to as the lateral walk by Howell (1944), the "false walk" (Brown, 1968), and as the diagonal sequence, diagonal couplets gait (Hildebrand, 1966), is very rare and is only employed by the kinkajou, the unguligrade giant armadillo, the aardvark, most apes, and all monkeys. Although Einarsen (1948) illustrates this type of walk for pronghorn, the illustrations are obviously in error. It would appear from the evidence of modern forms that the walk was undoubtedly the primitive system of locomotion employed by all terrestrial vertebrates (Muybridge, 1899). Boonstra (1967) and Magna de la Croix (1936) concluded that the walking gait was basic to the evolution of mammalian gaits.

In the walking gaits, as in most pronghorn gaits, speed is a product of rate and length of stride. As a pronghorn increases the tempo of a walk from a very slow walk to a fast walk, the rate of stride increases from .7 to 1.2 strides per second, while the length of stride increases from approximately 20 inches to 41 inches (51 to 104 cm.). Increased speed and body momentum appear to compensate for the relative instability of the fast walking gaits where there are more phases in a stride consisting of only two legs supporting the body.

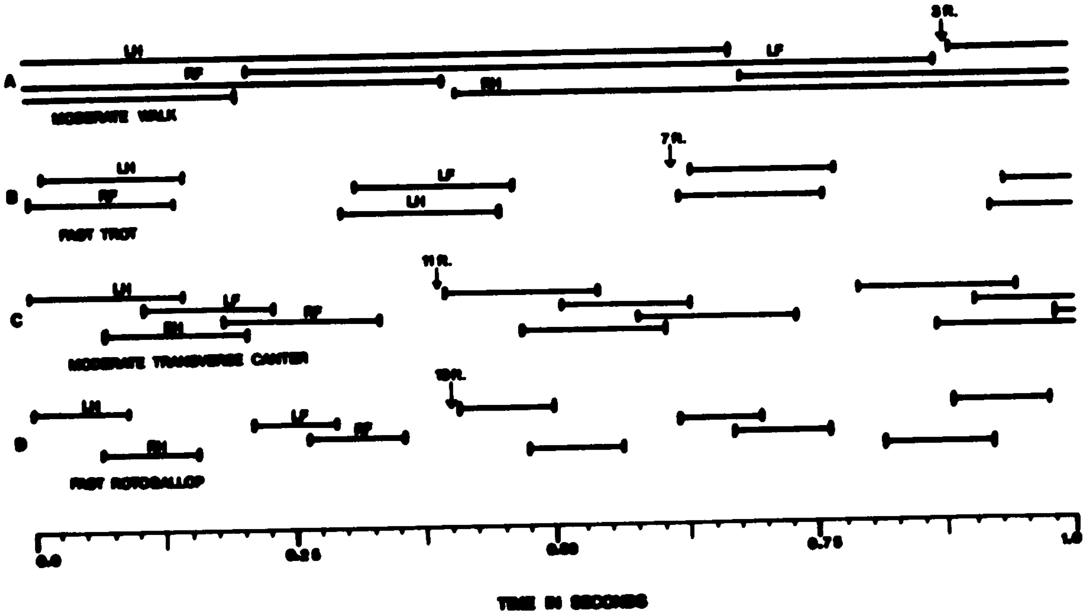
The disparity in support time of legs of a diagonal pair in a trotting stride is a result of the front legs of a pronghorn being somewhat shorter than the hind legs and not being able to match the stride of the longer hind legs. This discrepancy in the length of fore and hind legs is not unique to pronghorn, for Howell (1944) has pointed out that this condition is true for most mammals. The disparity in support would be greater, however, if it were not for the anatomical adaptations present in pronghorn and other cursorial mammals for lengthening the functional length of the forelimb. Loss of clavicle associated with the incorporation of the scapula (now free to swing) into the functional length of the forelimb increases length of stride and makes it possible for the front leg to match the stride of the longer hind leg more closely (Eaton, 1944). This allows the length of stride and the timing of fore and hind limb movements to approximate symmetry in walking and trotting gaits. As with the walk, the rate and length of stride increase as the trotting speed of a pronghorn increases.

