ABSTRACT

LEG MUSCLES AND THEIR FUNCTION: A COMPARATIVE STUDY IN COTURNIX AND BOBWHITE

By

Wayne V. Shooks

Although considerable work has been done on the leg muscles in birds, there are many groups and individual birds yet to be described. Furthermore, little is known about the functional aspects of leg muscles in vivo.

This study was undertaken to describe the gross morphology and function of the leg muscles in Coturnix (*Coturnix coturnix japonica*) and to compare the results with Bobwhite (*Colinus virginianus*).

Muscle origin, insertion, weight, and location are described in detail for Coturnix, followed by a comparison with Bobwhite. The action of each muscle is discussed.

Deductions of muscle action are based indirectly upon pulling of the tendon of freshly killed specimens. Muscle action was analyzed directly through experiments involving photographic analysis of motion pictures made of the walking pattern of birds in which the tendon of the

muscle being studied was cut. These results were compared to those of birds which had had a sham operation. Track patterns of the experimentals and shams were made and analyzed.

Based on the number of sesamoids, Coturnix is apparently not closely related to Bobwhite or to other gallinaceous birds. However, based on other characters such as the presence of M. adductor digiti II, Coturnix resembles other Phasianidae sufficiently to be placed in that family.

Differences between the Blue Grouse (Dendragapus obscurus) descriptions of Hudson et al. (1959) and my descriptions of Coturnix which could not be resolved as species variations included: (1) the insertion of M. adductor digiti II on the lateral side of digit II rather than on the medial side; and (2) the origin of M. popliteus on the tibiotarsus rather than on the fibula. The drawings of Hudson et al. (1959) from the lateral view failed to show M. ambiens after the removal of M. femoritibialis medius and appear to have the muscle lengths of MM. flexor perforans et perforatus digiti II and III reversed.

Muscle weight, which was used to determine the importance between size and action, was found to be variable. This problem was overcome by using several birds of the same age and genetic stock and obtaining a mean weight for each muscle. However, this is not possible in all studies, so I believe that for all future works a standardized formula should be used to determine muscle size:

$$\text{muscle size} = \frac{\text{individual muscle belly weight}}{\Sigma\text{belly weight of all leg muscles}}$$

Coturnix and Bobwhite each has its own species-specific locomotor pattern, which is similar from the time of hatching throughout life, with the exception of footstep length and footprint size. These characteristics increase rapidly after hatching and resemble the adults by seven weeks of age.

Coturnix and Bobwhite exhibit similar abnormalities in walking patterns following severance of a particular muscle.

Muscles were divided into four groups on the basis of their importance in walking: (1) those vital to survival in the wild; (2) those in which loss would result in greatly reduced chances of survival in the wild; (3) those that reduce efficiency, but are not vital to survival; and (4) those that have no effect on survival.

Importance of a muscle in walking was not necessarily correlated with muscle size or strength. The muscle formula devised by Garrod (1873) and expanded by Berger (1957) does include those muscles which were found to be of least importance in walking.

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While the muscle formula appears to have validity, the workers will be more apt to use computer analysis to make conclusions about avian phylogeny in the future. Workers who use numerical evaluations plugged into a computer are urged to refine their techniques to avoid overemphasizing leg muscles which are subject to a large amount of adaptation.

I suggest that this can best be accomplished by weighting the muscles of the muscle formula as proposed by Garrod (1873) and expanded by Berger (1957).

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INTRODUCTION

The purpose of this study was to compare leg muscles and their functions in *Coturnix coturnix japonica* and *Colinus virginianus* through the use of cinematography, track patterns, and analysis of fresh specimens.

There is a need for a fresh approach to the study of leg muscles and their function. In the past, the emphasis has been on anatomical studies based on preserved specimens.

Anatomical studies have passed through several phases of development. The earliest studies were done primarily to provide information in a descriptive sense about various muscles in birds. Hudson (1937) provides an excellent historical account of the development of this descriptive period.

Around the middle of the nineteenth century muscles were used to facilitate classification of birds. Sundevall (1851) isolated the Passeriformes from other birds on the basis of the absence of a vinculum between the flexors of the foot. Somewhat later Garrod (1873, 1874a) observed considerable variability in the presence or absence of particular leg muscles and on this basis proposed his muscle formula. This muscle formula had a major impact on subsequent studies and probably reached a peak when Hudson (1937) proposed additional muscles to supplement the original formula.

Berger (1959) expanded the formula by adding other muscles, but pointed out that probably the chief value of his expansion was to call attention of researchers to those muscles that exhibit the greatest variability.

Following Garrod's pioneer work there was a major surge in muscle studies which continued through the latter portion of the nineteenth and early part of the twentieth century. Many noteworthy descriptive studies which aided in classification were published. Garrod (1874b, 1874c, 1875, 1877, 1879) led the way with many additional studies of leg myology in several groups of birds. Beddard (1889, 1890, 1891, 1896a, 1896b) did a series of papers in which he classified birds by using the myological formula as his major criterion. In Beddard's (1898) ambitious attempt to classify all the known birds he used the muscle formula as one of his basic guidelines. Forbes (1882) studied the myology of some of the petrels, while Mitchell (1894, 1913) examined the flexor muscles and emphasized the importance of the peroneal muscle in classification. Fürbringer (1886, 1888) described many muscles including those of the leg. The only comprehensive myological work done in the United States during this period was that of Shufeldt (1890) on the Raven.

In the twentieth century, evolution became the motivating force for the study of muscles. The initial impetus was probably furnished by Howell (1936, 1938) who emphasized evolutionary relationships of vertebrate groups and whose influence carried over to others. Miller (1937), for example, studied the myology and adaptations of the Hawaiian Goose (Nesochen sandvicensis) and then through comparison with other geese proposed its evolutionary relationships. Burt (1930) analyzed adaptations in woodpeckers, including the leg muscles, and concluded that there were two major lines of descent. Fisher (1946) examined phylogenetic relationships of vultures. There were several other investigations which followed this general pattern and included leg myology, at least in part, as evidence for the conclusions reached (Avery, 1951; Berger, 1952, 1953, 1956a, 1956b, 1956c, 1957; Fisher and Goodman, 1955; Gaunt, 1969; Holmgren, 1955; Stallcup, 1954).

Hudson et al. (1959, 1964), increasingly aware of evolutionary relationships, applied numerical evaluations to taxonomic studies. In an even more extensive attempt to unravel the evolutionary relationships between groups of birds, Hudson et al. (1966, 1969) applied computer analysis to studies of bird appendages.

Unfortunately, this last approach, when done on preserved specimens, tends to restrict one to the evolution which has happened, subsequently ignoring what is taking place at the present time in an evolutionary sense. To understand what is occurring in evolution, one must look at the muscle in terms of function. For some reason this latter approach has been ignored. The point may readily be illustrated by the fact that George and Berger (1966) fail, in their book, to deal with muscle function at the gross anatomical level.

This is not to say that muscle function has been totally ignored. Watson (1869) decided to cut the M. ambiens in some chickens to challenge Borelli (1680) who had suggested that the M. ambiens was the perching muscle. Stolpe (1932) did research on joint mechanics which indirectly related to muscle function. Steinbacher (1935) studied muscle functions in the feet of various types of birds. Hudson (1937) mentioned what he considered to be the muscle function of each of the leg muscles. Berger (1952) analyzed muscle function in _Coccyzus_ and _Geococcyx_, applying general mathematical concepts to their types of locomotor movement. Miller (1937) analyzed the function of leg muscles in the Hawaiian Goose while Richardson (1942) did a similar study in woodpeckers. Both apparently based their results solely on the use of alcoholic specimens. Fisher (1957) pointed out that the results of gross dissection and study of muscle attachment, are frequently inconclusive and inaccurate because of differential action of the muscle and synergistic action of other muscles.

Therefore, Fisher cut the M. piriformis in vivo and studied the action of the muscle before and after this severance.

In contrast to the gross anatomical studies of muscle function, a more recent innovation at the other extreme of the continuum is the histophysiological approach, which emphasizes photomicrography plus histochemical and biochemical techniques. On the basis of fiber diameter, myoglobin content, metabolite load, and lipase and succinic dehydrogenase levels, George et al. (1965) attempted to explain the "nature" of the muscle function at the molecular level. While most of the work in this area pertains to flight muscles, Chandra-Bose (1967) used this method to study the M. gastrocnemius of a few birds.

Thus there exists a great gulf between the gross morphological studies and the molecular studies. There is a need to fill this void particularly in the nonhuman element of the animal kingdom. The physical education personnel, long interested in improving performance, have studied locomotion and muscle function. They have used cinematography to study locomotion and electromyography to investigate muscle function. By inserting a pair of electrodes in the muscle and then observing the electrical potential during a particular movement, one is able to deduce muscle function. Basmajian (1967) points out the real problem with this approach is the fact that the results are often difficult to interpret. Locomotor studies in physical education have been undertaken merely to improve performance of the individual, rather than to determine muscle function. Medical personnel have also been interested in muscle function and locomotor analysis because of their value in physical therapy and rehabilitation of patients.

The interest in locomotor analysis in birds through the use of some form of cinematography dates back to the nineteenth century. Hellbrandt (1960) points out that Leland Stanford, Jr. of California, who was interested in training race horses, hired Eadweard Muybridge to study the horse in motion. According to Hellbrandt (1960), Muybridge did this by having the horse run past a series of cameras placed parallel to the line of motion. As the horse passed each successive camera it broke a thread which tripped the shutter. Marey (1882, 1883) seized upon this concept and applied it to locomotor analysis of birds. Bangert (1960) studied the locomotor pattern of baby chicks. However, in no instance has there been an attempt to use locomotor analysis through cinematography as a tool to gain understanding of muscle function. By photographing and analyzing birds in which individual muscles have been cut, an understanding of the function of each muscle and its importance to the bird can better be understood. Therefore this study not only is an attempt to increase knowledge of muscle function in vivo, it is also an attempt to discover the importance of the individual muscles to the bird and consequently to the dynamic process of evolution.

Furthermore, a comparison of the leg myology of Coturnix was made with that of the Bobwhite. By correlating the new knowledge obtained about Coturnix with that which is known about Bobwhite from this and previous studies, it is hoped that the information obtained may help clarify the taxonomic position of Coturnix.

Finally, this study attempts to substantiate and broaden the work which Hudson et al. (1959, 1966) have done on the pelvic limb myology of galliform birds.

METHODS

Subjects

Birds used in this study were captive Coturnix (*Coturnix coturnix japonica*) and Bobwhite (*Colinus virginianus*) quail. For the sake of brevity, throughout the text the birds are referred to as Coturnix and Bobwhite.

All birds were obtained from the Department of Poultry Science at Michigan State University, East Lansing, Michigan. The birds, ranging in age from 0 to 33 months, were kept in a Petersime Brood Unit. Coturnix and Bobwhite used in muscle dissection and muscle severance portions of this study ranged in age from 11 to 16 months unless otherwise noted. All birds were fed a commercial preparation of quail breeder mash and had water available at all times.

Operative and postoperative care

Ether was used as the general anesthetic. The wing feathers were clipped and the bird was strapped by a sterilized gauze bandage to the surgical tray. The leg to be cut was held in place under the dissecting microscope by a sterilized gauze bandage tied from the leg to an adjacent stand. The leg was plucked of feathers and washed with an antiseptic followed by swabbing with alcohol.

All instruments were sterilized and the dissecting microscope was scrubbed with antiseptic solution to reduce the possibility of infection. A small incision was made through the skin in the appropriate area and the tendon or fleshy insertion of the muscle in question was isolated. In four Coturnix this tendon or fleshy insertion was then cut and in the fifth bird it was not. This fifth bird provided a sham operation. The same procedure was repeated on the other leg of all birds and care was taken to keep the entire procedure a constant length for a given muscle.

In Bobwhite the experimental procedure was the same for the M. gastrocnemius, M. tibialis anterior, and M. peroneus longus. In the remaining muscles the number of birds was reduced to one experimental and one sham.

The birds were then placed in a recovery box for one hour after which they were put back into a Petersime Brood Unit. They remained there until motion pictures and track patterns were made between 30 and 42 hours after the initial operative procedure had begun.

Just prior to the taking of the motion pictures, the tarsometatarsus joint and the posterior surface of the thigh were marked with a felt marker to assist in analyzing the film. After filming and tracking were completed, the birds were sacrificed to ascertain that only the appropriate cut had been made. This procedure was carried out on all leg muscles unless otherwise specified.

Determining locomotor pattern

To determine the walking pattern of the birds, slow motion photography and track patterns were employed. The birds were released on a track which they traversed while motion pictures were taken of their movements. The track consisted of a box 101 cm. long, 21 cm. deep, and 40 cm. high. The front and sides of the box were removed and a piece of gray illustration board was attached to the back. A grid pattern was constructed on the surface of the illustration board using 3.2 mm. wide Chart-Pak tape spaced 12 mm. apart. The substrate on which the birds walked consisted of a firm wood surface covered by a shag rug.

The 16 mm. Pallaird Bolex camera with a 70 mm. single reflex zoom lens was mounted two meters in front of the track on a tripod which could be moved parallel to the track. A 650 watt flood light was mounted directly above the camera. All motion was recorded at 64 frames per second using Kodak Plus-X Reversal film.

The film was analyzed by using a Centapix SR single frame motion picture analyzer. The step was divided into 13 different parts and only those 13 frames which correlated to those parts of the step were analyzed. These were: (1) last frame where digits of the right foot are completely on the substrate; (2) digits of the right leg clearly beginning to be lifted off substrate; (3) last frame before the digits of the right leg are totally free of the substrate; (4)

digits of the right leg pass the left leg; (5) right leg reaches its highest point anteriorly; (6) last frame before digits of right leg make contact with the substrate; (7) first frame where digits of right leg complete contact with the substrate; (8) digits of the left leg clearly beginning to be lifted off substrate; (9) last frame before the digits of the left leg are totally free of the substrate; (10) digits of the left leg pass the right leg; (11) left leg reaches its highest point anteriorly; (12) last frame before digits of left leg make contact with the substrate; (13) first frame where digits of left leg completes contact with the substrate.

For each frame analyzed, the angle at the distal end of the shank and proximal end of the tarsometatarsus was recorded. Hereafter that angle is referred to as the tarsometatarsus angle and merely the tarsus on the graphs. The angle of the posterior portion of the shank, using the line horizontal to the substrate as a reference line, was also recorded. In addition, the total angle of the leg from the tip of the third digit to the base of the tail was recorded by using a line perpendicular to the substrate as the reference line. The angle of the hallux to the tarsometatarsus was also recorded. Also the angle of the digits was measured from the tip through the highest point using a line parallel to the plane of the substrate as the reference line. The angle of the digits was considered to be 180 degrees if perfectly flat; as flexion increased this angle decreased. In the event the digit was inverted, the line was drawn through the lowest point and this angle was considered greater than 180 degrees.

One step of each of the four Coturnix experimentals and two steps of the Coturnix sham were analyzed. From these numbers a mean value for each measurement at each frame was obtained. The Bobwhite were used as comparisons, so only one experimental and one sham footstep were analyzed unless there appeared to be a difference from that found in Coturnix.

The information on the angle of the tarsometatarsus joint, digits, and hallux could be directly plotted on graphs; however, the angle formed at the distal end of the thigh and the proximal end of the shank, which hereafter is referred to as the tibiotarsus angle and merely as the tibia on the graphs, had to be extrapolated from other information that had been obtained. Likewise the angle formed at the proximal end of the thigh had to be extrapolated indirectly from the data obtained, since the loose skin on this part of the bird made direct measurements impossible. This angle is referred to as the angle of the femur in the remainder of this paper and merely the femur on the graphs.

To find the angles of the tibiotarsus and the femur, a model was constructed to duplicate the movement of the leg. Since the approximate length of the bones, the size of the leg, and the heretofore mentioned angles that were measured are known, the model can be set in the appropriate position and the angles sought can be directly read from the model. The two angles sought were extrapolated in the following manner. The angle of the femur was measured using a reference line perpendicular to the axis of the pelvic girdle at the level of the acetabulum. A point just distal to the base of the pelvic girdle was selected as the vertex and the angle formed between the perpendicular reference line and a line drawn to the point of division between the shank and thigh calculated. The angle of tibiotarsus was measured using the posterior surface of the shank as the one line, the point of division between the thigh and shank as the vertex, and a line drawn from this vertex to the vertex used to construct the angle of the femur. These angles were also plotted on graphs.

The track pattern was obtained by allowing the birds to walk on a transparent plastic surface covered by a thin layer of moist kitchen cleanser. When the cleanser dried the tracks made were transferred to transparent plastic sheets by tracing over the footprints with a felt marker.

Preparation of specimens for analysis

For description of muscle function through analysis of fresh specimens, one Bobwhite and one Coturnix were killed at the same time so that muscle action could be compared simultaneously. The tendon of the muscle being checked was then pulled and a description made. No bird was used for more than 30 minutes after death for this purpose.

Each muscle description was based on a dissection of at least four preserved specimens which varied in age from 11 to 24 months. These specimens were placed in a 10 percent formalin solution for eight hours, rinsed in fresh water for two hours and then placed in a 70 percent ethyl alcohol solution until used. In some instances fresh specimens were used in dissection since differences in color of muscles help isolate them.

Drawings were traced from actual projections made of the muscles by using a modified overhead projector. To prepare the specimens for this procedure the bird was sacrificed, the skin was removed and the exposed muscles were moistened immediately with a buffered formalin solution. They were kept moistened throughout the dissection and subsequent projection for tracing.

Skeletons for study and drawings were made from fresh specimens. The bird was killed, much of the muscle and viscera were removed, and then the bird was placed in a mixture of three parts of a bioenzyme soap to one part meat tenderizer. The solution was changed every two days until the remaining flesh was readily removed. (The length of this time is a function of the temperature; the higher the temperature, the shorter the time.)

Muscle weights were taken on eight specimens of each species. Birds were sacrificed, the muscles removed one at a time and weighed. Only the belly of the muscle was weighed. Weights were made to the nearest .0001 grams and rounded back to the nearest .001 grams. Caution was taken to keep the skin cover over the areas of the leg not being dissected to prevent drying out.

Hudson et al. (1959) was used as the main reference for all descriptions, drawings, and muscle abbreviations. In this way it is hoped that the information gathered in this paper can readily be compared to that already obtained by Hudson and his students. And at the same time the differences between Hudson's interpretations and mine can be quickly isolated for evaluation.

RESULTS AND DISCUSSION

Natural history of Coturnix and Bobwhite

In order to interpret better the meaning of variations of muscles and their function in terms of their importance in an evolutionary sense, it is necessary to summarize briefly the natural history of Coturnix and Bobwhite.

Distribution

Since Moreau and Wayre (1968) pointed out there is confusion on just what birds of the Far East constitute the species *Coturnix coturnix*, it is difficult to be certain of their range. The birds used in this study definitely occur in Japan and may be the same species as those of the far eastern mainland from Lake Baikal to Korea. Aldrich (1946) stated that the Bobwhite, including all the subspecies, occur over a vast area of the eastern, midwestern, and southern United States and southward through Central America.

Habitat

Yamashina (1961) indicated that Coturnix live on grasslands, riversides, and on seashores that have thick grass. According to Stoddard (1931), Bobwhite occur in open woodland, marshes, cultivated fields, and brushy regions wherever food is available.

Locomotion

Coturnix are poor fliers and when flushed fly only short distances (Yamashina, 1961). They depend primarily on their legs to move from one location to another. Stoddard (1931) states that Bobwhite are fast fliers, but are not capable of long sustained flights. Because they are rapid runners, flight is not essential to their survival except when escaping certain enemies.

Foraging

According to Etchecopar and Hue (1967), Coturnix are primarily seedeaters, taking an occasional insect. In captivity they were fed Quail breeder which contained some grain beetles which they ate eagerly. Judd (1905) found that approximately 80 percent of the Bobwhite diet was vegetative, consisting of grain, weedseeds, and fruits, while the remainder of the diet consisted of insects.

Reproduction

Coturnix in captivity are prolific producers of eggs at an early age. They begin laying at between 40 and 50 days of age and lay up to 200 eggs during their first year. Yamashina (1961) notes that in the wild Coturnix lay a clutch of seven to eight eggs. Bobwhite do not begin laying in captivity until six months of age even though Stoddard (1931) points out they reach a mature weight by 15 weeks. According to Bent (1932) Bobwhite clutch size ranges from 12 to 20 eggs.

Development and comparison of walking of Coturnix and Bobwhite

Coturnix and Bobwhite are precocial at hatching. Motion pictures taken within 24 hours after hatching indicate that the walking locomotor pattern of the young resembles that of the adult. Motion pictures taken of other age groups indicate that this general pattern of walking is continuous throughout life.

The basic differences observed between the young birds and the adults were that the young had a reduced step length and a smaller sized footprint. However, young Bobwhite develop rapidly, and young Coturnix even more rapidly, so that by seven weeks of age the step length and track pattern size resemble that of the adults.