Chubb (1929), Howell (1944), Dagg and de Vos (1968), and others have reported that the "galloping" gait of pronghorn antelope is the rotary gallop. It was found, however, that the transverse system of footfalls is also a natural and frequently employed gait at slower galloping speeds (canters). Such diversity in "galloping" gaits appears to be lacking in most other mammals. Authors reporting on the natural gaits of horses (Muybridge, 1899; Stillman, 1882; Howell, 1944; Grogan, 1951; and Hildebrand, 1965, to mention a few) have concluded or inferred that the horse employs the transverse gallop or canter exclusively. It has been reported by Chubb (1929) that the members of the Family Equidae, the cow, buffalo, goat, bear and others employ the diagonal (transverse) gallop, while some of the ruminants such as the deer, elk and antelope adhere to the rotatory system of the dog. The cheetah, a member of the cat family, employs the rotary gallop (Hildebrand, 1959). Film shot and analyzed during this study confirms the gaits of the horse, deer, elk and dog as reported above, and suggests that the exclusive galloping gait of the Rocky Mountain Bighorn Sheep (_Ovis canadensis_) and the Rocky Mountain Goat (_Oreamnos americanus_) is the transverse gallop. It would appear from the referencescited above and from film analyzed in this study, that there has been a selection for certain types of galloping gaits within phylogenetic groups: transverse for Families Equidae, Bovidae and Ursidae, rotary for Families Canidae, Felidae and Cervidae, and both for the Family Antilocapridae at cantering speeds with a preference for the rotary sequence at fast galloping speeds. Magna de la Croix (1928) noted the evolutionary trend toward the rotogallop in many artiodactvls and the transverse gallop in many perissodactyls.

As previously mentioned, speed is increased in the walking and trotting gaits by increasing both length and rate of stride. This was also found to be the case with canters. In the gallop, however, speed is increased by increasing the length of stride but the rate of stride is actually decreased in many cases. Figure 39 shows comparative stride lengths for various gaits according to time. Hildebrand (1962) noted that, as speed of travel increased, small rodents would decrease stride rate while increasing stride distance, but asserted that ungulates and carnivores increased stride distance considerably but increased stride rate only slightly. His statement holds true for all pronghorn gaits with the exception of some fast galloping strides. The most rapid stride rate recorded for a pronghorn was 2.8 strides per second, the longest stride length being 18 feet (5.5 m.). Both the cheetah and horse average about 23 feet (7 m.) per stride at a fast gallop but the rate of stride for the cheetah is 3.5 strides per second, whereas it is only 2.5 strides per second for the horse (Hildebrand, 1959). He also points out that the stride of the cheetah is 8½ to 11½ times its shoulder height, compared with 4½ to 5 for the horse. The stride of a mature pronghorn is about 6 to 6½ times its shoulder height. Therefore, the length of stride (relative to shoulder height) and rate of stride are greater in pronghorn than in the horse but somewhat slower than the cheetah with its flexible back.

McLean (1944) stated that when pronghorn are running most of their power seems to be generated by the hind legs and the forelegs are used mainly for stability. However, the body weight of a pronghorn is carried principally on the larger front feet when running, whereas the rear hooves do not strike the ground as forcefully and the hind legs act

Figure 39. Sequences of footfalls (gait diagrams) of various gaits shown in relation to time in seconds. Letters R, L, H and F, respectively, mean right, left, hind and front feet. Time intervals required to cover specified distances (one complete stride) are indicated.


3 fr.
LH
LF
A
RF
RH
MODERATE WALK
7 fr.
LH
LF
B
RF
LH
FAST TROT
11 fr.
LH
LF
C
RF
RH
MODERATE TRANSVERSE CANTER
15 fr.
LH
LF
D
RF
RH
FAST ROTOGALLOP
0.0
0.25
0.50
0.75
1.0
TIME IN SECONDS

merely as supports (Einarsen, 1948). The foregoing statements appear somewhat contradictory, but are in fact dealing with two different phenomena: propulsion and support. Although the propulsive-support ratio of limb function varies in mammals according to body conformation, speed, etc., if both limbs are approximately the same size, the support role is relatively higher in the pair nearest the center of gravity and the propulsive role in the other pair (Howell, 1944). Inasmuch as most mammals, including pronghorn, have the center of gravity near the front quarters, the main propulsive thrust is produced by the hind limbs and the forelimbs act more as struts. Taylor (1970), working with East African viverrids, and Hildebrand (1959) working with the horse and cheetah, reported similar results. An investigation of the walk in the cat (Manter, 1938) resulted in the conclusion that the forelimbs meet the ground with greater retarding thrust than do the hindlimbs.