There were differences in the walking locomotor pattern of Coturnix and Bobwhite. Coturnix flexes its digits to a greater degree than Bobwhite as the foot moves anteriorly. The tarsometatarsal angle is slightly smaller in Coturnix when standing, but the tarsometatarsal angle is greater in Coturnix as the leg reaches its highest point forward. At this highest point forward the digits are flexed more in Coturnix than in Bobwhite. In fact, at this point digit III is frequently inverted in Bobwhite.

When the foot is on the substrate, Coturnix bends its digits about 15 degrees in order that the nails may make contact with the substrate, while Bobwhite bends its digits only 10 degrees to make contact with the substrate. Coturnix has a smaller footprint and also takes a slightly shorter step when walking than does the Bobwhite.

Osteology of the hind limb

The pelvic girdle and limb of Coturnix (Figures 1 and 2) have the same general anatomical features as Bobwhite. Two osteological variations which are of importance to this study are the longer bones and larger nails on the foretoes in Bobwhite. The longer bones make it possible for the Bobwhite to take a longer step, while the longer nails make possible a reduction in the amount of flexion of the digit necessary to reach the substrate.

Muscles and their function

Since there is no justifiable reason to arrange the muscles in any one particular sequence, the arrangement of the muscle descriptions follows that used by Hudson et al. (1959). Muscle weights are given as the mean followed by standard error. All weights are rounded to the nearest

Figure 1.--(Coturnix coturnix japonica) Lateral view of the left half of the pelvic girdle and the left pelvic limb.

Abbreviations for pelvic girdle and limb:

ant. il. crest = Anterior iliac crest.

cap. fib. = Caput fibulae.

caud. vert. = Caudal vertebrae.

ext. condyle = External condyle.

fov. il. ant. = Fovea iliaca anterior.

ilio-isch. fenestra = Ilio-ischiatic fenestra.

inn. cn. crest = Inner cnemial crest.

med. dors. ridge = Median dorsal ridge.

post. il. crest = Posterior iliac crest.

obt. foramen = Obturator foramen.

out. cn. crest = Outer cnemial crest.

spine of fib. = Spine of Fibula.

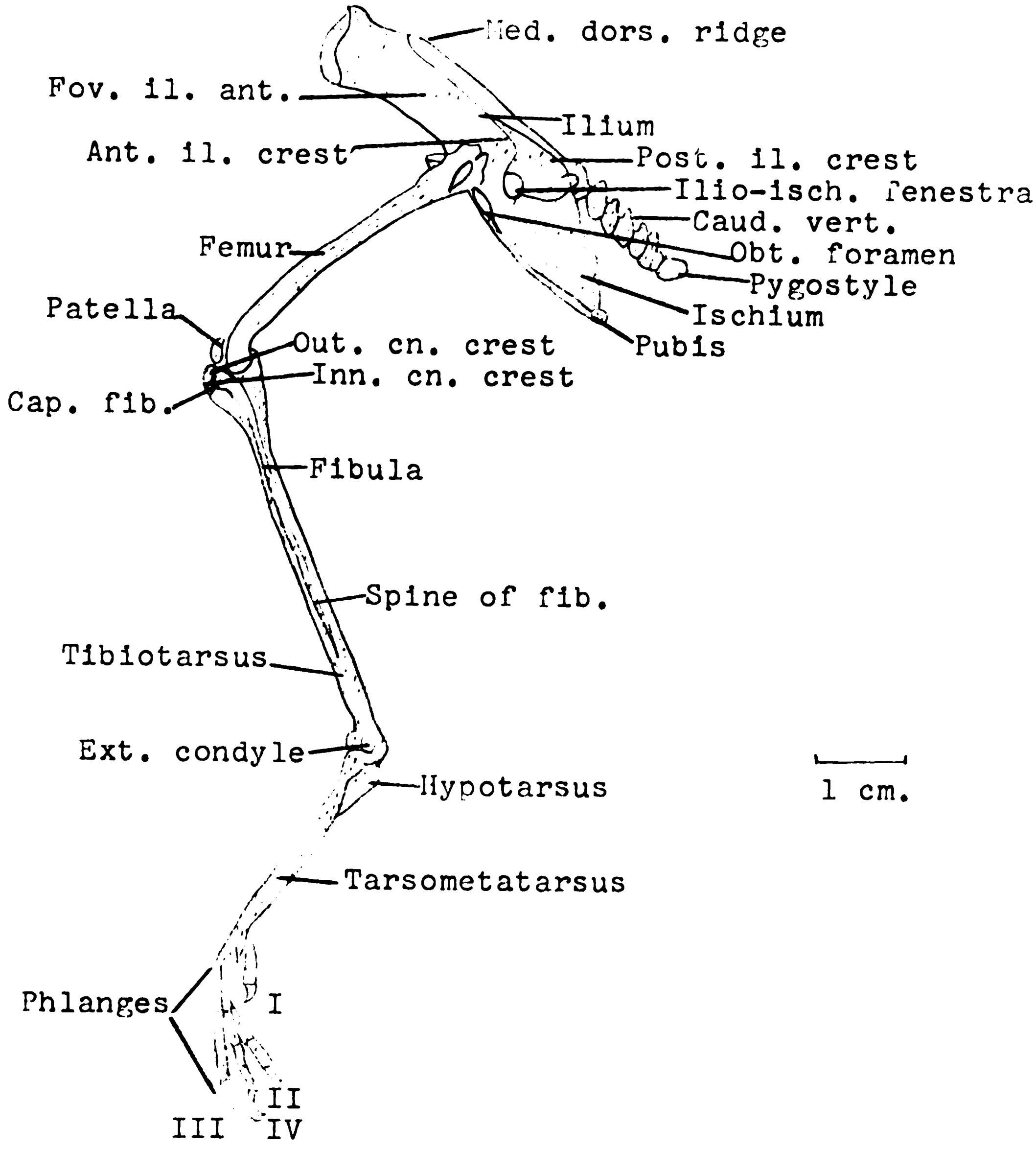
Med. dors. ridge
Fov. il. ant.
Ilium
Ant. il. crest
Post. il. crest
Ilio-isch. fenestra
Caud. vert.
Femur
Obt. foramen
Pygostyle
Patella
Ischium
Pubis
Out. cn. crest
Inn. cn. crest
Cap. fib.
Fibula
Spine of fib.
Tibiotarsus
Ext. condyle
Hypotarsus
1 cm.
Tarsometatarsus
Phlanges
I
II
III
IV

Figure 1

Figure 2.--(*Coturnix coturnix japonica*) Medial view of the left half of the pelvic girdle and the left pelvic limb.

Abbreviations for pelvic girdle and limb:

ilio-isch. *fenestra* = Ilio-ischiatic fenestra.

int. *condyle* = Internal condyle.

med. *dors*. *ridge* = Median dorsal ridge.

obt. *foramen* = Obturator foramen.

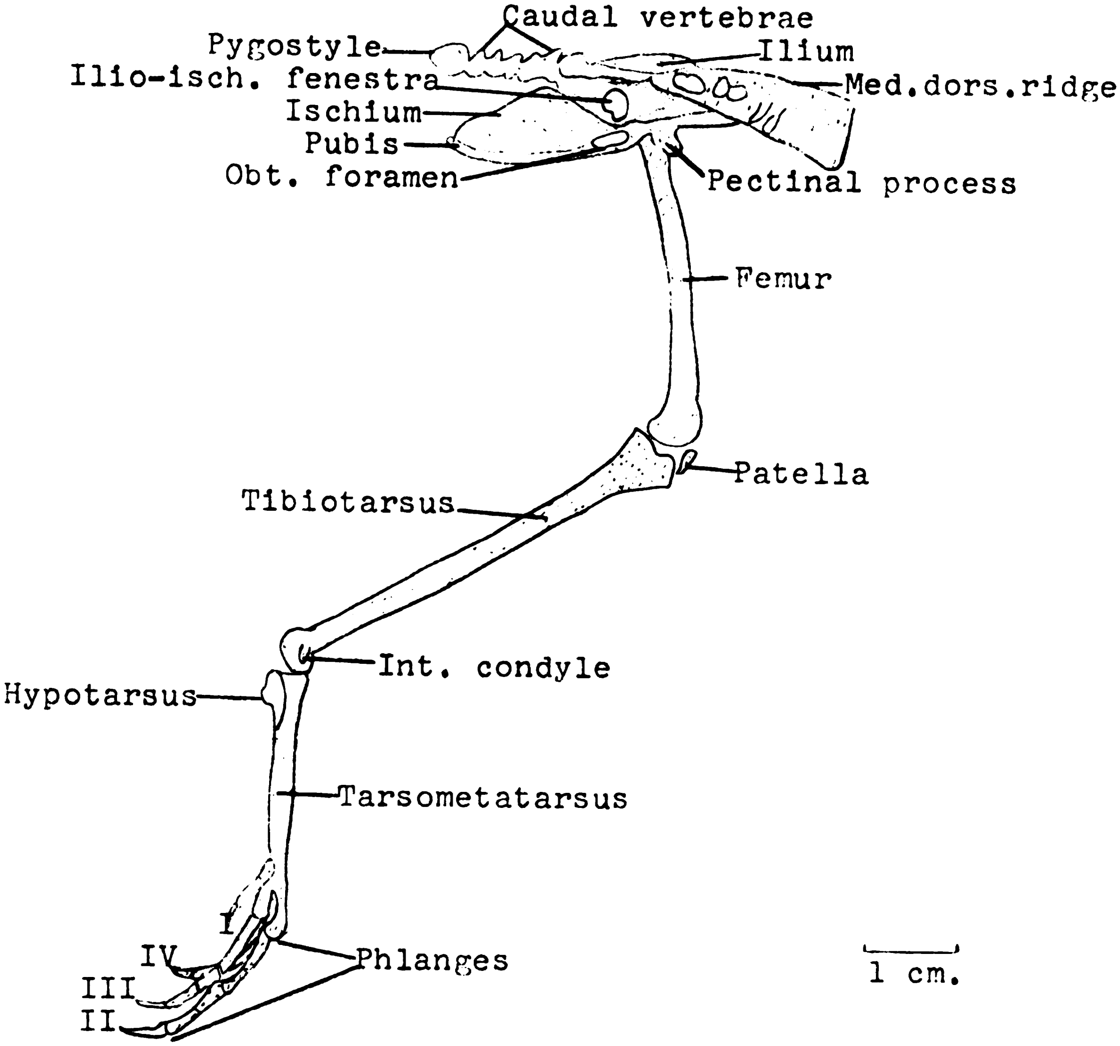
Caudal vertebrae
Pygostyle
Ilium
Ilio-isch. fenestra
Med.dors.ridge
Ischium
Pubis
Obt. foramen
Pectinal process
Femur
Patella
Tibiotarsus
Int. condyle
Hypotarsus
Tarsometatarsus
I
IV
III
II
Phlanges
1 cm.

Figure 2

.001 grams. Generally the muscles of Coturnix and Bobwhite are similar; in those cases where they are not, the variations are pointed out.

M. iliotrochantericus posterior

Description for Coturnix and comparison with Bobwhite.--(Figures 4, 5, 7, and 8.) This, the largest of the iliotrochantericus muscles, is located at the anterior proximal end of the femur below the M. sartorius and the aponeurosis of the M. iliotibialis. It occupies the anterior iliac fossa. It originates fleshy from the anterior iliac fossa and iliac crest, the belly remaining fairly wide up to the very short, stout tendon which inserts on the lateral surface of the trochanter of the femur. Coturnix Wt.: ♂0.367 ± 0.024, ♀0.384 ± 0.017; Bobwhite Wt.: ♂0.684 ± 0.025, ♀0.791 ± 0.086.

Action.--In Coturnix and Bobwhite this muscle pulls the head of the femur inward and slightly forward at the same time, thus causing the posterior portion of the thigh to move outward and forward. When the tendon was cut, differences in the track and locomotor pattern when walking were not measurable, but this muscle appeared to be more important in preventing leg rotation than in pulling the thigh forward.

M. iliotrochantericus anterior

Description for Coturnix and comparison with Bobwhite.--(Figures 4, 5, 6, 7, and 8.) This triangular muscle

Figure 3.--(*Coturnix coturnix japonica*) Lateral view of the superficial muscles of the left thigh and shank.

Abbreviations for muscles (after Hudson et al., 1959):

bic. *fem*. = M. biceps femoris.

f. *dig*. *l*. = M. flexor digitorum longus.

f. *p*. *et* *p*. *d*. *II* = M. flexor perforans et perforatus digiti II.

f. *p*. *et* *p*. *d*. *III* = M. flexor perforans et perforatus digiti III.

gas. (*p*. *ext*.) = M. gastrocnemius (pars externa)

gas. (*p*. *int*.) = M. gastrocnemius (pars interna)

il. *tib*. = M. iliotibialis.

per. *brev*. = M. peroneus brevis.

per. *long*. = M. peroneus longus.

pirif. (*p*. *caud*. *fem*.) = M. piriformis (pars caudofemoralis).

sar. = M. sartorius.

semit. = M. semitendinosus.

tib. *ant*. = M. tibialis anterior.

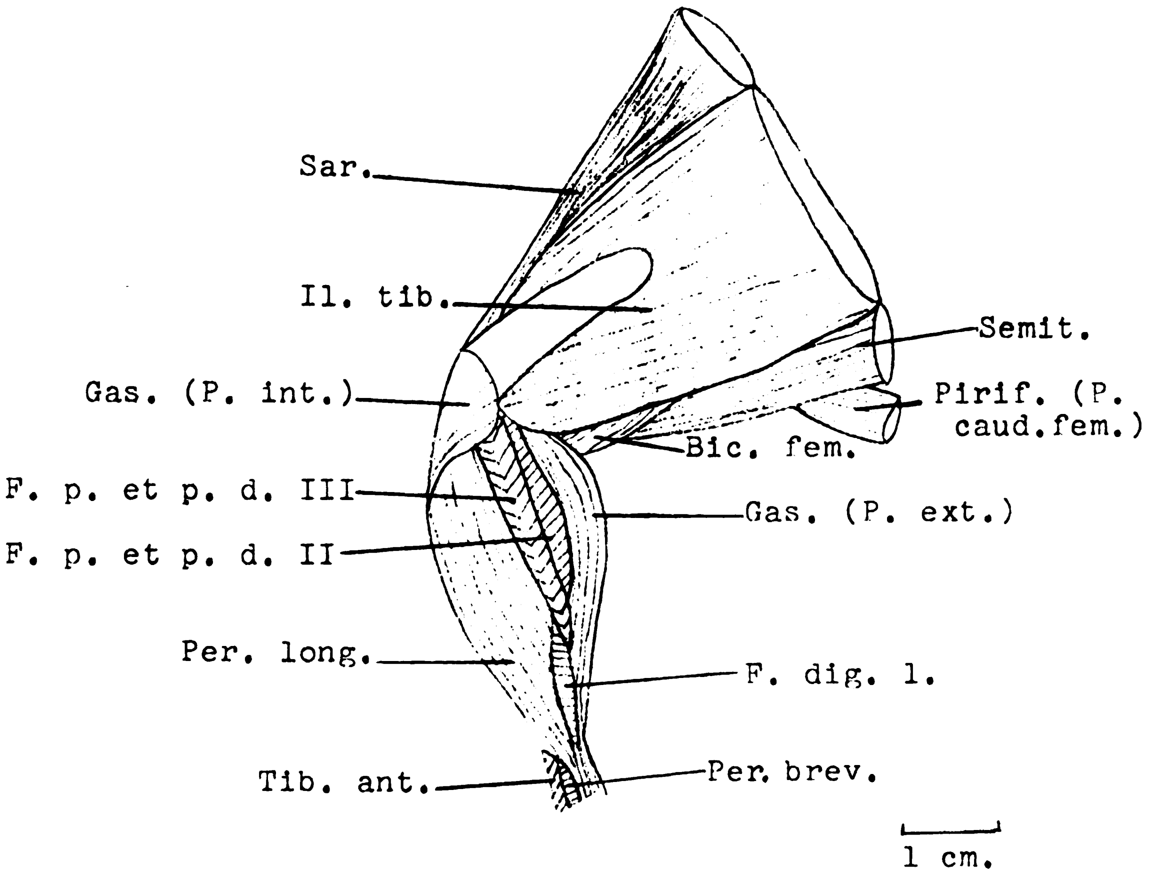
Sar.
Il. tib.
Gas. (P. int.)
F. p. et p. d. III
F. p. et p. d. II
Per. long.
Tib. ant.
Semit.
Pirif. (P. caud.fem.)
Bic. fem.
Gas. (P. ext.)
F. dig. l.
Per. brev.
1 cm.

Figure 3

Figure 4.--(*Coturnix coturnix japonica*) Lateral view of a second layer of muscles of the left thigh and shank. The following muscles have been removed wholly or in part: M. gastrocnemius, M. iliotibialis, M. sartorius, M. peroneus longus.

Abbreviations for muscles (after Hudson et al., 1959):

acc. = Accessory portion of M. semitendinosus.

add. *long*. = M. adductor longus et brevis.

bic. *fem*. = M. biceps femoris.

fem. *tib*. *med*. = M. femoritibialis medius.

flex. *dig*. *l*. = M. flexor digitorum longus.

f. *p*. *et p*. *d*. *II* = M. flexor perforans et perforatus digiti II.

f. *p*. *et p*. *d*. *III* = M. flexor perforans et perforatus digiti III.

flex. *per*. *d*. *III* = M. flexor perforatus digiti III.

flex. *per*. *d*. *IV* = M. flexor perforatus digiti IV.

il. *troc*. *ant*. = M. iliotrochantericus anterior.

il. *troc*. *med*. = M. iliotrochantericus medius.

il. *troc*. *post*. = M. iliotrochantericus posterior.

per. *brev*. = M. peroneus brevis.

pirif. (*p*. *caud*. *fem*.) = M. piriformis (pars caudofemoralis).

pirif. (*p*. *il*. *fem*.) = M. piriformis (pars iliofemoralis).

semit. = M. semitendinosus.

tib. *ant*. = M. tibialis anterior.

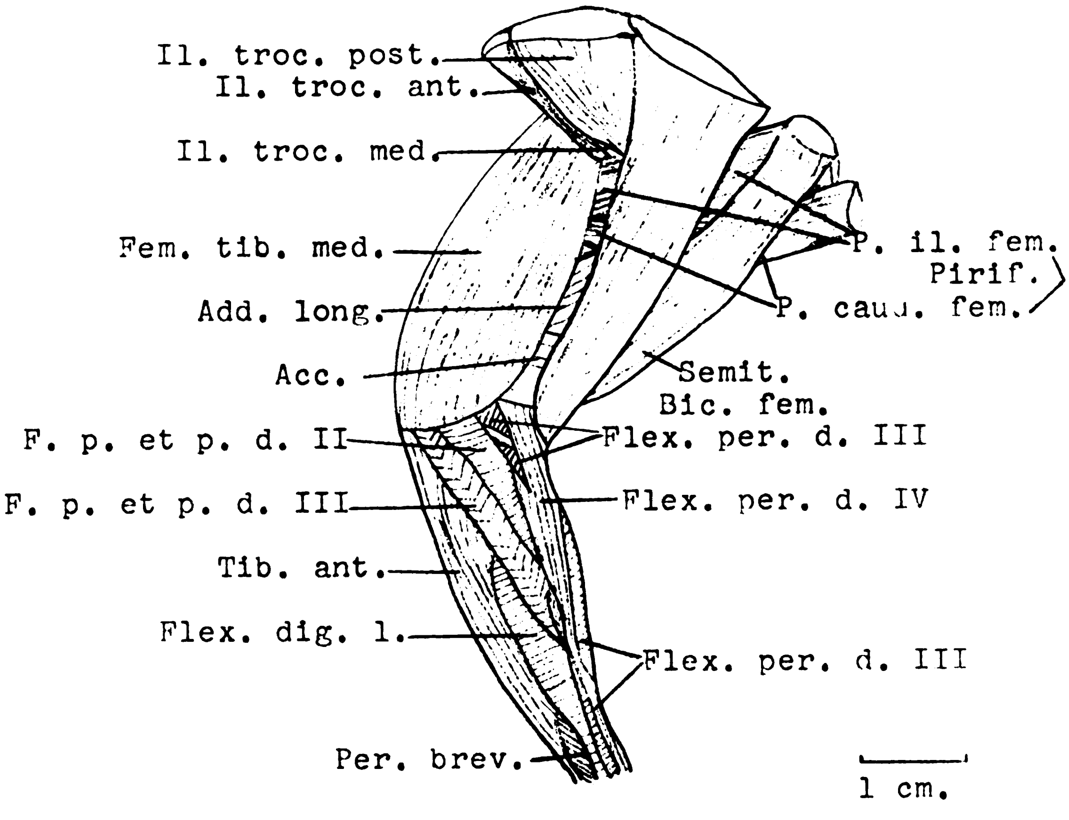
Il. troc. post.
Il. troc. ant.
Il. troc. med.
Fem. tib. med.
Add. long.
Acc.
F. p. et p. d. II
F. p. et p. d. III
Tib. ant.
Flex. dig. l.
Per. brev.
P. il. fem.
Pirif.
P. caud. fem.
Semit.
Bic. fem.
Flex. per. d. III
Flex. per. d. IV
Flex. per. d. III
1 cm.

Figure 4

Figure 5.--(*Coturnix coturnix japonica*) Lateral view of a third layer of muscles of the left thigh and shank. In addition to the muscles listed in Figure 4, the following muscles have been wholly or partly removed: M. biceps femoris, M. femoritibialis, M. flexor perforans et perforatus digiti II, M. flexor perforans et perforatus digiti III, M. semitendinosus, M. tibialis anterior.

Abbreviations for muscles (after Hudson et al., 1959):

acc. = Accessory portion of M. semitendinosus.

add. *long*. = M. adductor longus et brevis.

ambiens = M. ambiens.

bic. *fem*. = M. biceps femoris.

ext. *dig*. *l*. = M. extensor digitorum longus.

fem. *tib*. *ext*. = M. femoritibialis externus.

f. *dig*. *l*. = M. flexor digitorum longus.

flex. *per*. *d*. *III* = M. flexor perforatus digiti III.

flex. *per*. *d*. *IV* = M. flexor perforatus digiti IV.

glut. *med*. *et* *min*. = M. gluteus medius et minimus.

il. *troc*. *ant*. = M. iliotrochantericus anterior.

il. *troc*. *med*. = M. iliotrochantericus medius.

il. *troc*. *post*. = M. iliotrochantericus posterior.

isch. *fem*. = M. ischiofemoralis.

obt. *int*. = M. obturator internus.

per. *brev*. = M. peroneus brevis.

pirif. (*p*. *caud*. *fem*.) = M. piriformis (pars caudofemoralis).

pirif. (*p*. *il*. *fem*.) = M. piriformis (pars iliofemoralis).

semi. *m*. = M. semimembranosus.

semit. = M. semitendinosus.

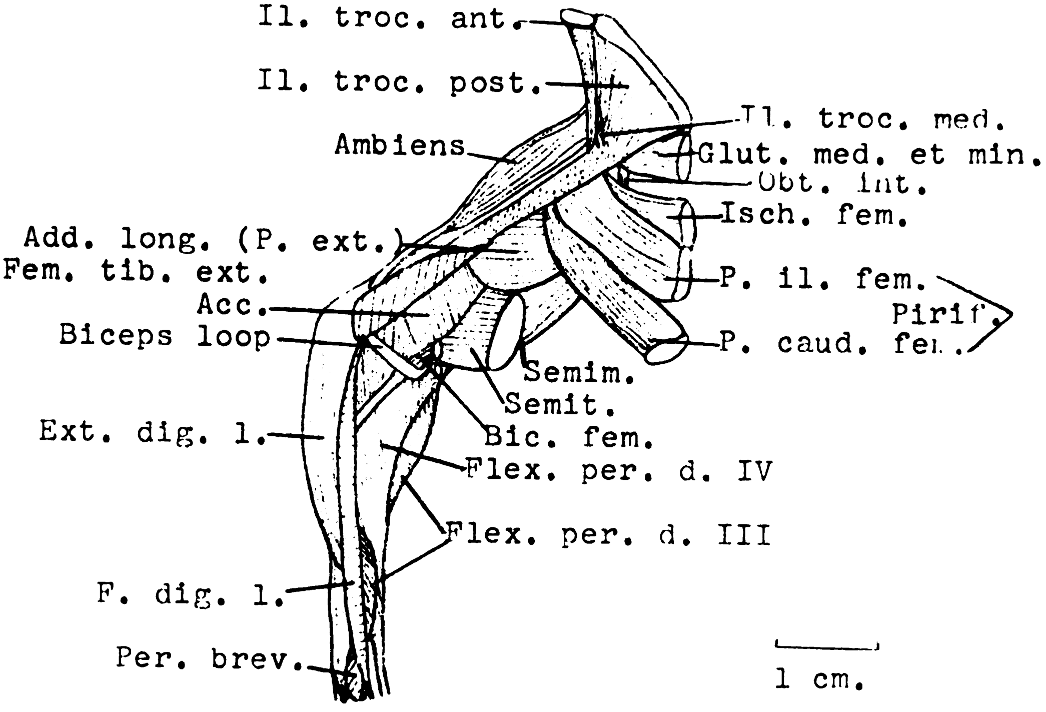
Il. troc. ant.
Il. troc. post.
Il. troc. med.
Glut. med. et min.
Ambiens
Obt. int.
Isch. fem.
Add. long. (P. ext.)
Fem. tib. ext.
P. il. fem.
Pirif.
Acc.
Biceps loop
P. caud. fem.
Semim.
Semit.
Ext. dig. l.
Bic. fem.
Flex. per. d. IV
Flex. per. d. III
F. dig. l.
Per. brev.
1 cm.

Figure 5

Figure 6.--(*Coturnix coturnix japonica*) Lateral view of a fourth layer of muscles of the left thigh and shank. In addition to the muscles listed in Figures 4 and 5 the following muscles have been removed wholly or in part: M. ambiens, M. extensor digitorum longus, M. flexor tibialis externus, M. flexor digitorum longus, M. flexor perforatus digiti III, M. flexor perforatus digiti IV, M. iliotrochantericus posterior, M. piriformis.

Abbreviations for muscles (after Hudson et al., 1959):

add. *long*. (*p*. *ext*.) = M. adductor longus et brevis pars externa).

add. *long*. (*p*. *int*.) = M. adductor longus et brevis pars interna).

f. *hal*. *l*. = M. flexor hallucis longus.

flex. *per*. *d*. *II* = M. flexor perforatus digiti II.

glut. *med*. *et min*. = M. gluteus medius et minimus.

il. *troc*. *ant*. = M. iliotrochantericus anterior.

il. *troc*. *med*. = M. iliotrochantericus medius.

isch. *fem*. = M. ischiofemoralis.

obt. *ext*. = M. obturator externus.

obt. *int*. = M. obturator internus.

per. *brev*. = M. peroneus brevis.

semim. = M. semimembranosus.

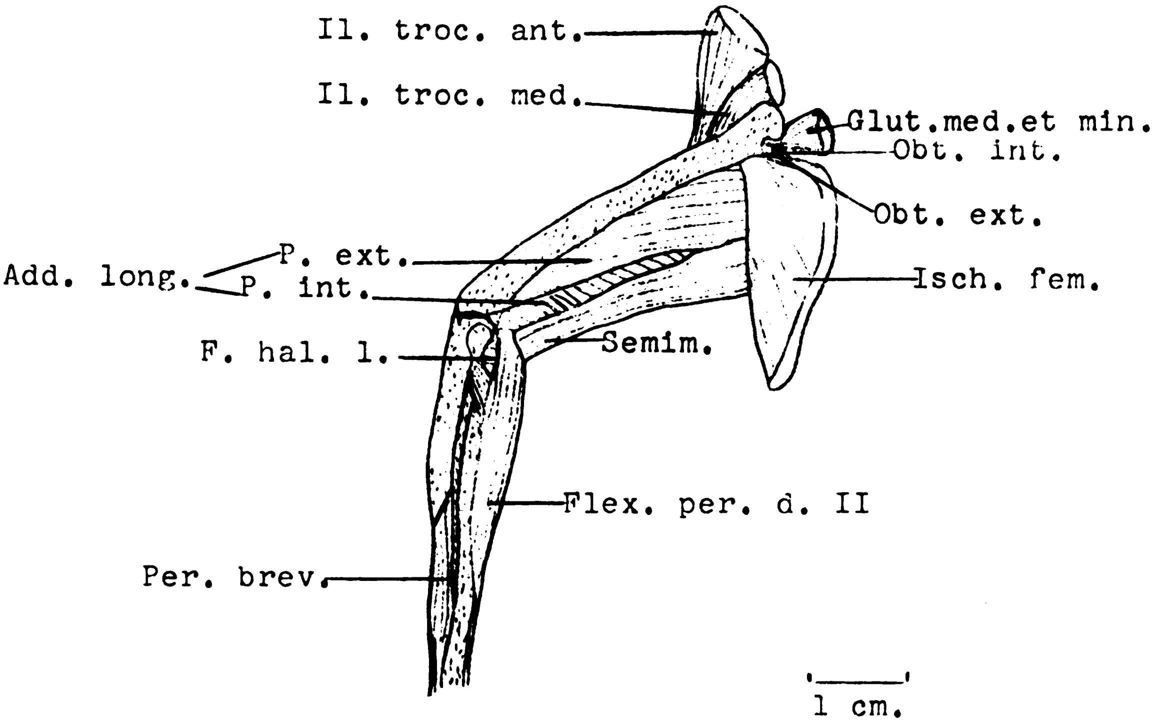
Il. troc. ant.
Il. troc. med.
Glut.med.et min.
Obt. int.
Obt. ext.
P. ext.
Add. long.
P. int.
Isch. fem.
Semim.
F. hal. l.
Flex. per. d. II
Per. brev.
1 cm.

Figure 6

Figure 7.--(*Coturnix coturnix japonica*) Medial view of the superficial muscles of the left thigh and shank.

Abbreviations for muscles (after Hudson et al., 1959):

acc. = Accessory portion of M. semitendinosus.

add. *long*. = M. adductor longus et brevis.

ambiens = M. ambiens.

ext. *dig*. *l*. = M. extensor digitorum longus.

fem. *tib*. *int*. = M. femoritibialis internus.

fem. *tib*. *med*. = M. femoritibialis medius.

gas. (*p*. *ext*.) = M. gastrocnemius (pars externa).

gas. (*p*. *int*.) = M. gastrocnemius (pars interna).

gas. (*p*. *med*.) = M. gastrocnemius (pars medius).

iliacus = M. iliacus.

il. *troc*. *ant*. = M. iliotrochantericus anterior.

il. *troc*. *med*. = M. iliotrochantericus medius.

il. *troc*. *post*. = M. iliotrochantericus posterior.

obt. *int*. = M. obturator internus.

per. *long*. = M. peroneus longus.

pirif. (*p*. *caud*. *fem*.) = M. piriformis (pars caudofemoralis).

sar. = M. sartorius.

semim. = M. semimembranosus.

semit. = M. semitendinosus.

tib. *ant*. = M. tibialis anterior.

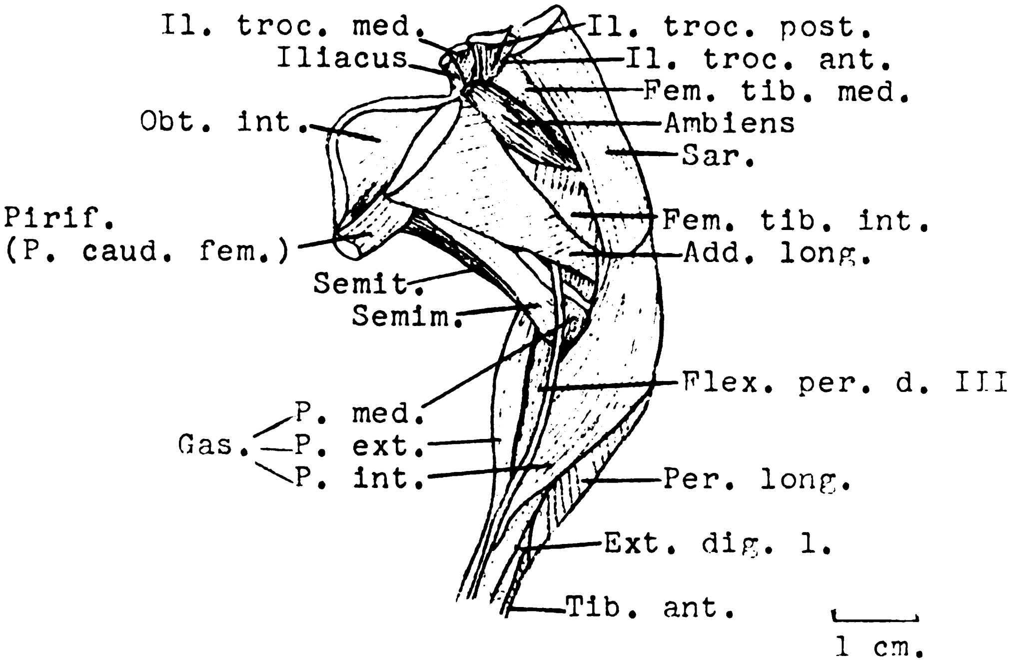
Il. troc. med.
Iliacus
Obt. int.
Pirif.
(P. caud. fem.)
Semit.
Semim.
Gas.
P. med.
P. ext.
P. int.
Il. troc. post.
Il. troc. ant.
Fem. tib. med.
Ambiens
Sar.
Fem. tib. int.
Add. long.
Flex. per. d. III
Per. long.
Ext. dig. l.
Tib. ant.
1 cm.

Figure 7

Figure 8.--(Coturnix coturnix japonica) Medial view of a second layer of muscles of the left thigh and shank. The following have been removed wholly or in part: M. gastrocnemius, M. peroneus longus, M. sartorius, M. semimembranosus.

Abbreviations for muscles (after Hudson et al., 1959):

add. long. = M. adductor longus et brevis.

ambiens = M. ambiens.

ext. dig. l. = M. extensor digitorum longus.

fem. tib. int. = M. femoritibialis internus.

fem. tib. med. = M. femoritibialis medius.

f. dig. l. = M. flexor digitorum longus.

f. hal. l. = M. flexor hallucis longus.

flex. per. d. III = M. flexor perforatus digiti III.

iliacus = M. iliacus.

il. troc. ant. = M. iliotrochantericus anterior.

il. troc. med. = M. iliotrochantericus medius.

il. troc. post. = M. iliotrochantericus posterior.

obt. int. = M. obturator internus.

pirif. (p. caud. fem.) = M. piriformis (pars caudofemoralis).

plan. = M. plantaris.

semim. = M. semimembranosus.

semit. = M. semitendinosus.

tib. ant. = M. tibialis anterior.

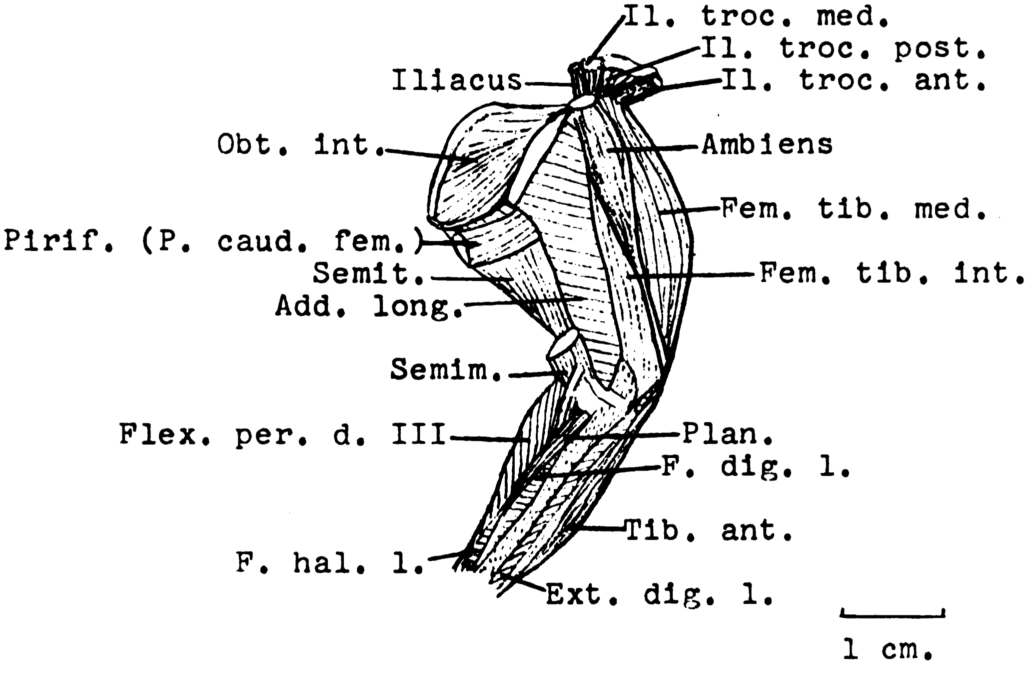
Il. troc. med.
Il. troc. post.
Iliacus
Il. troc. ant.
Obt. int.
Ambiens
Fem. tib. med.
Pirif. (P. caud. fem.)
Semit.
Fem. tib. int.
Add. long.
Semim.
Flex. per. d. III
Plan.
F. dig. l.
Tib. ant.
F. hal. l.
Ext. dig. l.
1 cm.

Figure 8

of the anterior proximal portion of the thigh is located medial to the M. iliotibialis, M. femoritibialis medius, and M. sartorius. It is distal to the adjacent M. iliotrochantericus posterior which covers it proximally. It has a partly fleshy origin from the anterior preacetabular ilium. The broad origin tapers rapidly to form a flat tendon which inserts on the anterolateral surface of the femur, just distal to the M. iliotrochantericus medius. Coturnix Wt.: ♂0.033 ± 0.006, ♀0.047 ± 0.004; Bobwhite Wt.: ♂0.122 ± 0.028, ♀ 0.154 ± 0.026.

Action.--In Coturnix and Bobwhite this muscle pulls the femur forward slightly as it pulls it inward, causing a slight movement of the posterior portion of the thigh outward and slightly forward. When the tendon was cut, no differences were noted in the locomotor or track pattern when walking.

M. iliotrochantericus medius

Description for Coturnix and comparison with Bobwhite.--(Figures 4, 5, 6, 7, and 8.) This, the smallest of the iliotrochantericus muscles, lies medial to the M. iliotrochantericus medius and occupies the region immediately in front of the acetabulum. Its fleshy origin is from the ventral portion of the preacetabular ilium. The belly tapers rapidly to form a tendon which inserts on the anterolateral portion of the femur just distal to the M.

iliotrochantericus posterior. Coturnix Wt.: ♂ 0.028 ± 0.003, ♀ 0.026 ± 0.002; Bobwhite Wt.: ♂ 0.031 ± 0.004, ♀ 0.038 ± 0.003.

Action.--In Coturnix and Bobwhite this muscle moves the femur forward and inward a slight amount. No visible movement of the thigh was noted as the femur moved anteriorly. When the tendon was cut no observable differences were noted in the locomotor or track pattern when walking.

M. gluteus medius et minimus

Description for Coturnix and comparison with Bobwhite.--(Figures 5 and 6.) This small triangular muscle is located under the M. iliotibialis at the proximal end of the femur. It arises mostly fleshy from the dorsolateral edge of the ilium. The belly of the muscle is very short and soon forms a broad tendon which then tapers to insert on the anterolateral surface of the femur. The muscle is slightly stouter in Bobwhite. Coturnix Wt.: ♂ 0.009 ± 0.001, ♀ 0.011 ± 0.002; Bobwhite Wt.: ♂ 0.013 ± 0.001, ♀ 0.012 ± 0.001.

Action.--In Coturnix and Bobwhite this muscle is an extremely weak abductor of the femur. When cut, no differences were noted in the locomotor or track pattern when walking.

M. iliacus

Description for Coturnix and comparison with Bobwhite.--(Figures 7 and 8.) This muscle, deeply situated in the proximal end of the thigh, has a fleshy origin from the ilium ventral to the origin of the M. iliotrochanter medius. It passes behind the femur and inserts fleshy on the posteromedial side of the proximal end of the femur. Coturnix Wt.: ♂0.014 ± 0.001, ♀0.017 ± 0.002; Bobwhite Wt.: ♂0.030 ± 0.006, ♀0.029 ± 0.004.

Action.--In Coturnix and Bobwhite, this muscle adducts the femur at the same time rotating it slightly as it pulls the femur forward. Although it was not cut, the size and type of origin and insertion suggests that it is very weak and of little value to the walking locomotor pattern of the bird.

M. ambiens

Description for Coturnix and comparison with Bobwhite.--(Figures 5, 7, and 8.) This long, narrow, thin muscle located on the medial side of the thigh slightly posterior to M. sartorius originates partly fleshy from the pectinal process of the ilium. The belly extends two-thirds the length of the thigh tapering distally into a tendon which passes between the M. femoritibialis medius and M. sartorius bending diagonally around the knee, transversing the patellar tendon and then inserting on the common tendon to the head of the fibula of the flexor perforatus digiti muscles. This insertion occurs on the lateral side of the shank proximal to the M. biceps femoris tendon. The muscle is more fleshy at the origin in Bobwhite. Coturnix Wt.: ♂ 0.040 ± 0.004, ♀ 0.037 ± 0.003; Bobwhite Wt.: ♂ 0.039 ± 0.004, ♀ 0.052 ± 0.005.

Action.--In Coturnix and Bobwhite this muscle extends the shank and at the same time there is very slight flexion of digits III and IV and somewhat more flexion of digit II. The bending occurs at the proximal end of the digits beyond which the digits remain straight as flexion occurs. When the tendon was cut, no observable differences were noted in the track or locomotor pattern of walking. Morrison (1869), however, observed toe inversion in chickens when he cut this muscle.