Hildebrand (1965) states that his limited data show no significant differences between the gaits of colts and adult horses. Pronghorn, however, were not observed to employ the trot until they were about two weeks old. Although the footfall sequences of cantering and galloping fawns are comparable to those of the adult animals, there was considerably less suspension, or no suspension, during each stride of a fawn's gait. As fawns have longer legs in proportion to their bodies than mature animals and, because of their apparent lack of muscular coordintion at a very young age, it would appear that the stability acquired from very short periods of suspension, or lack of such, would be of great value. A considerable maturation of the coordinating mechanism of the body appears to be necessary before fawns can execute the intricate footfall sequences of the symmetrical gaits. The fact that the rotary sequence of footfalls was the only one observed in running fawns, and is the exclusive sequence of mature animals at fast speeds, suggests that perhaps the rotary sequence is more basic or primitive to the species than is the transverse one.

Straddling of the front legs by the hind legs to prevent interference of ipsilateral legs was observed to some extent in all gaits, being most pronounced in the rotogallop, especially the rotogallop of fawns. The manner in which straddling occurs in the pronghorn is widespread among mammals. Chubb (1929) pointed out that even an English bulldog with broad shoulders and narrow hips will execute the stereotyped straddling procedure even though it appears very awkward in doing so.

Gregg (1955) maintains that the bound (bounding gallop) is a distinct and isolated gait that does not develop from or into any other gait. He also reports that the frequency of the bounds is usually over 150 per minute, compared to a frequency of 120 per minute for mule deer. Although data from this study agree with the frequencies reported, they do not corroborate the statement concerning the isolation of the gait. It was found that although pronghorn do usually use the bounding gallop to initiate flight, the gait would usually grade into a trot, boundlike canter or normal canter sequence.

Film sequences analyzed in this study indicate that the footfall sequence of the bounding gallop of mule deer is very similar to that of the pronghorn. However, the magnitude (vertical and horizontal) of the bounds is greater in the mule deer, while the frequency of the bounds is somewhat less. As was the case with the pronghorn the pure form of the gait is rarely encountered. Usually all four feet strike and leave the ground at separate, but closely spaced intervals of time.

General Gait Analysis

Pronghorn spend a greater percentage of each trotting stride on diagonal supporting legs at slower speeds than at faster speeds, 62 percent being the average for the slower trots and 48 percent for the faster trots. These percentages are low when compared to the trotting gaits of the twelve pecoran species reported by Dagg and de Vos (1968). The average percentage times of the trotting strides of these species (relative speed was not indicated) ranged from 72 to 92 percent (e.g. *Alces americana*, 80; *Cervus canadensis*, 75; *Rangifer tarandus*, 83; *Odocoileus hemionus*, 86; *Dama dama*, 72; *Odocoileus virginianus*, 77; and *Gazella thomsonii*, 92). As with the pronghorn, most of the twelve species were reported to have short periods of time during the trotting stride when one front and/or one hind leg gave sole support to the body, with the hind leg usually having a greater percentage time than the front leg. However, the total percentage time spent on one leg alone was considerably higher for most of the twelve species than for the pronghorn. A longer one-leg support phase would, of course, result in a shorter total suspension. Whereas in the pronghorn total suspension is from 33 percent (moderate trot) to 45 percent (fast trot) of the total duration of stride and four-point support is very rare, Dagg and de Vos (1968) report that there is no period of suspension in the trotting strides of moose, elk, gazelle, etc., a very small percentage (3 to 20%) in other forms, and that several animals, including the moose, elk, caribou and mule deer, have a very short (1 to 4%) period of four-point support. It would appear, therefore, that the trotting stride of the pronghorn is more symmetrical than many other species and that the body is suspended for a greater percentage of the stride.

Hildebrand (1966) asserts that large animals accelerating from a moderate gallop to a fast gallop decrease the duration of those intervals when all feet are off the ground. Although pronghorn are not "large" animals compared to many ungulate groups, nonetheless the trend is true for the pronghorn if only canters (one period of flexed suspension) are considered (Table 2). However, when a pronghorn increases speed from a fast canter to a gallop a period of extended suspension is incorporated into the gait, thus increasing the total suspension time per stride for the gallop to more than that of the moderate canter. During the speed increase from slow canter to fast gallop the footfalls are spread out to accommodate the extended period of suspension. Therefore, the percentage of stride time spent on four legs and three legs decreases while the time spent on two-leg and one-leg support is increased. Dagg and de Vos (1968) maintain that theoretically the fastest gait would be one in which two-leg support is completely eliminated in favor of one-leg support.

According to Dagg and de Vos (1968) heavy animals such as moose and elk never have an extended suspension and the period of flexed suspension is often missing, particularly when galloping slowly. They also report that the mule deer has a period of extended suspension but no period of flexed suspension, and that the white-tailed deer has both a flexed and extended period of suspension with the extended period being the larger of the two. Howell (1944) depicted a light horse that had a very brief period of extended suspension. Although the cheetah is quite different from ungulates in many respects, it is interesting to note that it is reported to be the fastest of animals for a short dash and like the pronghorn has two periods of suspension in its gallop (rotogallop). The suspension periods of the cheetah's gallop increase in duration with increased speed, the extended suspension period increasing proportionately more (Hildebrand, 1961).

Limited data indicate that pronghorn change front leads during slow and moderate canters more frequently than rear leads. A possible explanation for this could be that the heavy front quarters with head attached (center of gravity being a few inches behind the shoulders) puts considerable stress on the front legs during the rocking action of canters where the body is thrust vertically into a period of flexed suspension at slow speeds with little body momentum. At a fast gallop the hind legs are required to increase their propulsive force (hence stress), the front legs displace the shoulders less vertically, and the front and hind lead changes approach the same frequency. As pronghorn maintain the rotary sequence of footfalls at fast galloping speeds, front and rear lead changes must occur together, hence leads change at the same frequency.

The changing of front and rear leads independently, resulting in a change from transverse to rotary canter or vice versa, appears to be unique to the pronghorn according to the available literature. The inference from the works of Jacobsen (1960), Grogan (1951) and Howell (1944) is that the horse retains the transverse footfall sequence, although front and rear lead changes occur regularly to postpone fatigue. It follows that front and rear leads must be changed simultaneously during the execution of one stride if the transverse footfall sequence is to be maintained. Reporting on lead changes in the horse and cheetah, Hildebrand (1959) states that lead reversal is usually accomplished by the forelimbs first but that the motion of the hind limbs must be coordinated to avoid the interference that would otherwise follow. Apparently leads are changed simultaneously because the cheetah maintains a rotogallop and the horse a transverse gallop. The pronghorn, however, even when maintaining a fast rotogallop will usually change the front lead during one stride and the rear lead during the following stride. Therefore, a stride consisting of a transverse footfall sequence is often interjected into the stride between front and rear lead changes.

When progressing faster than a walk, adult pronghorn and fawns usually employ the canter or gallop. Lack of heavy antlers and moderate body size are probably two reasons responsible for the selection of the asymmetrical canters and gallops as the most commonly used fast gaits. Dagg and de Vos (1968) point out that animals with heavy antlers or horns use the symmetrical trot more frequently than the gallop since the center of gravity changes less radically than in the gallop, and the heavy head is more easily controlled. They also point out that in a gallop all of the animal's weight must be launched into a period of suspension from one foot. Galloping, therefore, requires less energy for moderate-sized animals than for heavy ones. Inasmuch as the force of contraction of a muscle varies as the square of linear measure while the mass of the body varies as the cube of linear measure, largeness places muscles at a disadvantage. Although skeletal and muscular adaptations can help to reduce the load placed on the muscles of larger animals, size is still important. Pronghorn appear to be in the size range that is best suited for rapid locomotion.

The observation that pronghorn will usually crawl under or occasionally through a fence rather than jump over it has been reported by many writers. Pronghorn have, however, been reported to have jumped a six-foot (1.8 m.) trap fence (Buechner, 1950), a 34.3 inch (87 cm.) four-strand barbed wire fence (Bruns, 1969) and barriers up to and over eight feet (2.4 m.) high (Spillett et al., 1967). A study on the effects of various livestock fences on pronghorn movement (Spillett et al., 1967) concluded that, with few exceptions, pronghorn appear to be unaware of their ability to jump vertical barriers and rarely jump fences over 32 inches (81 cm.) high unless under severe stress or active pursuit.

It is a general consensus that the cheetah is the fastest of animals for a short sprint. Speeds of over 70 miles per hour have been reported for this remarkable cat. The pronghorn with recorded speeds of up to 60 miles per hour appears to be the fastest pecoran (ruminating artiodactyls) species followed by the smaller true antelope, with the cervids being the slowest of these families (Dagg and de Vos, 1968). Speed and endurance are both important factors in cursorial mammals such as the cheetah and pronghorn. The cats are typical short distance sprinters whereas the larger herbivores, particularly the horses and their relatives, are stayers par excellence among mammals (Slijper, 1966). Hildebrand (1959) reports that a horse ran 50 miles at an average speed of 15 miles per hour. Although pronghorn can only maintain extremely rapid speeds for a mile or so, they can run at approximately 30 miles per hour for eight or nine miles. Thus, the pronghorn with its moderate body size would appear to be a good sprinter with a good endurance capacity. Inasmuch as the length of stride varies in direct proportion to leg length but the intrinsic rate of muscle contraction, and hence rate of stride, varies inversely with linear measure (Hill, 1950), the pronghorn's body would appear to be a rather successful compromise with reference to size. It should be pointed out, however, that even animals the size of pronghorn must have considerable anatomical adaptations to make fast speeds possible: increased functional length of limb through unguligrade foot posture, limb muscles massed close to body to decrease the amount of energy needed to swing the long limbs back and forth, muscle insertions relatively near to the joints they move to produce limb velocities even though power is sacrificed, evolution of hinge joints (allowing motion only in the line of travel) accompanied by the elimination of most adductor, abductor and rotator muscles at the expense of more developed flexor and extensor muscles, to mention a few.