M. sartorius

Description for Coturnix and comparison with Bobwhite.--(Figures 3 and 7.) This straplike fleshy muscle constituting the anterior margin of the thigh originates laterally and sweeps around the front of the thigh distally toward the medial surface. The origin is fleshy from the anterior iliac crest. The posterior margin is fused very closely to the M. iliotibialis. There is also a tendinous connection to the underlying M. iliotrochantericus posterior. Insertion is on the anteromedial surface of the tibial crest and patellar tendon in common with the tendons of the

M. iliotibialis and M. femoritibialis. It is frequently hidden laterally by a layer of fat covering its surface. While the muscle is closely fused posteriorly to the M. iliotibialis, the line of demarcation between the two muscles is more distinct proximally in Bobwhite. In Bobwhite the muscle belly is somewhat wider and the posterior part of the muscle inserts on the tendon of the M. femoritibialis internus above the patellar tendon. Coturnix Wt.: ♂ 0.289 ± 0.008, ♀ 0.287 ± 0.016; Bobwhite Wt.: ♂ 0.790 ± 0.078, ♀ 0.810 ± 0.075.

Action.--In Coturnix and Bobwhite this muscle flexes the thigh as it extends the shank. It can also move the thigh inward a slight amount. Cutting (Figure 10) causes a reduction in the angle of the tibiotarsus joint when walking and a change in the femoral movement. This indicates that it plays a role in extending the shank in walking, although it is not so important as the M. femoritibialis and that it is important in pulling the femur forward in walking.

M. iliotibialis

Description for Coturnix and comparison with Bobwhite.--(Figure 3.) This large muscle covers nearly the entire lateral portion of the thigh. It originates from the ilium by means of an aponeurosis anteriorly and is fleshy in origin posteriorly. As the muscle narrows distally, the central portion is aponeurotic. The muscle is fused to the M. sartorius anteriorly, to the M. semitendinosus posteriorly, and to the M. femoritibialis medially. It unites at the knee with the M. sartorius and the underlying M. femoritibialis to form the patellar tendon which inserts on the outer cnemial crest. Coturnix Wt.: ♂1.155 ± 0.100, ♀1.229 ± 0.062; Bobwhite Wt.: ♂1.877 ± 0.234, ♀1.842 ± 0.231.

Action.--In Coturnix and Bobwhite this muscle pulls on the knee region to cause the leg to move up and away from the body. It also causes slight extending of the shank in both birds. Cutting (Figure 11) caused a decrease in the tibiotarsus angle indicating that it does extend the shank, although it is not nearly so important as the M. femoritibialis muscle in doing this. No differences in the track pattern were observed following severance of this muscle.

M. femoritibialis

Description for Coturnix and comparison with Bobwhite.--(Figures 4, 5, 7, and 8.) This muscle which makes up the bulk of the anterior portion of the thigh has three parts. The small M. femoritibialis externus arises fleshy from the distal posterolateral half of the femur. It inserts on the patellar tendon in common with the M. femoritibialis medius and M. iliotibialis internus. The largest of the three, the M. femoritibialis medius, makes up the bulk of the thigh anterior to the femur. It arises somewhat tendinous at the proximal end of the femur and has a fleshy origin nearly the entire length of the femur. Its insertion is in common with the M. iliotibialis internus and M. femoritibialis externus to help form the patellar tendon. The M. femoritibialis internus arises fleshy from the distal four-fifths of the posteromedial surface of the femur. At the distal end it forms a tendon which inserts on the outer cnemial crest of the tibiotarsus in common with the patellar tendon. There is a division of the M. femoritibialis internus into a superficial and deep layer in Bobwhite. The origin of M. femoritibialis externus has more tendinous fibers in Bobwhite. Coturnix Wt.: ♂ 1.306 ± 0.126, ♀ 1.376 ± 0.186; Bobwhite Wt.: ♂ 1.846 ± 0.136, ♀ 2.027 ± 0.137.

Action.--All three muscle heads in Coturnix and Bobwhite pull the tibiotarsus forward, thus causing extension of the shank. In addition the M. femoritibialis internus rotates the tibiotarsus medially. Cutting the three parts (Figure 12) shows that it is extremely important in pulling the shank forward in walking, as indicated by the smaller angles during leg movement. The smaller angles throughout the step also indicate that this muscle is an important antagonist to the flexors.

M. piriformis

Description for Coturnix and comparison with Bobwhite.--(Figures 3, 4, 5, 7, and 8.) This muscle is deeply situated in the posterior portion of the thigh musculature lateral to the M. biceps femoris, M. adductor longus et brevis, and M. semitendinosus. It is divided into the pars caudofemoralis and the pars iliofemoralis. The pars caudofemoralis arises mostly fleshy from the ventral side of the pygostyle and passes down to the femur where it inserts mostly tendinous on the posterolateral surface. The pars iliofemoralis originates fleshy from the ilium and passes down to the femur where its fleshy insertion is just proximal to the insertion of the pars caudofemoralis. This muscle is stouter in Bobwhite than in Coturnix. The pars caudofemoralis portion originates tendinous and is proportionately narrower at the origin in Bobwhite. Coturnix Wt.: ♂0.264 ± 0.016, ♀0.243 ± 0.012; Bobwhite Wt.: ♂0.309 ± 0.015, ♀0.379 ± 0.023.

Action.--In Bobwhite and Coturnix both parts pull the femur backward thus causing flexion of the thigh. This is, however, the only function of the pars iliofemoralis. The pars caudofemoralis pulls on the pygostyle causing the tail to move downward and outward. This muscle was not cut, but Fisher (1957), by cutting the pars caudofemoralis in pigeons, caused a reduction in the ability to depress the tail.

M. semitendinosus

Description for Coturnix and comparison with Bobwhite.--(Figures 3, 4, 5, and 7.) This fleshy muscle constituting the posterior margin of the thigh originates laterally and sweeps around the posterior part of the thigh distally toward the medial surface. The origin is fleshy from the posterior iliac crest, the ischium, and first two caudal vertebrae. Proximally it is closely fused to the adjacent M. iliotibialis. Distally it forms a tendon which fuses with the underlying tendon of the pars media of the M. gastrocnemius and then extends on to an insertion on the tibia just below the head of the tibia. At the distal end the anterior portion of the belly is connected by a fibrous raphe to the accessory portion of the M. semitendinosus. The accessory portion inserts on the posterior lateral surface of the femur. In Bobwhite there is a significant difference in that the tendon of the M. semitendinosus fuses with the tendon of M. semimembranosus to form a common tendon which inserts on the tibiotarsus. Coturnix Wt.: ♂ 0.500 ± 0.041, ♀ 0.462 ± 0.028; Bobwhite Wt.: ♂ 1.222 ± 0.116, ♀ 1.198 ± 0.120.

Action.--This muscle pulls on the femur, tibiotarsus, and M. gastrocnemius. It pulls the thigh posteriorly in Coturnix and Bobwhite. The tibiotarsus is pulled back by a separate tendon in Coturnix and by a common tendon with the M. semimembranosus in Bobwhite. In both cases the end result is flexion of the shank. The attachment to the M. gastrocnemius causes slight extension of the tarsometatarsus in both species of birds. Cutting (Figure 13) results in a reduction in flexion of the tibiotarsus during walking, indicated by the indrease of the angle of the tibiotarsus particularly at frame three. However, it is not so important as the M. biceps femoris in pulling the tibiotarsus posteriorly. Furthermore, there was no observable difference in the movement of the femur following severance. No observable differences were noted in the track pattern.

M. semimembranosus

Description for Coturnix and comparison with Bobwhite.--(Figures 5, 6, 7, and 8.) This weak straplike band occupies the medial posterior portion of the thigh. The anterior position arises tendinous while the posterior portion arises fleshy from the ischium and pubis lateral to the M. adductor longus et brevis. Posterior to the knee the M. semimembranosus is intimately associated with the three parts of the M. gastrocnemius and sends a tendon to the proximal lateral side of the tibia just distal to the M. semitendinosus tendon. The origin of the muscle in Bobwhite is more tendinous. In Bobwhite the M. semimembranosus fuses with the M. semitendinosus posterior to the knee to form a common tendon which inserts on the tibiotarsus. Coturnix Wt.: ♂ 0.049 ± 0.007, ♀ 0.049 ± 0.010; Bobwhite Wt.: ♂ 0.088 ± 0.008, ♀ 0.084 ± 0.005.

Action.--This muscle pulls primarily on the tibiotarsus with some pull exerted on the M. gastrocnemius to flex the shank in Coturnix. In Bobwhite the pull on the tibiotarsus is by means of a common tendon with the M. semitendinosus; some pull is exerted on the M.

gastrocnemius. M. semimembranosus also flexes the shank in Bobwhite. In Bobwhite and Coturnix the attachment to the M. gastrocnemius causes slight extension of the tarsometatarsus. When the tendon was cut, no observable differences were noted in track or locomotor patterns when walking.

M. biceps femoris

Description for Coturnix and comparison with Bobwhite.--(Figures 3, 4, and 5.) This muscle located below the M. iliotibialis in the posterior region of the thigh originates from the iliac crest just below the M. iliotibialis. The origin is aponeurotic anteriorly and the posterior portion is fleshy. This muscle tapers rapidly until it forms a powerful tendon at the level of the knee. The tendon passes through the biceps loop under the pars externa of the M. gastrocnemius and between the two heads of the M. flexor perforatus digiti IV and M. flexor perforatus digiti II to its insertion on the posterolateral surface of the fibula. Coturnix Wt.: ♂ 0.354 ± 0.031, ♀ 0.319 ± 0.010; Bobwhite Wt.: ♂ 0.816 ± 0.081, ♀ 0.946 ± 0.051.

Action.--In Coturnix and Bobwhite the fibula and tibiotarsus are pulled, thus causing flexion of the shank. Since the point of insertion on the fibula is also the point of the strongest fusion of the fibula to the tibiotarsus, this muscle does not appear to move the fibula independently. Cutting (Figure 14) shows that this muscle plays two vital roles in walking. The large tibiotarsus angle particularly at frames two and three verify that it flexes the shank, while the larger than normal angles that occur while the foot is moving forward indicate that it is also an important antagonist of the extensor muscles. The total length of the step was also reduced in the experimentals.

M. ischiofemoralis

Description for Coturnix and comparison with Bobwhite.--(Figures 5 and 6.) This muscle located in the proximal end of the shank, medial to the M. piriformis originates fleshy from much of the lateral surface of the ischium. It forms a tendon which inserts on the lateral surface of the femur just proximal to the insertion of the M. piriformis. The origin does not cover so extensive an area as the ischium in Bobwhite. Coturnix Wt.: ♂ 0.147 ± 0.007, ♀ 0.135 ± 0.005; Bobwhite Wt.: ♂ 0.141 ± 0.008, ♀ 0.145 ± 0.005.

Action.--In Coturnix and Bobwhite this muscle pulls medially and posteriorly on the head of the femur causing the anterior portion of the thigh to move away from the body and slightly posteriorly. Cutting (Figure 5) shows it not only pulls the thigh posteriorly, but also is an important antagonist. No observable differences were noted in the track pattern.

M. obturator internus

Description for Coturnix and comparison with Bobwhite.--(Figures 5, 6, 7, and 8.) This large muscle occupies the internal surface of much of the postacetabular ventral area of the pelvic girdle. It originates from the pubis, much of the medial side of the ischium, and a small part of the ilium. The muscle tapers, forming a tendon which passes through the obturator foramen after which it inserts on the posterolateral side of the head of the femur. Coturnix Wt.: ♂ 0.078 ± 0.009, ♀ 0.082 ± 0.006; Bobwhite Wt.: ♂ 0.199 ± 0.017, ♀ 0.204 ± 0.012.

Action.--In Coturnix and Bobwhite this muscle pulls from the posterolateral surface of the femur causing the femur to rotate inward as it moves backward, thus causing the anterior portion of the thigh to move slightly outward and posteriorly. Cutting (Figure 16) causes a slight alteration in the walking locomotor pattern. Its importance appears to be more that of an antagonist to the iliotrochanterus muscles to keep the femoral joint stable rather than one of moving the thigh, thus the differences reflected in the locomotor pattern are probably due to a reduction in the stability of the femoral joint. No differences were noted in the track pattern while the bird was walking.

M. obturator externus

Description for Coturnix and comparison with Bobwhite.--(Figure 6.) This short, deeply situated muscle arises fleshy just in front of the obturator foramen. It passes tightly along the posterior surface of the head of the femur and inserts fleshy on the posterolateral edge of the head of the femur. Coturnix Wt.: ♂ 0.006 ± 0.002, ♀ 0.008 ± 0.001; Bobwhite Wt.: ♂ 0.016 ± 0.003, ♀ 0.015 ± 0.004.

Action.--In Coturnix and Bobwhite this muscle pulls very slightly on the posterolateral portion of the femur causing it to move inward and posteriorly. No movement of the thigh was observed. Although this muscle was not cut, it would probably be very weak and have no effect on the walking locomotor pattern because of its small size, type of origin, and insertion.

M. adductor longus et brevis

Description for Coturnix and comparison with Bobwhite.--(Figures 4, 5, 6, 7, and 8.) This large muscle located on the surface of the medial side of the thigh has two heads. The medial head arises from the pubis and is tendinous except for a small anterior portion which arises fleshy. The lateral head arises fleshy from the ventral portion of the ilium. Insertion is mostly fleshy on the entire length of the posterior portion of the femur distal to the insertion of the M. piriformis. Coturnix Wt.: ♂ 0.301 ± 0.008, ♀ 0.290 ± 0.014; Bobwhite Wt.: ♂ 0.432 ± 0.026, ♀ 0.481 ± 0.028.

Action.--In Coturnix and Bobwhite this muscle pulls the femur backward, thus causing extension of the thigh. Cutting (Figure 17) illustrates the fact that this muscle is important in pulling the thigh backward when the bird is walking. This is indicated by the abnormally large joint angle of the femur particularly in frame three. Furthermore, the femur moved farther anteriorly after severance, indicating that it not only extends, but also is an important antagonist during walking. The track pattern showed a reduction in step length.

M. tibialis anterior

Description for Coturnix and comparison with Bobwhite.--(Figures 3, 4, 7, and 8.) This two-headed muscle located on the anterior portion of the shank lies below the M. peroneus longus. The larger anterior head has its fleshy origin from the overlying M. peroneus longus in addition to the outer cnemial crest. The much smaller lateral head passes behind the outer cnemial crest under the patella to originate by a small tendon on the external condyle of the femur. The two bellies of this muscle unite in a bipennate fashion and continue nearly to the fibrous loop where it tapers into a flat tendon. The tendon passes over the anterior surface of the tarsometatarsal joint and under the fibrous loop after which it enlarges and thickens prior to inserting on the anterior surface of the medial side of the tarsometatarsal joint. The belly of this muscle is much shorter in Bobwhite. Coturnix Wt.: ♂ 0.267 ± 0.005, ♀ 0.265 ± 0.010; Bobwhite Wt.: ♂ 0.565 ± 0.035, ♀ 0.520 ± 0.033.

Action.--In Coturnix and Bobwhite, M. tibialis anterior pulls on the tarsometatarsus resulting in its flexion. Cutting (Figure 18) causes a great increase in the tarsometatarsal joint angle, indicating that it is an extremely powerful flexor and vital to the locomotor walking pattern. The track pattern indicated a reduction in the total step length. At frame five, a unique variation in the locomotor pattern took place: in most birds the digits were inverted at this point following muscle severance. However, this variation did not occur in all the experimental Coturnix nor in all the experimental Bobwhite. Some birds that did not display this phenomenon immediately were kept alive a few days for study but never did invert the digits, while in other birds the phenomenon was observed two or three days after muscle severance.

M. extensor digitorum longus

Description for Coturnix and comparison with Bobwhite.--(Figures 5, 7, and 8.) This deeply situated muscle is located on the anterior side of the shank, posterior and medial to the M. tibialis anterior. Its origin is fleshy from the proximal three-fifths of the anterolateral surface of the tibiotarsus. A tendon formed in the distal end of the shank passes through the fibrous loop and a bony canal in the tibiotarsus, then onto the anteromedial side of the tarsometatarsus. This muscle then passes through another fibrous loop, onto the anterior surface of the tarsometatarsus where the tendon bifurcates into two parts. The smaller medial branch sends a tendon to digit II and the medial side of digit III. The larger branch bifurcates again sending one branch to the lateral side of digit III and another branch to digit IV. Because of the tight fascial sheath all branches have the "effect" of inserting the entire length out to the proximal end of the distal phalanx of each digit. In one bird of the 15 examined the tendon of this muscle was ossified. Tendon ossification did not occur in any Bobwhite examined. Coturnix Wt.: ♂ 0.094 ± 0.008, ♀ 0.093 ± 0.009; Bobwhite Wt.: ♂ 0.167 ± 0.011, ♀ 0.166 ± 0.009.

Action.--In Coturnix and Bobwhite this muscle pulls on the foretoes in such a way that the digits are extended the entire length and at the same time the toes are spread apart. Thus this muscle is an abductor as well as an extensor of the foretoes. Cutting (Figure 19) causes the foretoes to bend under, greatly impeding the locomotor pattern. The footprint is reduced due to the digits curling under and the length of the step is likewise reduced. Thus this muscle is very vital in extending the foretoes and in performing this function helps to maintain continuity in the locomotor pattern.

M. peroneus longus

Description for Coturnix and comparison with Bobwhite.--(Figures 3 and 7.) This large muscle is located on the anterolateral surface of the shank. It has an extensive origin from the fascia of the knee joint, tibial crest, anterior surface of the M. flexor perforans et perforatus digiti III, the proximal end of M. flexor digitorum longus, and the proximal end of M. tibialis anterior. From its origin it sweeps around toward the lateral surface of the shank ending in a lateral tendon at the distal one-third of the shank. This tendon bifurcates into a deep tendon which proceeds posteriorly to insert on the lateral side of the tibial cartilage and into an approximately equal size branch which narrows as it passes distally over the intertarsal joint after which it broadens gradually until it inserts on M. flexor perforatus digiti III one quarter of the way from the proximal end of the tarsometatarsus. Coturnix Wt.: ♂0.409 ± 0.040, ♀0.383 ± 0.033; Bobwhite Wt.: ♂0.715 ± 0.053, ♀0.764 ± 0.067.

Action.--In Coturnix and Bobwhite M. peroneus longus pulls the tibiotarsus forward, the tarsometatarsus backward, and pulls on the M. flexor perforatus digiti III, thus causing slight extension of the shank, extension of the tarsometatarsus and a small amount of flexion of the entire length of digit III. When cut, no differences that were being measured were noted in the track or locomotor pattern during walking. However, there appeared to be a slight "toeing in" of the foot.

M. peroneus brevis

Description for Coturnix and comparison with Bobwhite.--(Figures 4, 5, and 6.) This muscle lies on the lateral distal three-fifths surface of the shank. It originates fleshy from the surface of the fibula and tibiotarsus. The tendon formed at the distal end of the tibiotarsus expands on the side of the lateral malleolus and remains expanded as it inserts on the posterolateral surface of the proximal end of the hypotarsus. Coturnix Wt.: ♂ 0.032 ± 0.007, ♀ 0.027 ± 0.005; Bobwhite Wt.: ♂ 0.050 ± 0.003, ♀ 0.066 ± 0.002.

Action.--In Coturnix and Bobwhite M. peroneus brevis pulls on the lateral side of the tarsometatarsus causing abduction of the tarsometatarsus. No differences were observed in locomotor or track patterns of birds walking when this muscle was cut.

M. gastrocnemius

Description for Coturnix and comparison with Bobwhite.--(Figures 3 and 7.) This large muscle is located in the shank occupying the superficial portion of the medial, posterior, and proximal anterior surfaces. It has three heads. The pars externa has its origin from the lateral side at the external condyle of the femur by a short stout tendon. The belly extends down the posterior portion of the leg and unites with the other two heads in the distal one-quarter of the shank. The pars media, the smallest head, originates on the internal condyle of the femur by a tendinous attachment. The belly ends near the proximal one-fifth of the shank and then continues on as a conspicuous tendon fused to the posterior surface of the pars interna. The large pars interna originates from the inner cnemial crest, the head of the tibiotarsus and patellar tendon. The pars interna unites with the tendon of the pars media, and slightly farther down near the distal one-fifth of the shank the pars externa also fuses to become the Achilles' tendon. This tendon passes over the posterior portion of the tarsometatarsal joint, inserting on the hypotarsus and the entire length of the tarsometatarsus thus providing a sheath for the underlying flexor tendons. Coturnix Wt.: ♂ 1.125 ± 0.056, ♀ 1.068 ± 0.058; Bobwhite Wt.: ♂ 1.839 ± 0.189, ♀ 1.846 ± 0.160.

Action.--In Coturnix and Bobwhite M. gastrocnemius pulls on the posterior portion of the tarsometatarsus causing extension of this bone. In addition it causes a slight spreading of the foretoes, particularly in Bobwhite. Cutting (Figure 20) shows that this is one of the most vital muscles in walking and is an extremely powerful extensor of the tarsometatarsus. When cut, the bird no longer stands up, but walks on its tarsometatarsal joint, the tarsometatarsal bone being in a nearly horizontal plane. This is shown in the graph by the extremely reduced tarsometatarsal angle. Because of the new position of the tarsometatarsal bone, the digits flex more than usual to make contact with the substrate. The angle of the tibiotarsus and femur joints are also altered somewhat as the bird adjusts to this new locomotor pattern. No track pattern could be made of these experimental birds.

M. plantaris

Description for Coturnix and comparison with Bobwhite.--(Figure 8.) This muscle located just posterior to the femur and medial to the pars interna of the M. gastrocnemius originates fleshy from the posteromedial surface of the tibiotarsus. It forms a tendon slightly proximal to the middle of the shank which inserts on the tibial cartilage. Coturnix Wt.: ♂0.051 ± 0.004, ♀0.046 ± 0.003; Bobwhite Wt.: ♂0.081 ± 0.005, ♀0.074 ± 0.004.

Action.--In Coturnix and Bobwhite the pull is from the tibial cartilage causing extension of the tarsometatarsus. When the tendon was cut, no observable differences were noted in the track or locomotor pattern when walking.

M. flexor perforans et perforatus digiti II

Description for Coturnix and comparison with Bobwhite.--(Figures 3 and 4.) This superficial muscle lies on the posterolateral side of the shank bordered anteriorly by

M. flexor perforans et perforatus digiti III and posteriorly by pars externa of M. gastrocnemius. Its origin is partly fleshy from the external condyle of the femur and the biceps loop. It becomes tendinous near the middle of the leg. The tendon passes over the hypotarsus on down the tarsometatarsus. At the level of the proximal phalanx of digit II it perforates M. flexor perforatus digiti II and then splits as it is perforated by M. flexor digitorum longus and inserts on the distal end of phalanx I and proximal end of phalanx II. In Bobwhite more of the origin is on the biceps loop. The belly length is .4 the length of the shank in Bobwhite while in Coturnix it is .5 the length of the shank. Coturnix Wt.: ♂ 0.053 ± 0.005, ♀ 0.056 ± 0.004; Bobwhite Wt.: ♂ 0.088 ± 0.013, ♀ 0.072 ± 0.005.

Action.--In Coturnix and Bobwhite the pull is such that it causes flexion of digit II. The bending occurs at the proximal end of the first phalanx with the remainder of the digit remaining straight as flexion occurs. Cutting (Figure 21) causes an inversion of this digit as well as a reduction in flexion. This is also reflected in a reduction in the length of the toeprint of digit II in the track pattern when walking. Thus, this muscle is not only important in flexing digit II during leg movement, but also in keeping the digit on the substrate.

M. flexor perforans et perforatus digiti III

Description for Coturnix and comparison with Bobwhite.--(Figures 3 and 4.) This superficial muscle located on the anterolateral surface of the shank is bordered anteriorly by the M. peroneus longus and posteriorly by the M. flexor perforans et perforatus digiti II. It has a fleshy origin from the outer cnemial crest, patellar tendon, and biceps loop. It tapers into a tendon near the middle of the shank which then passes over the hypotarsus in the tendon of M. flexor perforatus digiti III down the posterior surface of the tarsometatarsus to the proximal phalanx where it perforates the tendon of M. flexor perforatus digiti III; then it is perforated by the M. flexor digitorum longus and inserts on the distal end of phalanx II and proximal end of phalanx III. At the level of the hallux it is connected by a vinculum to M. flexor perforatus digiti III. Coturnix Wt.: ♂ 0.116 ± 0.009, ♀0.111 ± 0.009; Bobwhite Wt.: ♂ 0.261 ± 0.020, ♀0.297 ± 0.030.

Action.--In Coturnix and Bobwhite the pull is such that it causes flexion of digit III and slight flexion of digits II and IV. Unlike the action of M. flexor perforans et perforatus digiti II, this muscle flexes in such a way that it causes digit III to curl over its entire length. The major bend that causes this "curling effect" occurs between phalanges I and II. Cutting (Figure 22) causes inversion of the digit which is also reflected in the track pattern in the reduction in the amount of digit III in contact with the substrate. It also shows a decrease in flexion when walking following muscle severance. Thus it is not only important in flexing digit III during leg movement, but also is important in helping keep the distal end of digit III on the substrate.

M. flexor perforatus digiti II

Description for Coturnix and comparison with Bobwhite.--(Figure 6.) This muscle located posterior to the M. flexor digitorum longus has two heads. The one head arises in common with the M. flexor perforatus digiti IV from the region of the head of the fibula, while the other head arises in common with the M. flexor perforatus digiti IV and M. flexor perforatus digiti II from the distal end of the femur. The belly is closely fused to the other two flexor perforatus muscles. The belly extends four-fifths the length of the tibiotarsus, from where a tendon passes over the posterior surface of the tarsometatarsus to the second digit where the tendon splits and inserts on the proximal end of the first phalanx. Coturnix Wt.: ♂ 0.050 ± 0.008, ♀ 0.054 ± 0.005; Bobwhite Wt.: ♂ 0.113 ± 0.013, ♀ 0.125 ± 0.019.

Action.--In Coturnix and Bobwhite the pull is from the first phalanx of digit II. As it flexes this digit, the major bend is at the proximal end of the first phalanx, thus the remainder of the digit remains straight as it flexes at this point. Cutting (Figure 23) causes an "S shape" bending configuration of digit II when on the substrate and a reduction in the amount of flexion during leg movement. The track pattern of the experimentals varied from the control in that the length of the print of digit II was slightly decreased due to the proximal inversion. Thus this muscle is not only important in flexion during walking, but also in keeping the proximal end of digit II on the substrate.

M. flexor perforatus digiti III

Description for Coturnix and comparison with Bobwhite.--(Figures 4, 5, and 8.) This muscle located on the posterior portion of the shank has two heads. The smaller head arises from the region of the head of the fibula by a tendon while the larger head arises in common with the M. flexor perforatus digiti II and M. flexor perforatus digiti IV from the distal end of the femur. This muscle forms a tendon near the distal one-quarter of the shank. This tendon then continues on to form a sheath which surrounds the M. flexor perforatus digiti IV and M. flexor perforans et perforatus digiti III. Just distal to the hypotarsus the tendon becomes ossified. This ossification extends to the vinculum which attaches it to M. flexor perforans et perforatus digiti III. The tendon then continues onto the third digit where it bifurcates and inserts on the distal end of phalanx I and proximal end of phalanx II. Coturnix

Wt.: ♂ 0.107 ± 0.010, ♀ 0.107 ± 0.008; Bobwhite Wt.: ♂ 0.172 ± 0.012, ♀ 0.182 ± 0.008.

Action.--In Coturnix and Bobwhite this muscle pulls on digits III and IV causing them to flex. The primary bending point is between phalanges I and II in digit III and at the proximal end of phalanx I in digit IV. Beyond these points the digits remain straight when flexion occurs. Cutting (Figure 24) causes a sharp "S shaped" bending configuration of digit III when on the substrate and a reduction in the amount of flexion during leg movement. Digit IV did not appear to change. The length of the print of digit III decreased due to the inversion toward the proximal end of the toe. Thus, this muscle is not only important in flexion during walking, but also in keeping the proximal end of digit III on the substrate.

M. flexor perforatus digiti IV

Description for Coturnix and comparison with Bobwhite.--(Figures 4 and 5.) This muscle located on the posterolateral side of the shank, medial to the pars externa of the M. gastrocnemius has two heads. The smaller lateral head arises by a tendon from the biceps loop and the region of the head of the fibula. The larger posteromedial head originates on the femur just distal to the insertion of the accessory portion of M. semitendinosus. The tendon of the M. biceps femoris passes between the two heads after which the two heads of M. flexor perforatus digiti IV unite to form a tendon which passes over the posterior portion of the intertarsal joint in the sheath formed by M. flexor perforatus digiti III and on down the tarsometatarsus. Insertion is on the fourth digit by means of three tendinous branches. One small lateral branch goes to the distal end of phalanx I. The middle branch goes to the distal end of phalanx II and proximal end of phalanx III, and the longest branch inserts on the distal end of the third phalanx and the proximal end of the fourth phalanx. In one bird this tendon was ossified. There was no trace of ossification in any of the Bobwhite examined. Coturnix Wt.: ♂ 0.177 ± 0.005, ♀ 0.155 ± 0.009; Bobwhite Wt.: ♂ 0.269 ± 0.022, ♀ 0.251 ± 0.017.

Action.--In Coturnix and Bobwhite the pull of this muscle is from the proximal end of the digit causing it to flex. The primary bending point is at the proximal end of the first phalanx beyond which the digit remains straight as flexion occurs. Cutting (Figure 25) causes a very sharp "S shape" bending configuration of digit IV when on the substrate and a reduction in the amount of flexion during leg movement. The track pattern varied from the control in that the length of the print of digit IV decreased due to the inversion toward the proximal end. Thus, this muscle is not only important in flexion during walking, but also in keeping the proximal end of the digit on the substrate.

M. flexor hallucis longus

Description for Coturnix and comparison with Bobwhite.--(Figures 6 and 8.) This muscle located directly lateral to the M. plantaris arises fleshy from the intercondyloid area of the femur. Near the middle of the shank it forms a tendon which passes down over the back of the tarsometatarsus through a groove on the hypotarsus and unites by means of a vinculum to the M. flexor digitorum longus. It has a small region of ossification just before the vinculum. Beyond the vinculum the tendon continues until it inserts on the distal end of the hallux. In Bobwhite the tendon is ossified over much of the proximal end of the tarsometatarsus prior to the formation of the vinculum. Coturnix Wt.: ♂ 0.045 ± 0.004, ♀ 0.043 ± 0.004; Bobwhite Wt.: ♂ 0.105 ± 0.011, ♀ 0.111 ± 0.010.

Action.--In Bobwhite and Coturnix, pulling this muscle flexes the foretoes in the manner described for M. flexor digitorum longus. In addition it flexes the hallux. The hallux flexion occurs near the distal end of the digit creating a curling or grasping effect. Because of the arrangement of the vinculum this muscle cannot operate independently of the M. flexor digitorum longus but the M. flexor digitorum longus can act independently of the M. flexor hallucis longus. When cut, no difference in locomotor or track pattern when walking was observed.

M. flexor digitorum longus

Description for Coturnix and comparison with Bobwhite.--(Figures 3, 4, 5, and 8.) This muscle located on the posterolateral side of the shank is situated deeply within the musculature proximally and is superficial distally. The fibular head originates fleshy from the fibula and the tibial head arises from the posterior portion of the fibula and nearly the entire lateral surface of the tibiotarsus. The tendon passes through a bony canal in the hypotarsus and then becomes ossified near the distal one-third of the tarsometatarsus. The tendon has a vinculum formed between it and the M. flexor hallucis longus near the distal one-third of the tarsometatarsus. The tendon forms three branches at the distal end of the tarsometatarsus. Branches go to digit II, digit III, and digit IV. Each branch inserts on the distal end of the ventral side of the respective digit. In Bobwhite the belly of the muscle is somewhat shorter. Coturnix Wt.: ♂ 0.144 ± 0.007, ♀ 0.135 ± 0.008; Bobwhite Wt.: ♂ 0.296 ± 0.010, ♀ 0.268 ± 0.008.

Action.--In Coturnix and Bobwhite the pull is from the distal end of the three digits causing flexion of digits I, II, and III. Since the major bend in each digit occurs between the distal phalanges of each digit, the flexion creates a curled, or grasping effect. Cutting (Figure 26) shows that this muscle is important in keeping the distal end of the digits on the substrate as well as flexing them. All three foretoes show an inversion at the tip when on the substrate as well as a decrease in the amount of flexion during leg movement. The footprint is reduced in length in the track pattern due to the inversion, but the length of the step is not adversely affected by muscle severance.

M. popliteus

Description for Coturnix and comparison with Bobwhite.--(Figure 9c.) This small triangular muscle is deeply situated in the proximal end of the shank. It has a fleshy origin from the posterolateral surface of the proximal end of the shank. It passes horizontally across the shank and inserts partly fleshy on the posterior surface of the head of the fibula. Coturnix Wt.: ♂ 0.010 ± 0.001, ♀ 0.009 ± 0.001; Bobwhite Wt.: ♂ 0.022 ± 0.004, ♀ 0.026 ± 0.002.

Action.--In Coturnix and Bobwhite this muscle moves the fibula toward the tibia a very small amount. Evidence gathered by stimulating this muscle in a chicken with a stimulator and recording fibular movement with a strain gauge transducer indicates that this muscle does in fact move the fibula toward the tibiotarsus. This muscle was not cut.

M. extensor hallucis longus

Description for Coturnix and comparison with Bobwhite.--(Figure 9a.) This small muscle located on the anteromedial surface of the tarsometatarsus arises fleshy

Figure 9.--(Coturnix coturnix japonica) (a) Anterior view of the left tarsometatarsus showing intrinsic foot muscles. (b) Posterior view of the left tarsometatarsus showing intrinsic foot muscles. (c) Posterior view of muscle of tibiotarsus showing the deeply situated M. popliteus.

Abbreviations for muscles (after Hudson et al., 1959):

abd. *d*. *II* = M. abductor digiti II.

abd. *d*. *IV* = M. abductor digiti IV.

add. *d*. *II* = M. adductor digiti II.

ext. *brev*. *d*. *III* = M. extensor brevis digiti III.

ext. *brev*. *d*. *IV* = M. extensor brevis digiti IV.

ext. *hal*. *l*. = M. extensor hallucis longus.

f. *hal*. *brev*. = M. flexor hallucis longus.

pop. = M. popliteus.

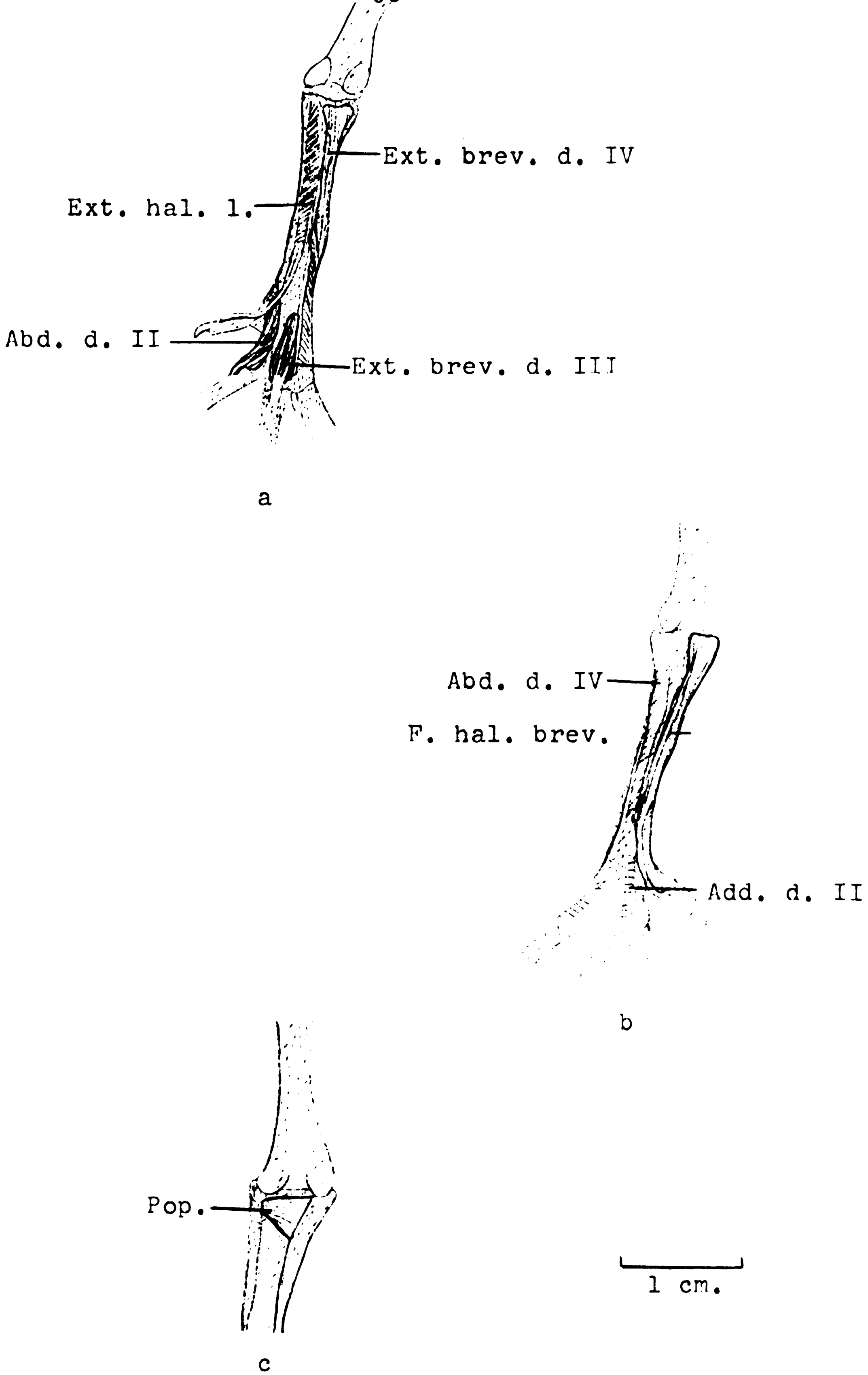
Ext. brev. d. IV
Ext. hal. l.
Abd. d. II
Ext. brev. d. III
a
Abd. d. IV
F. hal. brev.
Add. d. II
b
Pop.
1 cm.
c

Figure 9

from the proximal end of the tarsometatarsus. It also has some fleshy fibers which originate from much of the length of the tarsometatarsus and join the tendon that curls around to the medial surface where it inserts on the top of the distal end of the hallux. Coturnix Wt.: ♂ 0.006 ± 0.002, ♀ 0.005 ± 0.001; Bobwhite Wt.: ♂ 0.012 ± 0.002, ♀ 0.013 ± 0.003.

Action.--In Coturnix and Bobwhite the tendon of this muscle pulls on the hallux. When pull is exerted, the hallux extends with the bend occurring at the proximal end of the digit. When the tendon is cut (Figure 27), the angle the hallux makes with the tarsometatarsus is greatly increased. Furthermore, when you pick up a normal bird it usually extends its hallux, but the experimentals did not, even when under stress of handling. The cutting had no effect on the track pattern of birds walking. While the results were dramatic, they had little effect on the overall ability of the bird to walk.

M. extensor brevis digiti III

Description for Coturnix and comparison with Bobwhite.--(Figure 9a.) This small fleshy muscle is located on the anterior surface of the proximal end of the tarsometatarsus. Its origin is fleshy from the distal one-third of the tarsometatarsus. It inserts by a tendon on the proximal end of phalanx I of digit III. Coturnix Wt.: ♂ 0.004 ± 0.001, ♀ 0.005 ± 0.001; Bobwhite Wt.: ♂ 0.006 ± 0.002, ♀ 0.008 ± 0.001.

Action.--In Coturnix and Bobwhite this muscle extends digit III. The extension occurs at the proximal end of phalanx I. When cut, no differences were observed in the track or locomotor patterns.

M. extensor brevis digiti IV

Description for Coturnix and comparison with Bobwhite.--(Figure 9a.) This muscle located on the anterior surface of the tarsometatarsus originates fleshy from the anterolateral surface of the proximal end of the tarsometatarsus. It also has some fleshy attachment to the bone over the entire length to the point where it passes through a bony canal in the tarsometatarsus and inserts on the posteromedial side of phalanx I of digit IV. Coturnix Wt.: ♂ 0.012 ± 0.002, ♀ 0.009 ± 0.001; Bobwhite Wt.: ♂ 0.009 ± 0.002, ♀ 0.010 ± 0.003.

Action.--In Coturnix and Bobwhite this muscle extends digit IV adducting it at the same time. Both movements occur at the proximal end of the digit. Cutting (Figure 28) caused a very slight increase in the flexion of digit IV while the track pattern showed a slight increase in the angle formed between digit III and digit IV. It did not, however, interfere in the overall ability of the bird to walk.

M. abductor digiti II

Description for Coturnix and comparison with Bobwhite.--(Figure 9a.) This small muscle located on the posterolateral surface of the proximal end of the tarsometatarsus has a fleshy origin. It forms a tendon which inserts on the dorsal medial surface of the first phalanx of digit II. Coturnix Wt.: ♂ 0.006 ± 0.001, ♀ 0.006 ± 0.001; Bobwhite Wt.: ♂ 0.009 ± 0.002, ♀ 0.010 ± 0.001.

Action.--In Coturnix and Bobwhite this muscle abducts digit II. The movement occurs at the proximal end of phalanx I. Although the locomotor pattern was not affected when the bird was walking, the track pattern showed a small decrease in the angle formed between digit II and digit III.

M. flexor hallucis brevis

Description for Coturnix and comparison with Bobwhite.--(Figure 9b.) This muscle located on the posteromedial side of the tarsometatarsus has a fleshy origin from the hypotarsus and nearly the entire length of the tarsometatarsus. The tendon inserts on the proximal end of the first phalanx of the hallux. Coturnix Wt.: ♂ 0.007 ± 0.001, ♀ 0.007 ± 0.001; Bobwhite Wt.: ♂ 0.015 ± 0.002, ♀ 0.012 ± 0.001.