Functional Analysis of Body Structures

As speed increases (walk through gallop) the strike-departure angles of the legs of pronghorn become more acute and the paths followed by the front and rear hooves in relation to pivot points at the shoulder and hip scribe larger trajectory paths. The front legs (back legs as well) travel farther in moving to the ground from the position of maximum forward extension in fast gaits than in slower gaits, thus it can be assumed that they have a greater backward acceleration when they strike the ground. This results in less deceleration of the animal's body while in motion (Hildebrand, 1959). If a foot is placed on the ground with less backward speed than the forward speed of the whole body relative to the ground, the foot acts as a brake and the body drives the limb instead of the limb driving the body (Gray, 1953). A high stepping action is very important at high speeds as it reduces the amount of energy required to swing the limb forward (Gray, 1953). This is accomplished by flexing several of the leg joints, thus shortening the limb and decreasing the load on the muscles (Hildebrand, 1959). Keeping the front legs fully extended until contact with the ground is made facilitates the maximum stride length possible and increases speed. In all of the fast gaits employed by pronghorn, the front legs remain in full extension until contacting the ground. This is also true for the fast gaits of the horse and cheetah (Hildebrand, 1959).

Although the pronghorn's body levels out at fast galloping speeds and remains relatively close to the ground, there is still some vertical movement of the hips and shoulders. The vertical movement of the body is minimized by the cushioning effect of the digital ligaments when the pasterns are flexed (Camp and Smith, 1942) and by the muscles and tendons that suspend the thorax between the shoulder blades preventing excessive vertical movement of the forequarters as they pass over the stiff front legs which are pivoting on the support feet. The smoothness of the fast galloping gait probably results in a greater amount of energy being expended in moving the legs and less energy being used in raising the center of gravity.

As previously mentioned, the vertebral column of pronghorn and other large runners is relatively rigid to minimize stresses resulting from locomotor movements. The arrangement of vertebral processes restricts lateral bending of the spine restricting movement to the sagittal plane only (Slijper, 1946). Ottaway (1955) points out, however, that although movement of the back in such forms is mainly restricted to vertical flexion of the lumbo-sacral junction, slight lateral roll occurs which increases the stride somewhat. This slight lateral roll was more apparent in pronghorn employing a rotogallop, with its accompanying exaggerated ipsilateral overstride, than in those employing a transverse gallop. Perhaps this lateral roll, resulting in slight increase in stride length, is one factor involved in the pronghorn's exclusive use of the rotogallop at fast speeds.

Carnivores such as the dog and the cheetah have very supple spines that are sharply flexed and extended when running (Hildebrand, 1960). Hildebrand further points out that such an animal is several inches longer when the body is extended than when it is flexed and that by flexing and extending its back as its legs swing back and forth the animal increases its length of stride considerably. In the flexed position the chest-buttock length of the cheetah is only 67 percent of its length in the extended position, while the flexed length of the horse is 80-90 percent of its extended length (Hildebrand, 1959). At a fast gallop the chest-buttock length of a pronghorn during the flexed position is 79-80 percent of its length in the extended position. Although both the horse and the pronghorn have rigid backs, it would appear that the pronghorn utilizes its spine to a slightly greater advantage during fast gaits.

Inasmuch as the neck-back angles of pronghorn employing the canters and gallops are lower (more acute) than in the walking and trotting gaits but have a greater average difference between maximal and minimal values, the neck would appear to be playing a more important role in locomotion. This deduction is given more credence when one considers that it is only during the canters and the gallops that the neck moves backward and forward once for each complete stride (during the walk and trot the neck completes two cycles per stride), thus facilitating the shifting of the center of gravity as the series of leaps is executed. A possible reason for the speed advantage of the canters and gallops is that the rhythm of these gaits is timed so that the upward swing of the head helps advance the front leg by making greater use of the large brachiocephalic muscle passing from the skull to the humerus (Howell, 1944). The rhythm of the symmetrical walk and trot appears to be too fast for the movement of the neck to be of much help. The general patterns of neck movements for the walking and galloping gaits of the giraffe (Dagg, 1962) are similar to, but more pronounced than, those of the pronghorn.

According to skeletal proportions the pronghorn is a highly developed cursorial ungulate. Gregory (1912) reported femorometatarsal, femorotibial, humerometacarpal and humeroradial ratios for 56 different species of hoofed mammals including the pronghorn antelope. His ratios indicate that the giraffe is the most highly developed cursorial ungulate followed by the gazelle and then the pronghorn. Graviportal forms such as the elephant had very low ratios while most cursorial forms had ratios approaching or over 100. Some of his ratios for the pronghorn were slightly higher than those calculated in this study. As his method of measurement was not indicated, one can only speculate on the reasons for this discrepancy. Perhaps his measurements were not according to functional length, or maybe a skeleton of a younger animal was used for the measurements. The few pronghorn ratios reported by Howell (1944) are very similar to those of this study.

Skeletal proportions of pronghorn indicate that the newborn fawn is more specialized cursorially than its parent. Apparently individual skeletal elements of a limb grow at different rates because their ratios change as body size increases. Like most ungulates pronghorn are born in a very advanced state with flight being one of their chief means of defense. It would appear, therefore, that the ability of fawns to keep up with the herd and outrun pursuing enemies would be a very important factor in the survival of the species. Undoubtedly their adaptation for speed at a very early age is an important factor in fawn survival, and hence survival of the species.

SUMMARY AND CONCLUSIONS

1. The analysis of gaits and other related information was made by studying 16 mm slow motion movie film frame by frame through a viewer. Tracings of pronghorn made from successive frames of slow motion moving-picture sequences arranged in correct spatial relation to one another were used to analyze body movements.

2. The walking gait of pronghorn is a four-time symmetrical gait. Pronghorn employ the very slow, slow and fast diagonal walks. According to Hildebrand's symmetrical gait graph the corresponding terminology would be very slow, slow and moderate lateral-sequence, single-foot walks respectively. An increase in both length and rate of stride accounts for the increase in speed of the fast walk over the slower walks. Trots, canters and some gallops demonstrate the same phenomenon. In many fast galloping sequences, however, it was found that speed increase was a result of an increase in the length of stride but a slight decrease in rate of stride.

3. The trot is a two-time symmetrical gait with support being furnished by alternating diagonal pairs of limbs moving either in unison or approaching synchronization. In most trotting sequences the hind foot of a diagonal pair is in contact with the ground for a longer period of time (6 to 11%) than the front foot owing to the front legs of pronghorn being somewhat shorter than the hind legs. It is difficult, therefore, for a full stride of the hind legs to be matched by the front legs, particularly at fast trotting speeds. Lack of clavicle, associated with the incorporation of the scapula into the functional length of the forelimb, increases stride length of the shorter forelimb and makes it possible for the fore and hind limb movements to approximate symmetry in trotting and walking gaits. The pronghorn

employs the slow, moderate and fast running trots according to Hildebrand's graph. Several different footfall sequences are used by trotting pronghorn.

4. Trotting pronghorn spend most of each stride on diagonal supporting legs; the hind leg of a diagonal pair usually has a slightly longer interval of support. Diagonal support decreases and total suspension increases as trotting speed is increased. The average percentage time spent on diagonal pairs during a complete stride is less for pronghorn than for other pecoran species according to the literature; the total suspension time is greater.

5. The pronghorn employs the transverse and rotary canter, both having one phase of flexed suspension during each stride. These gaits can be executed in a variety of footfall patterns. At fast speeds the exclusive gait of the pronghorn is the rotary gallop having both a flexed and an extended period of suspension. In the cantering gaits of pronghorn, like those of larger animals, the duration of the flexed suspension phase decreases as speed increases. However, when a pronghorn increases speed from a fast canter to a gallop a period of extended suspension is incorporated into the gait and the total suspension time per stride is greater than for the moderate canter. As speed is increased footfalls are spread out and fewer phases occur in each stride consisting of four-leg and three-leg support but there is an increase in two and one leg phases.

6. According to the literature and the film analyzed in this study, it is apparent that through the process of evolution there has been a selection for certain types of gallops within phyletic lines. In most cases just one type of gallop has been selected. The pronghorn, however,

demonstrates great versatility in this respect employing both the transverse and rotary sequence of footfalls.

7. When pronghorn are running, the main propulsive thrust is produced by the hind legs and the forelegs are used more for support and stability.