Action.--In Coturnix and Bobwhite this muscle pulls on the hallux. This pull flexes the hallux at the same time moving it medially. The bend occurs at the level of the first joint. It pulls the hallux more medially than does M. flexor hallucis longus. However, when this muscle was cut the track and locomotor patterns of walking were not affected.

M. adductor digiti II

Description for Coturnix and comparison with Bobwhite.--(Figure 9b.) This small flat muscle deeply situated on the bottom side of the tarsometatarsus has a fleshy origin. Near the distal one-third of the tarsometatarsus, M. adductor digiti II forms a tendon which inserts laterally on the proximal end of phalanx I of digit II. Coturnix Wt.: ♂ 0.003 ± 0.001, ♀ 0.004 ± 0.001; Bobwhite Wt.: ♂ 0.007 ± 0.001, ♀ 0.007 ± 0.001.

Action.--In Coturnix and Bobwhite this muscle adducts digit II. The adduction occurs at the proximal end of the digit. This muscle was not cut.

M. lumbricalis

Description for Coturnix and comparison with Bobwhite.--This muscle must consist of but a few small fibers in Coturnix and Bobwhite. Hudson et al. (1959) describes it as "a single small fleshy slip arising from the anterior surface of the trifurcated tendon of the M. flexor digitorum longus . . ." in the Blue Grouse. George and Berger (1966) state that "for all practical purposes, the muscle appears to be absent in the majority of birds." This latter statement applies to Coturnix and Bobwhite.

M. abductor digiti IV

Description for Coturnix and comparison with Bobwhite.--(Figure 9b.) This small muscle located on the posterolateral surface of the tarsometatarsus has a fleshy origin from the hypotarsus and much of the posterolateral surface of the tarsometatarsus. It inserts on the lateral surface of the proximal end of the first phalanx of digiti IV. Coturnix Wt.: ♂ 0.010 ± 0.001, ♀ 0.010 ± 0.001; Bobwhite Wt.: ♂ 0.014 ± 0.002, ♀ 0.015 ± 0.002.

Action.--In Coturnix and Bobwhite this muscle abducts digit IV. The bend for the outward movement occurs at the proximal end of the digit. Although there was no effect on the locomotor pattern when walking, the track pattern showed a very slight decrease in the angle formed between digits III and IV when this muscle was cut.

Significant morphological findings

Hudson et al. (1959) have done a monumental work of a descriptive nature on most genera of gallinaceous birds. They did not use Coturnix in that study, but in their computer analysis of the appendages of the gallinaceous birds (Hudson et al., 1966), they found that Coturnix have sesamoids in the M. extensor digitorum longus and M. flexor perforatus digiti IV. I found sesamoids in these muscles in only one of 15 Coturnix examined, a seven month old bird. The 15 birds ranged in age from six to 28 months.

Hudson et al. (1966) noted that *Coturnix pectoralis* did not have these sesamoids. Perhaps future studies will reveal that some birds in this species do have them.

Differences were found between the descriptions of Blue Grouse (Hudson et al., 1959) and my findings in Coturnix which could not be resolved as species variations. They stated that M. adductor digiti II inserts on the medial side of digit II. I found that in Coturnix and Bobwhite this muscle inserts on the lateral side where it would have to insert to be an adductor of digit II.

Another point of confusion exists over the origin and insertion of M. popliteus. Miller (1937) concluded that this muscle originates from the tibiotarsus and inserts on the fibula. Hudson et al. (1959) stated that it inserts on the tibiotarsus and takes its origin from the fibula. My research on this muscle indicates that it moves the fibula.

If one considers the stable element to be the origin and the movable element the insertion, then Miller is correct. If one agrees with Romer (1962) that the most proximal end of the muscle in an appendage is always the origin, then Hudson et al. are correct.

I believe that Miller is correct for the following reasons: (1) the difference in proximity to the body of the two ends of the muscle would be minute even in large birds, since the muscle lies nearly perpendicular to the body axis; (2) origin and insertion generally carries the connotation of the first definition, therefore to use Romer's definition would be misleading; (3) this would be the only muscle in the limb where action did not correlate with insertion.

Thus, in the interest of continuity and clarity, I have adopted the Miller concept of the origin and insertion of this muscle.

I also found M. flexor perforans et perforatus digiti II to be longer than M. flexor perforans et perforatus digiti III in Bobwhite and Coturnix. The illustration of these muscles in the Blue Grouse in Hudson et al. (1959) gives the impression that M. flexor perforans et perforatus digiti III is the longer of the two muscles. M. flexor perforans et perforatus digiti III is heavier, but it is the shorter of the two muscles in Coturnix and Bobwhite. This could have been a species variation but was not noted as such by Hudson et al. (1959). Furthermore, a lateral view of the musculature of the leg following removal of the M. femoritibialis medius should reveal the M. ambiens. This was not illustrated by Hudson et al. (1959).

Compared to most other gallinaceous birds, Bobwhite had a greatly reduced number of sesamoids. Bobwhite had sesamoids in M. flexor perforatus digiti III, M. flexor hallucis longus, and M. flexor digitorum longus. Coturnix was found to have additional sesamoids in the M. extensor digitorum longus and M. flexor perforans digiti IV.

Hudson et al. (1959) suggested that sesamoids are not adaptive. If this is, in fact, a valid phylogenetic criterion, Coturnix does not appear to be closely related to Bobwhite. Since no other known gallinaceous bird has this combination or number of sesamoids, it appears that Coturnix is not closely related to any other birds included in this order. This supports the research of Mainardi (1959) who found on the basis of serology that Coturnix is not closely related to other gallinaceous birds. Sibley (1960) drew similar conclusions based on egg protein analysis. The long tendons, the presence of M. adductor digiti II, and the fact that the leg resembles conditions characteristic of the Phasianidae clearly indicates that Coturnix belongs to this family.

Most of the muscles in Coturnix and Bobwhite were found to be similar. The weight of each was greater in Bobwhite, but origin and insertion were generally similar. The greatest variation in origin and insertion occurred in the fusion of the tendon of the M. semitendinosus with the tendon of the M. semimembranosus in Bobwhite, which is not the case in Coturnix. Another difference is the insertion of the M. sartorius, which in Bobwhite inserts in part on the tendon of the M. femoritibialis internus above the patellar tendon, whereas in Coturnix it inserts in the patellar tendon and tibial crest. However, since these muscles have such an important role in walking, their phylogenetic value is questionable. In Coturnix the separate tendon of the M. semimembranosus inserting below the

M. semitendinosus may be an adaptive feature to increase the running speed at the expense of power, perhaps a survival factor. Similarly, the attachment of the M. semimembranosus to the M. semitendinosus in Bobwhite may be to increase leverage of the tibiotarsus.

If, indeed, the birds are not closely related as suggested by the sesamoids, serology, and egg protein analysis, the similarity of the muscles can best be explained by the fact that they depend on nearly identical patterns of locomotion in somewhat similar habitats.

Since I was interested, in part, in the relationship between muscle size and action, it was necessary to find a means of measuring this factor. I selected weight because there appears to be little evidence in the literature of its value or lack of it, and partly because it would provide a satisfactory criterion of size. Individual muscle weight has been considered a poor measure of muscle size because of its variability within a species. Even though the birds used for this portion of the study were the same age and from the same genetic stock, there was considerable variability in weight of the individual muscles. However, using several birds, I was able to get a fairly accurate picture of size relationships. The advantage, I believe, of using actual weights is that it gives a clearer visual image of size relationships. A ratio, for example, only projects an abstract relationship. It is difficult to obtain several birds of one known age for some studies, while simply obtaining more than one bird is an impossibility in others. Therefore, in many cases, some other type of measurement has to be used, and the ratio appears to be the best alternative.

If a ratio to determine muscle weight is to be used, it must be selected carefully. For example, even though the females weighed approximately 20 percent more than the males, the individual muscle weights of the female birds were not greater than those of the males. There was no observable relationship between individual muscle weight and body weight.

Another measure which has been used to estimate muscle size in legs is a ratio of individual muscle weight to total leg muscle weight. This appears to be a more valid measure. Anyone who uses this should clearly indicate what the criterion for total leg weight is based upon. I suggest standardizing the ratio as follows:

$$\text{muscle size} = \frac{\text{individual muscle belly weight}}{\Sigma\text{belly weights of all leg muscles}}$$

If this formula were used in all future studies, muscle ratio would become a valuable tool of comparison.

Finally, muscle volume was found to be of little additional value when the weight of the muscle was known, so after the first few birds, I discontinued measuring it.

Significant findings of functional analysis

Pulling on a particular muscle in a freshly killed specimen caused similar actions in Coturnix and Bobwhite. Therefore it is not surprising to see remarkably similar abnormalities in the walking patterns following severance of a particular muscle.

This similarity may be explained in part by the fact that both birds depend primarily on terrestrial locomotion in somewhat similar habitats for their means of movement. Thus, there has been a convergence in muscle function to facilitate terrestrial movement. Both species exhibit several features which, according to Miller (1937), are characteristic of terrestrial locomotion: (1) large bulk of the legs relative to body size; (2) large M. sartorius; (3) large M. iliotibialis; (4) large M. peroneus longus; (5) strong tendons to the toes; and (6) arrangement of M. tibialis anterior, M. biceps femoris and M. gastrocnemius for speed rather than power.

Each leg segment had some muscles which were more important than others in moving that portion of the leg. The more important muscles were the same ones in Coturnix and Bobwhite. First of all the muscles most important in flexing and extending the thigh during walking were the M. sartorius, M. adductor longus et brevis, and M. ischiofemoralis. Of the cut muscles which pull the femur forward, the M. sartorius caused the greatest reduction in femoral movement. Cutting verifies that the iliotrochantericus muscles, because of their close proximity to the head of the femur and consequently shorter power arm, are more vital in rotating the femur than in pulling it forward. Rather than actually rotating the femur, however, they act against the obturator muscles on the posterior surface of the proximal end of the femur to provide a solid support for the head of the femur in the acetabulum. Of the three iliotrochantericus muscles only the M. iliotrochantericus posterior had any visible effect on the locomotor pattern of walking.

Of those muscles pulling the thigh posteriorly, cutting indicates that M. adductor longus et brevis and M. ischiofemoralis cause the greatest reduction in extension during walking.

In moving the shank there are two muscles which are very important in the walking locomotor pattern. Loss of either of these by severing the tendon would greatly impair its chances of survival in the wild. Cutting of the M. biceps femoris causes a great reduction in the ability of the bird to flex its tibiotarsus as evidenced in the reduction of shank movement; therefore it is extremely important in tibial flexion. Another muscle which proved to be of lesser importance in tibial flexion was the M. semitendinosus. Cutting all the parts of the M. femoritibialis greatly impaired the ability of the bird to extend the shank. Another muscle which also proved to be of lesser importance in shank extension was the M. iliotibialis.

For moving the tarsometatarsus two muscles were found to be vital in maintaining continuity in the walking locomotor pattern. The loss of either through muscle severance would most certainly remove any chance of survival in the wild. Unlike the heretofore mentioned "muscle systems" which acted synergistically and assumed more of the load when another muscle was cut, the M. gastrocnemius and the M. tibialis anterior do not have any other synergistic muscle to assume their function. They are the muscles that move the tarsometatarsus.

It is true that M. peroneus longus may pull the tibiotarsus forward slightly, but cutting it indicated that its functional value in pulling the tibiotarsus forward is minimal. It is therefore not surprising to find that cutting the M. gastrocnemius and M. tibialis anterior caused nearly total impairment of walking. This indicates that the M. gastrocnemius is vital for extension, while the M. tibialis anterior is necessary for flexion of the tarsometatarsus.

In the digits there is only one important extensor of the foretoes. Thus when this muscle, the M. extensor digitorum longus, is cut, it results in a very adverse effect on the walking locomotor pattern. Since the bird's toes do not extend as its foot hits the ground, the bird's balance, as well as size of step, is altered. Since the hallux does not play a vital role in walking, the effect of cutting its major extensor, the M. extensor hallucis longus, has a dramatic effect on the ability of the hallux to extend, but has no observable effect on the overall ability of the bird to walk.

In contrast to having one major extensor, there are many flexors of the foretoes. They nearly all cause some effect on the walking pattern when cut, but no single one impeded greatly the birds ability to walk. The flexors of the hallux do not have an effect on the locomotor pattern.

Thus there are certain muscles vital to walking which are associated with each part of the limb. Other muscles were found to be of less importance in the walking pattern. From information gained in this study I have divided the muscles into four groups on the basis of their importance in walking in Coturnix and Bobwhite.

Group 1--Those muscles vital to survival: M. gastrocnemius, M. femoritibialis, M. tibialis anterior, and M. extensor digitorum longus.

Group 2--Those muscles the loss of which would result in a greatly reduced probability of survival in the wild: M. sartorius, M. iliotibialis, M. semitendinosus, M. biceps femoris, M. flexor digitorum longus, and M. adductor longus et brevis.

Group 3--Those muscles that reduce efficiency, but are not vital to survival: the remaining flexors and extensors of the foretoes, M. iliotrochantericus posterior, M. obturator internus, and M. ischiofemoralis.

Group 4--Those muscles that have no observable effect on survival: M. iliacus, MM iliotrochantericus anterior and medius, M. gluteus medius et minimus, M. ambiens, M. piriformis, M. semimembranosus, M. obturator externus, MM. peroneus longus and brevis, M. plantaris, the flexors and extensors of the hallux, the abductors and adductors of the digits, and the M. lumbricalis.

Those muscles which fall in groups one and two would not be desirable to use for phylogenetic purposes since they are subject to great degrees of convergent and divergent evolution. Similarly those muscles of group four appear to be more valid to use in phylogenetic studies. Most of these muscles are small, but others, such as M. peroneus longus, are large so that size is not a sole criterion of importance of action in walking.

Strength of a muscle is usually associated with its bulk and shape. On this basis the M. extensor digitorum longus, for example, does not appear to be extremely powerful, yet it is one of the most vital muscles for walking. Thus neither strength nor size should be considered the sole criterion for importance of a muscle in walking.

If scratching, running, and other types of locomotor studies prove that muscles in group four are of little functional value, then these muscles can and should be weighted in future numerical studies using computer analysis.

Finally, those muscles which fall into group four include those which Berger (1957) proposed to add to the muscle formula. Group four includes other muscles, such as the flexors and extensors of the hallux, which are not in the formula because they are probably important in other types of leg movements even though their role in walking is minimal. Additional studies of the role of these muscles are necessary before one could determine the validity of inclusion or exclusion of them in the muscle formula.

SUMMARY AND CONCLUSIONS

This investigation was undertaken to study and compare leg muscles and their function in Coturnix and Bobwhite.

The muscles of Coturnix are described and compared with Bobwhite as to origin, insertion, location, and weight, including any unique variation noted in a particular muscle.

Several variations were found between the two species. Probably the most important of these is the greater number of sesamoids in Coturnix, which has two more than Bobwhite. Since this feature is apparently nonadaptive, Coturnix does not appear to be closely related to Bobwhite on the basis of this one characteristic. Furthermore, since Coturnix does not resemble any other known gallinaceous bird in the number of sesamoids present, it does not appear that Coturnix is closely related to any other gallinaceous bird on the basis of this characteristic.

Other variations, such as type of attachment, shape, and presence or absence of a muscle slip resemble those of other members within the family Phasianidae.

Differences were found between the descriptions of Blue Grouse (Hudson et al., 1959) and my findings in

Coturnix which could not be resolved as species variations. I found that M. adductor digiti II inserts on the lateral, rather than the medial, surface of digit II. While perhaps technically correct, the description of Hudson et al. (1959) of the origin and insertion of M. popliteus is misleading; therefore, I have followed Miller (1937) in reversing this description. Their drawings of the lateral view should show M. ambiens after the removal of M. femoritibialis medius. A difference which could be a species characteristic, but which was not noted as such, was the length of M. flexor perforans et perforatus digiti III as appearing longer than M. flexor perforans et perforatus digiti II. It was the reverse of this condition in all the gallinaceous birds observed in this study.

Since I was interested in muscle size in relation to action, it was necessary to find a means of studying size. Weight was selected because it is a measure which can be readily understood. The major problem with using this measure is that it is variable even in birds of a known age and stock. It was possible to overcome this by using several birds, but this might not be feasible in some other studies. Therefore, I propose that the most valid means of estimating size in future studies is the standardized ratio:

$$\text{muscle size} = \frac{\text{individual muscle belly weight}}{\Sigma\text{belly weights of all leg muscles}}$$

If all myologists use the same formula, the muscle ratio would become a valuable tool of muscle comparison.

In addition to this classical approach to muscle study, the action was studied indirectly through pulling the leg muscle tendons in freshly killed specimens. In order to obtain direct evidence of function, the tendon of the muscle being studied was cut, after which motion pictures and tracks of their walking patterns were made and analyzed. The results were compared to a sham operated bird to see if any differences in locomotor or track pattern had occurred.

The locomotor pattern from the time of hatching resembles that of the adult in both species except for length of step and footprint, although there were differences between the species. Furthermore, Coturnix and Bobwhite exhibit similar abnormalities in walking patterns following severance of a particular muscle.

There are a few muscles which, if cut, totally impair walking in both species. The ones which had the greatest negative effect on the locomotor pattern when cut were M. gastrocnemius, M. femoritibialis, M. tibialis anterior, and M. extensor digitorum longus. The bird could not survive in the wild without these. Another larger group of muscles, including the other major extensors and flexors of the leg, would greatly reduce the chances of survival in the wild. A third group of muscles would reduce efficiency, but not inhibit survival. This group includes the major abductors and adductors, as well as those muscles which hold the femur in place. Finally, there was a group of muscles that could be lost without any adverse effect on walking. These include many of the smaller muscles such as the M. gluteus medius et minimus.

However, importance in walking is not necessarily correlated with muscle size. Of the muscles which are most important in maintaining continuity of step, M. extensor digitorum longus and M. tibialis anterior are not particularly large. The M. peroneus longus, on the other hand, is larger, but is not vital to the walking locomotor pattern. Its only role in walking may be to prevent toeing in.

Strength of a muscle is usually associated with shape and bulk. On this basis the M. extensor digitorum longus, for example, does not appear to be extremely powerful, yet it is vital to survival. Thus, neither size nor strength should be considered as the sole criterion for importance of a muscle in a particular locomotor activity.

On the basis of this study, the muscles which would be of least importance in walking, and thus subject to least adaptation, correspond to the muscle formula as proposed by Garrod (1873) and expanded by Berger (1957). A word of caution must be interjected in that some of these muscles may be of greater value in some other type of locomotor patterns, such as scratching; therefore, further studies are necessary to determine their role in such activity. However the muscle formula is of taxonomic value and should be retained.

Future studies using any numerical evaluations of characteristics, such as the recent computer analysis studies to determine relationships, should refine their techniques to weight the above mentioned group of muscles. Unless this is done, there is a very real danger of masking true relationships. If this happens, characteristics which are subject to much adaptation may be overemphasized.

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APPENDIX

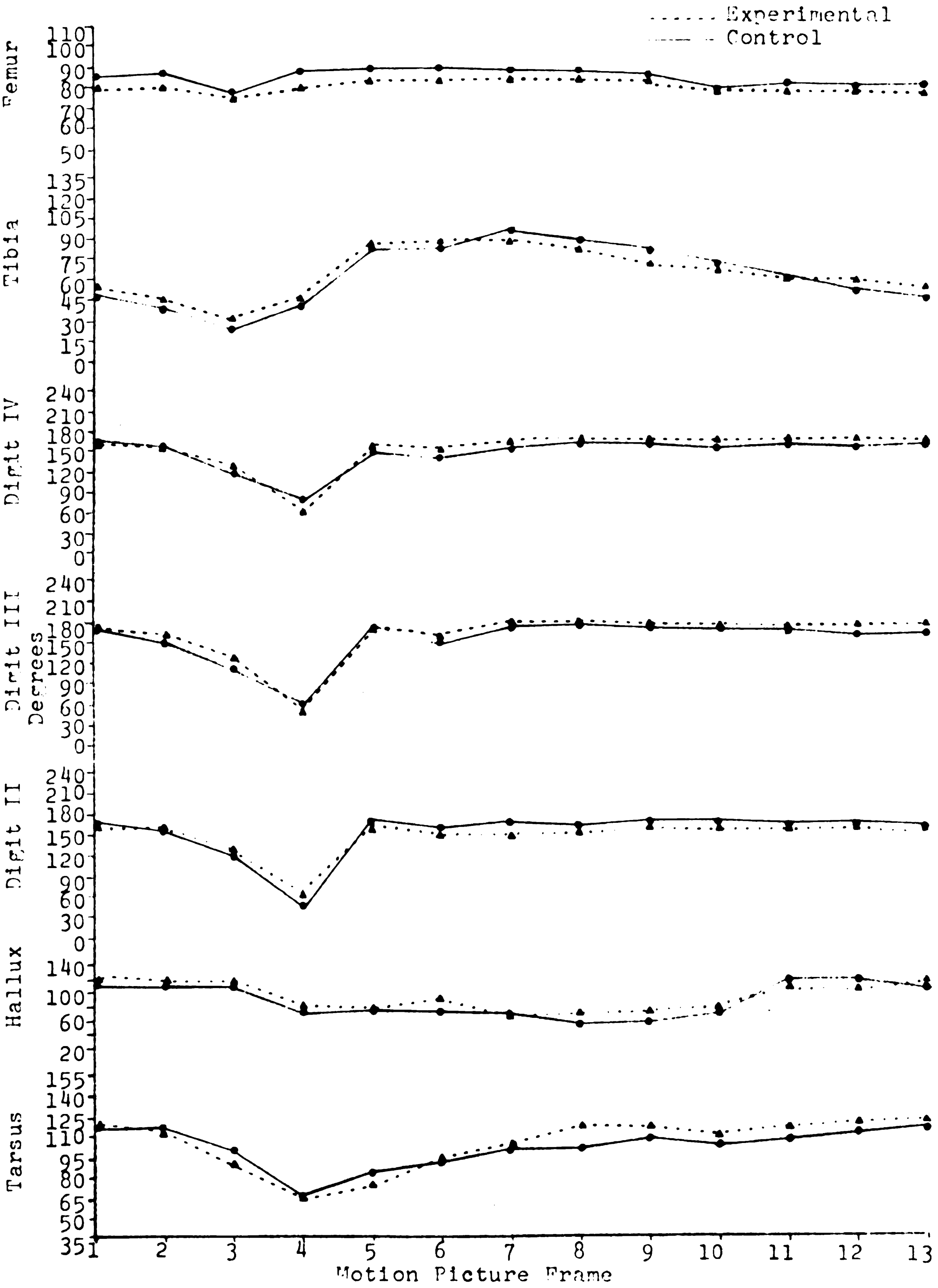

Figure 10. The locomotor pattern of Coturnix following severance of M. sartorius.