8. Until a fawn is about two weeks old its gait repertoire is limited to a rather awkward rotary canter or gallop and a feeble walk. Their fast gaits average less suspension per stride than older animals and the straddling of front legs by hind legs is far more pronounced in fawns. Legs long in proportion to body, poor muscular and nervous coordination and rough terrain are thought to be partly responsible for the awkward appearance of fawn gaits. The footfalls of fawns are spread out over the stride in such a way that a large percentage of each cantering or galloping stride is spent on two legs, a very small percentage on three legs and no four-leg support is present. Galloping fawns have at least one foot on the ground all, or practically all, of the time for added stability.

9. The bound and half-bound are gaits rarely employed in their pure form by pronghorn. The bounding gallop is most often employed when initiating a rapid start. The symmetry of the gait is usually broken after a few strides resulting in a boundlike canter. When the bounding gallop is employed in its pure form the period of suspension is usually slightly greater than half of the total stride duration. The bounding gallop of mule deer was found to be very similar to that of pronghorn except that the magnitude of the bounds was greater in mule deer, and the frequency of the bounds somewhat less. Stotting was observed most frequently during the mating season.

10. Pronghorn change front and rear leads during the canter and gallop to postpone fatigue. At slow speeds the lagging hind foot and forefoot are usually on the ground for about the same length of time or slightly less than their leading counterparts. With increased speed the duration of contact of the lagging forefoot is reduced, while that of the lagging hind foot is increased to as much as, or more than, its leading counterpart. Lead changes usually occur most frequently at fast speeds. Front and rear leads usually change at about the same frequency. The actual lead changes are accomplished during the period (or periods) of suspension when the feet are off the ground. When changes in front and rear leads occur independently, the sequence of footfalls also changes and so does the type of canter or gallop, e.g., rotary canter to transverse canter. While maintaining a fast rotogallop a pronghorn will usually change the front lead during one stride and the rear lead in the subsequent stride, thus introducing one stride of a transverse gallop into the main rotogallop sequence.

11. When making a sharp turn a pronghorn will employ the rotogallop and lead with the inside forefoot. Leads are frequently changed a few strides in advance of a turn.

12. Changes from one gait to another are made very smoothly in pronghorn. Occasionally pronghorn will execute complete cycles of locomotion with only three of the four feet striking the ground during a change in gait. In all cases analyzed the leg being held through the stride was a front leg and was the first foreleg to strike the ground in the following stride. Apparently holding one front leg during the transitional stride of a gait change is often advantageous to the reorientation of legs in preparation for the footfall sequence of the new gait.

13. Pronghorn exhibit a considerable degree of synchronization in both lead and type of canter or gallop employed, especially when the members of the herd are closely bunched. There appears to be no correlation between the leading foot (left or right) and the type of gallop or canter being employed.

14. When progressing faster than a walk, adult pronghorn and fawns usually employ the canter or gallop. Trotting is most frequently employed to initiate and/or complete a burst of locomotion. Lack of heavy antlers and moderate body size are thought to be two reasons responsible for the selection of the asymmetrical gaits as the most commonly used fast gaits.

15. From the data collected it would appear that pronghorn will usually crawl under a fence rather than jump over it if the bottom wire is at least 17 inches (43 cm.) from the ground. Although pronghorn are often reluctant to jump vertical barriers, they have been reported to jump eight foot (2.4 m.) fences when pressed. Broad jumps of 20 to 25 feet (6.1 to 7.6 m.) to cross horizontal obstacles are relatively common.

16. It has been reported that speeds of up to 60 miles per hour can be reached and maintained for a short distance by exceptional pronghorn under ideal conditions. Speeds of 30 to 40 miles per hour can be maintained for several miles. The cheetah is undoubtedly the fastest mammal (recorded speeds of over 70 miles per hour) but the pronghorn is probably the swiftest ungulate.

17. The angles at which the legs strike and leave the ground become more acute as speed is increased from a walk to a gallop, resulting in the pronghorn getting lower to the ground with each leg moving through a greater arc while in contact with the ground. This enables the propelling

limbs to exert their propulsive effort through a relatively longer swing. The feet are lifted higher at fast speeds than at slower speeds. Therefore, the legs travel farther and faster in moving to the ground and cause less deceleration of the animal's body. The front legs are kept fully extended until contact is made with the ground, thus extending the length of stride to its maximum limit. Limited data indicate that the leading feet (front and rear) usually scribe a larger trajectory path in relation to the body than do their lagging counterparts.

18. As speed increases from a canter to a gallop, the pronghorn's body levels out somewhat and remains closer to the ground. Thus, a greater amount of energy is expended in moving the legs and less energy used in raising the center of gravity. Vertical movement of the body is reduced by flexion of pasterns and by the thorax being suspended by muscles and tendons between two pillars formed by the leg bones and shoulder blades.

19. Movement of the spine in pronghorn, as in most ungulates, is limited to vertical flexion of the posterior lumbar region near its juncture with the sacrum. As speed increases the degree of spine flexion also increases and a larger stride is accomplished. The chest-buttock length is indicative of the degree of spinal flexure and hence speed. At a fast gallop the chest-buttock length of a pronghorn during the flexed position (flexed suspension phase of stride) is approximately 79 to 80 per cent of its length in the extended position (extended suspension phase of stride), compared to 80-90 per cent for the horse. It would appear, therefore, that the pronghorn utilizes its spine to a slightly greater advantage during fast gaits than does the horse. Carnivores such as the dog and cheetah have very supple spines that are

flexed and extended to a greater degree than the more rigid spines of ungulates. Lateral flexion of the pronghorn's spine, although very slight, appears to be more pronounced during the rotogallop. Perhaps the slight increase in stride length resulting from this lateral roll is one factor involved in the pronghorn's exclusive use of the rotogallop at fast speeds.

20. In the gaits faster than a walk the average neck-back angles are greater (head held more erect) in the trot and slower canters than in the fast canter and gallop, but the average difference between maximal and minimal values is greater in the faster gaits. Therefore, the head has more vertical movement in the faster gaits and appears to play a larger role in the shifting of the center of gravity and in the maintenance of equilibrium. During the canters and gallops the neck moves backward and forward once for each complete stride, while in the walk and trot the neck completes two cycles per stride and probably plays a lesser role in locomotor progression.

21. The skeleton of the pronghorn exhibits the basic cursorial adaptations that are found in other ungulates of similar body conformation. Lack of dew-claws in pronghorn is an adaptation to hard dry terrain. Skeletal proportions as indicated by various indices show that fawns are more specialized cursorially but not as well adapted for jumping as adult pronghorn. Comparisons of indices related to jumping ability were made between the pronghorn and the saltatorially adapted mule deer to give a better indication of adaptations for jumping. Adaptation for speed at a very early age is of value to an ungulate such as the pronghorn where flight is one of the chief means of defense.

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APPENDIX I

Table A. **Length, in millimeters, of mule deer limb bones for various sexes and ages.**

Sex	Age	Humerus	Radius	Olecranon	Metacarpal	Lateral digit (Manus)	Medial digit (Manus)	Scapula	Femur	Tibia	Metatarsal	Lateral digit (Pes)	Medial digit (Pes)	Calcaneum
♂	10 yrs.	230	257	66	231	86.5	86	250	289	346	282	93.5	91	77
♀	3 yrs.	188	208	65	201	87	86.5	165	242	285	337	92.5	91.5	65
♂	Juv.	175	195	--	190	73.5	72.5	---	225	264	229	80	79.5	—

Table B. **Length, in millimeters, of mule deer phalanges for various sexes and ages.**

		Manus				Pes			
Sex	Age	First lateral phalanx	First medial phalanx	Second lateral phalanx	Second medial phalanx	First lateral phalanx	First medial phalanx	Second lateral phalanx	Second medial phalanx
♂	10 yrs.	55	55	38	37.5	59	58.5	41	40
♀	3 yrs.	53.5	53.5	38	38	57	57	41	40.5
♂	Juv.	46.5	46	32.5	32.5	50.5	50.5	35	34.5

Table C. Limb segments of mule deer expressed as per cent of total limb length.

		Front leg				Hind leg			
Sex	Age	Humerus	Radius	Metacarpus	Phalanges	Femur	Tibia	Metatarsus	Phalanges
♂	10 yrs.	28.5	32.0	28.7	10.8	28.6	34.3	27.9	9.2
♀	3 yrs.	27.5	30.4	29.4	12.7	28.2	33.3	27.7	10.8
♂	Juv.	27.6	30.8	30.0	11.6	28.2	33.1	28.7	10.0

Table D. Skeletal proportions of mule deer as indicated by a few selected indices.

Sex	Age	Metapodial Index	Leg Index	Intermembral Phalangeal Index	Scapular Index	Olecranon Index	Calcaneum Index
♂	10 yrs.	82	80	93	25	11	21
♀	3 yrs.	85	80	94	24	13	20
♂	Juv.	83	79	92	--	10	--