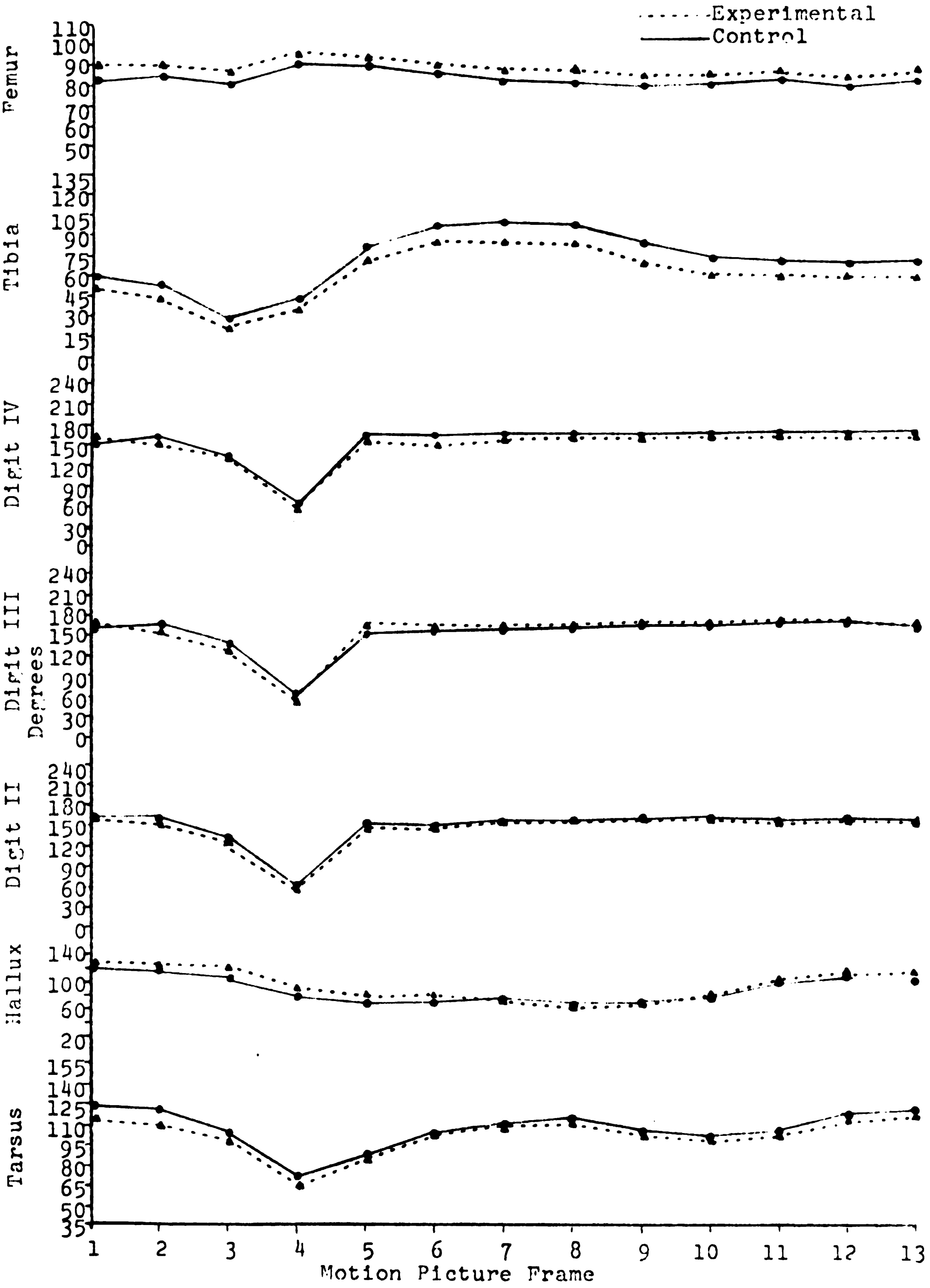

Figure 11. The locomotor pattern of Coturnix following severance of M. iliotibialis.

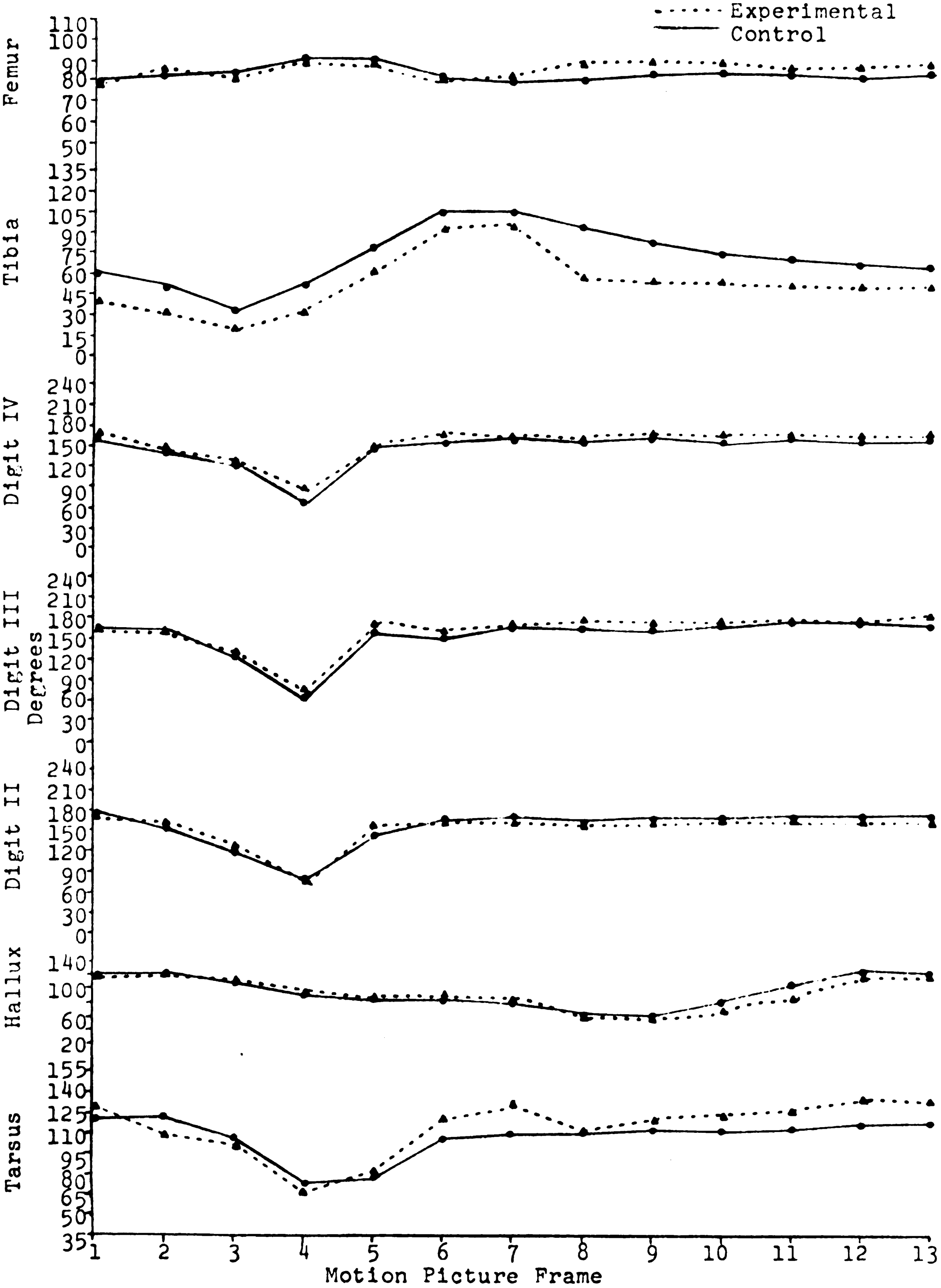

Figure 12. The locomotor pattern of Coturnix following severance of M. femoritibialis.

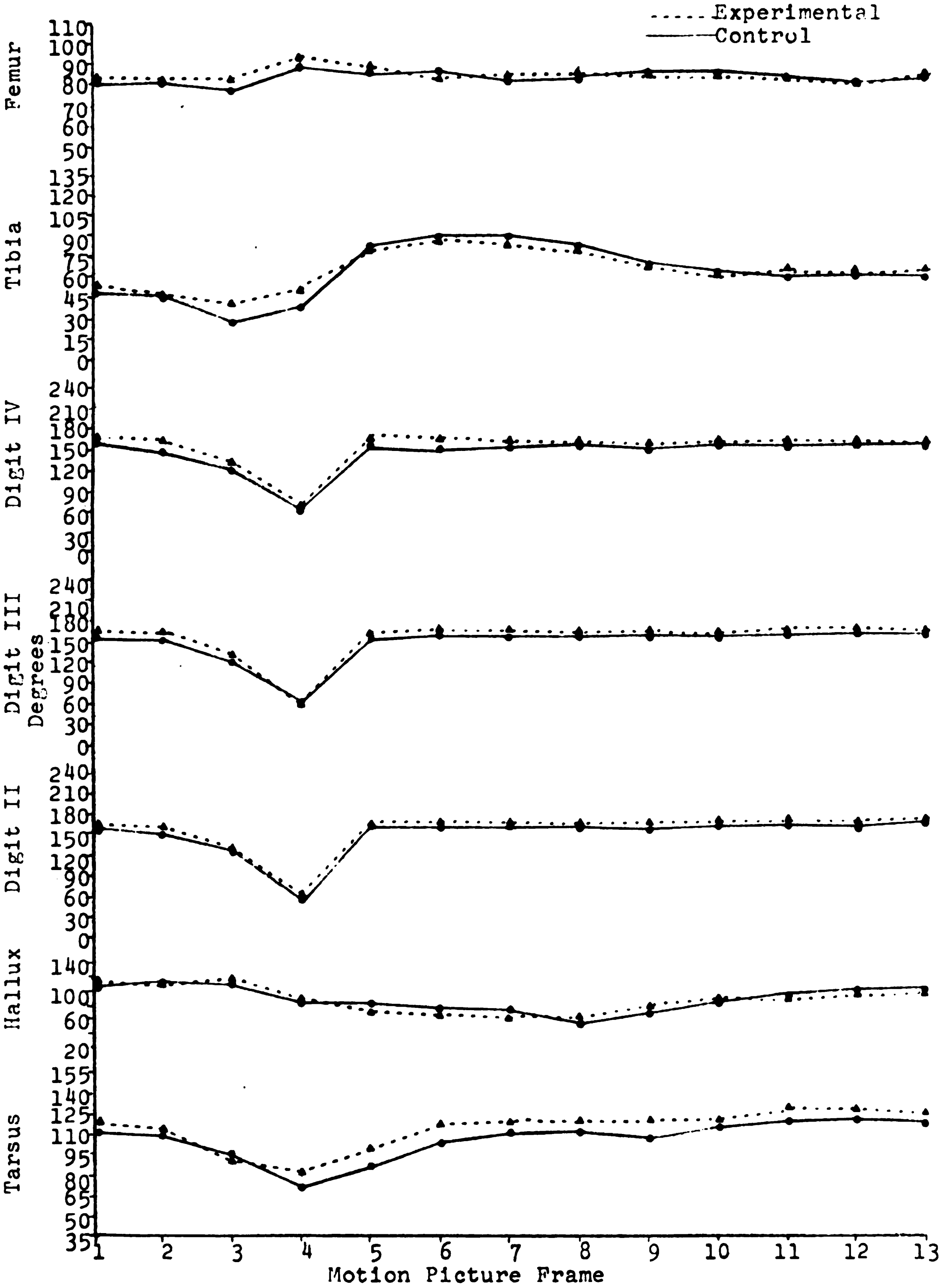

Figure 13. The locomotor pattern of Coturnix following severance of M. semitendinosus.

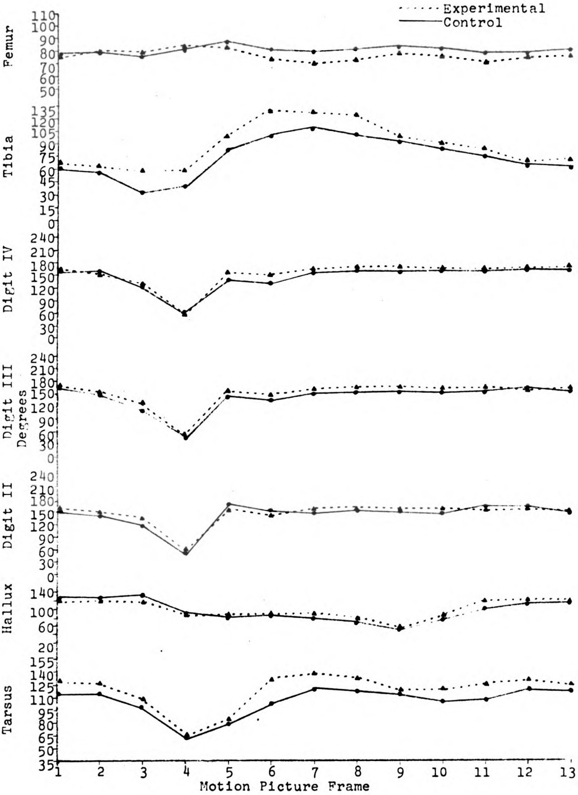

Figure 14. The locomotor pattern of Coturnix following severance of M. biceps femoris.

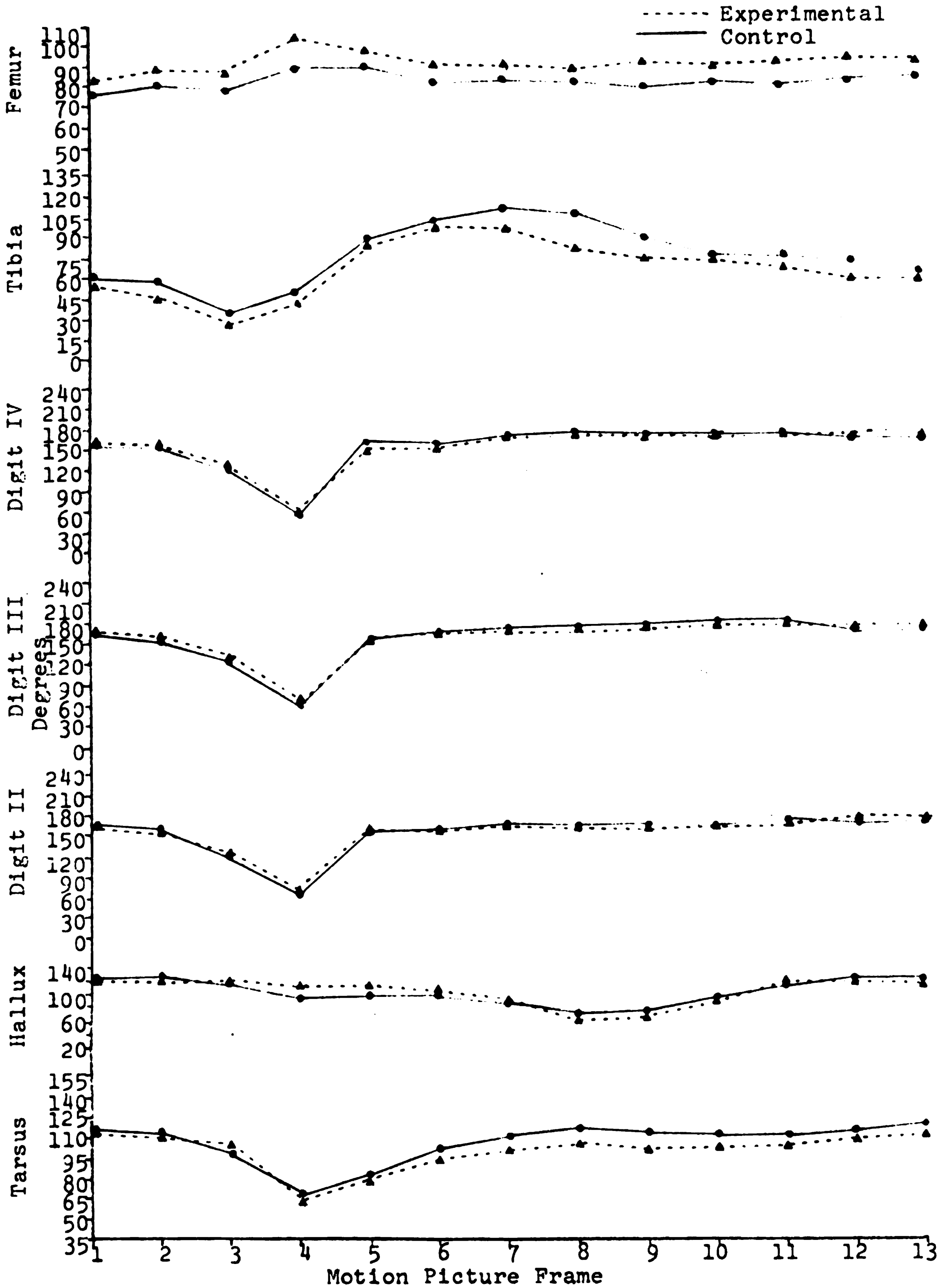

Figure 15. The locomotor pattern of Coturnix following severance of M. ischiofemoralis.

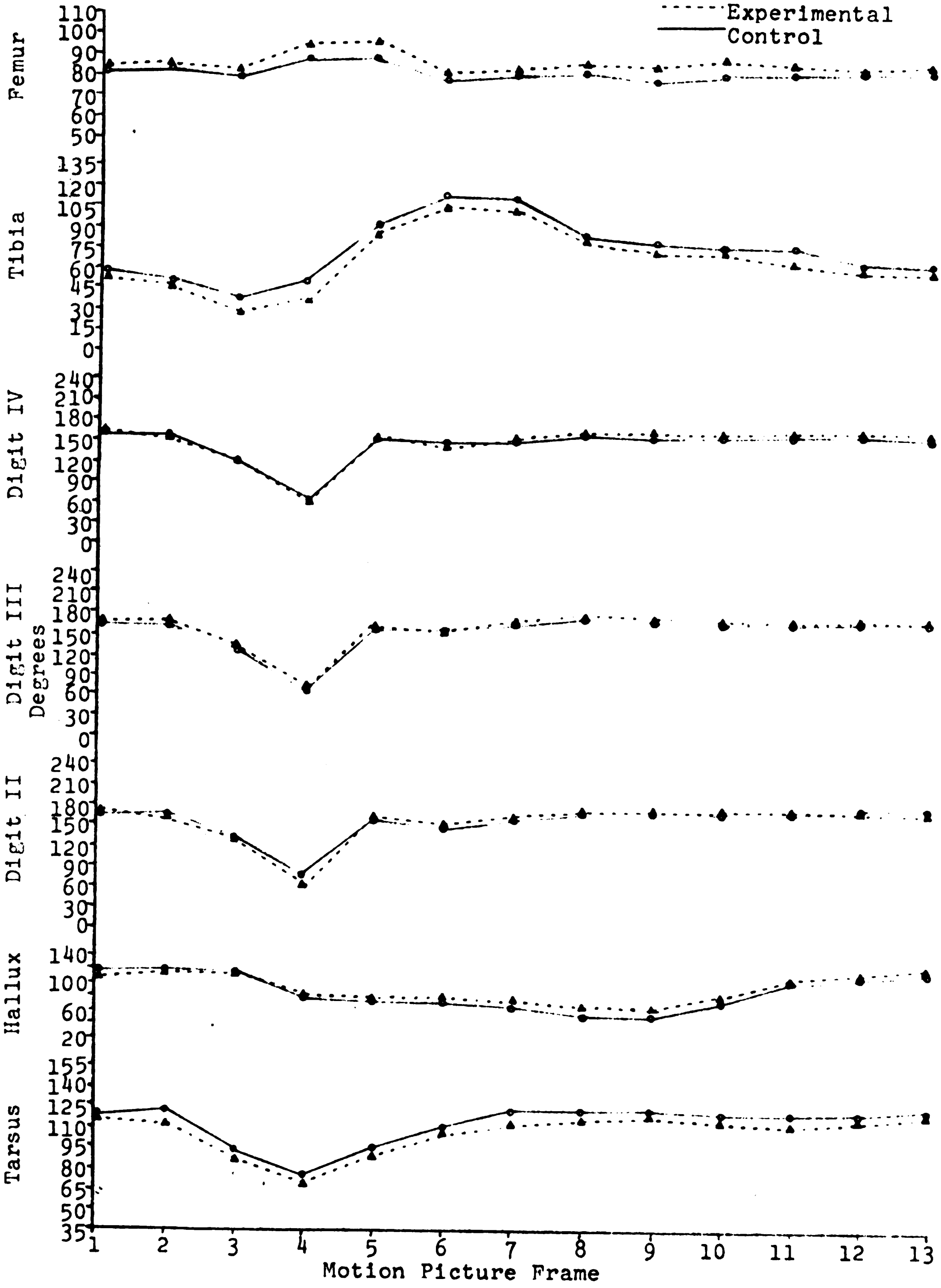

Figure 16. The locomotor pattern of Coturnix following severance of M. obturator internus.

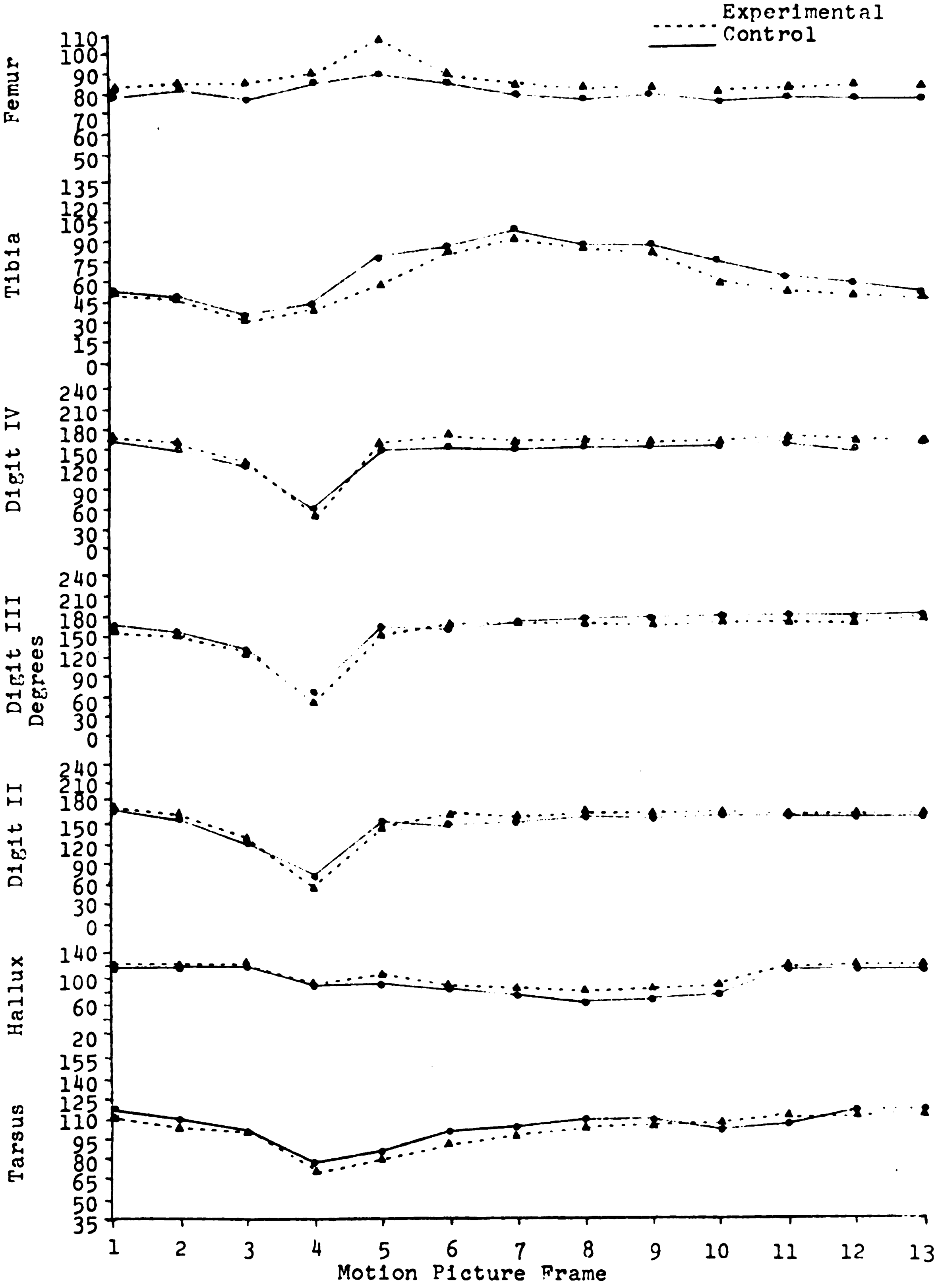

Figure 17. The locomotor pattern of Coturnix following severance of M. adductor longus et brevis.

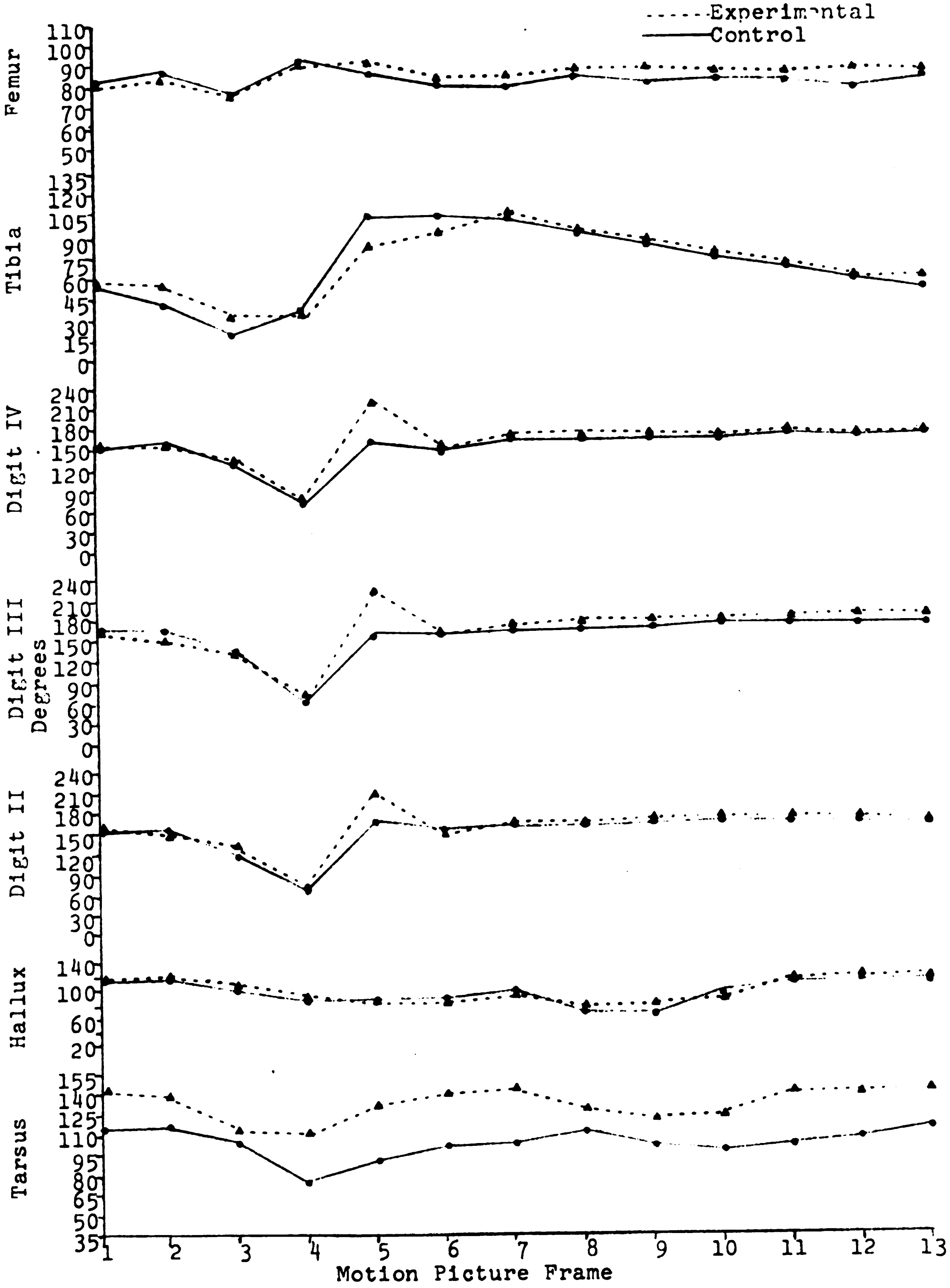

Figure 18. The locomotor pattern of Coturnix following severance of M. tibialis anterior.

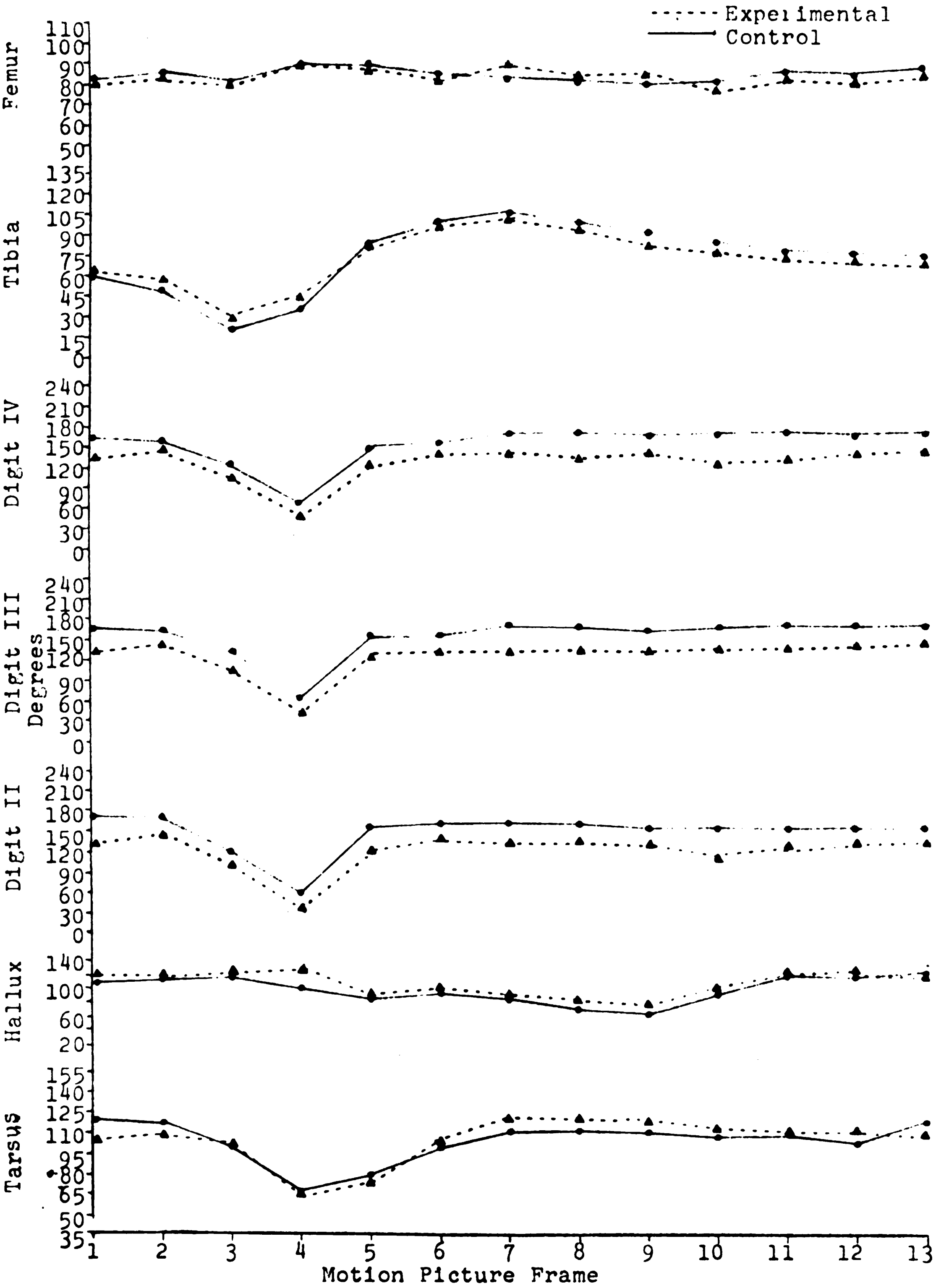

Figure 19. The locomotor pattern of Coturnix following severance of M. extensor digitorum longus.

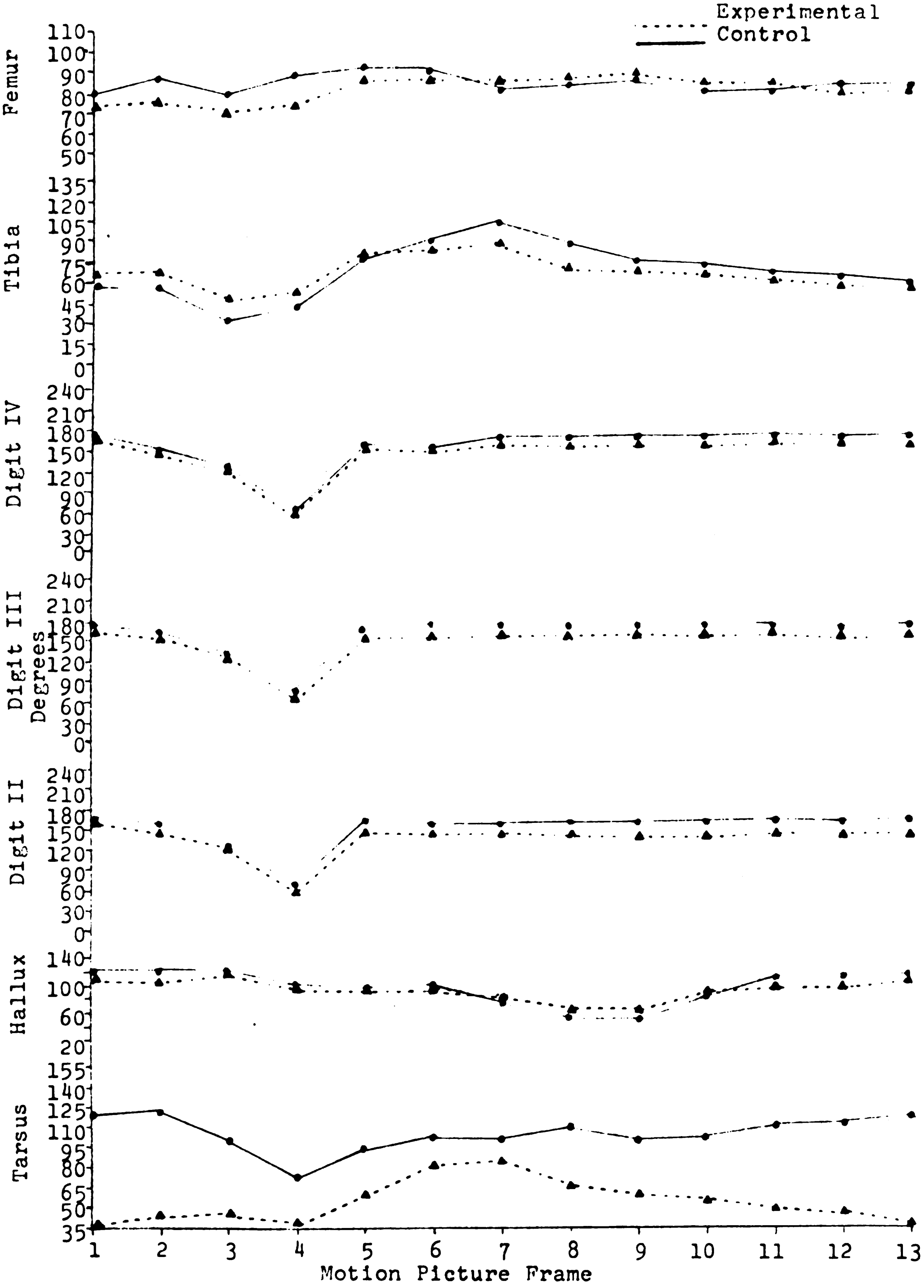

Figure 20. The locomotor pattern of Coturnix following severance of M. gastrocnemius.

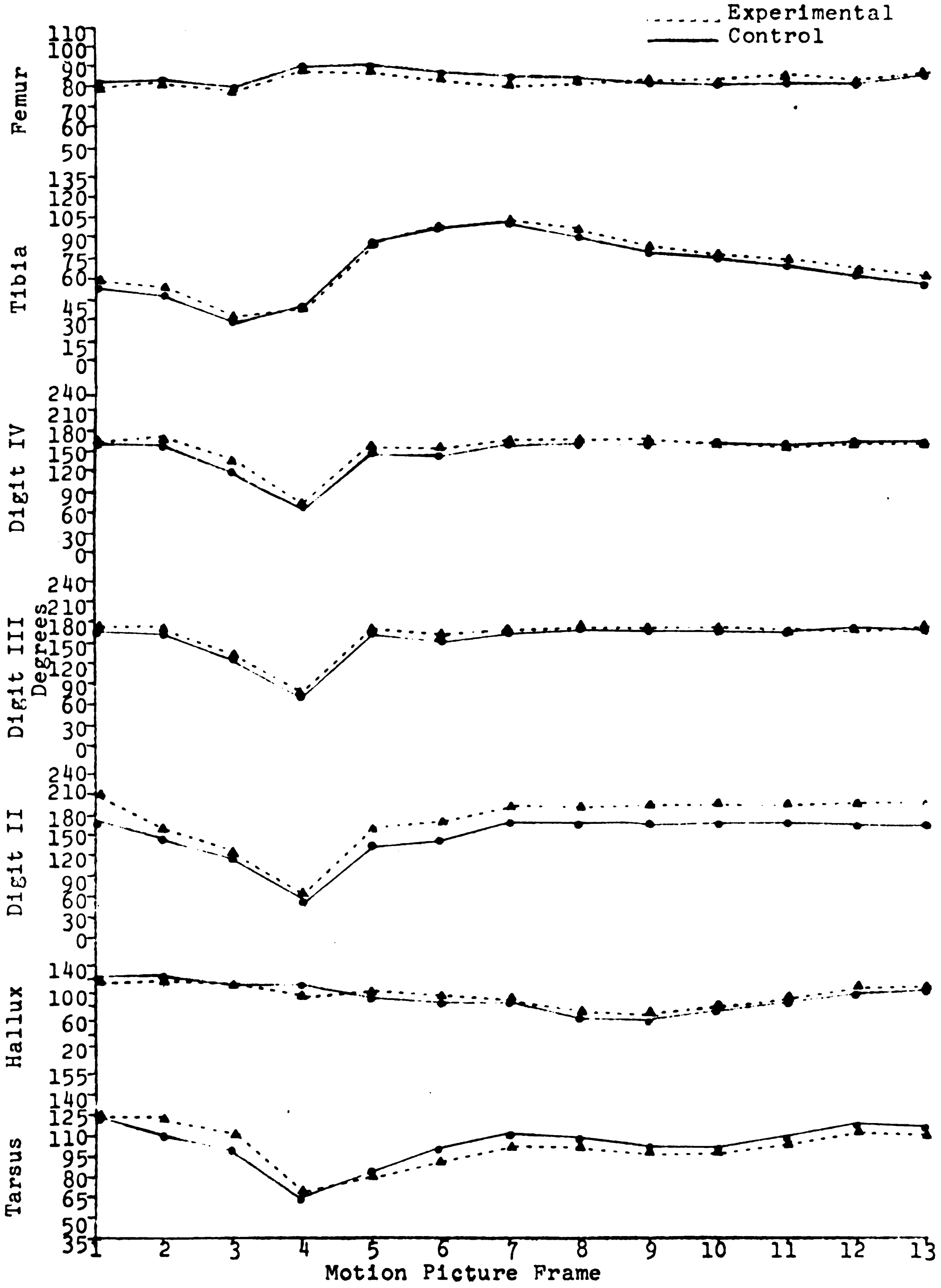

Figure 21. The locomotor pattern of Coturnix following severance of M. flexor perforans et perforatus digiti II.

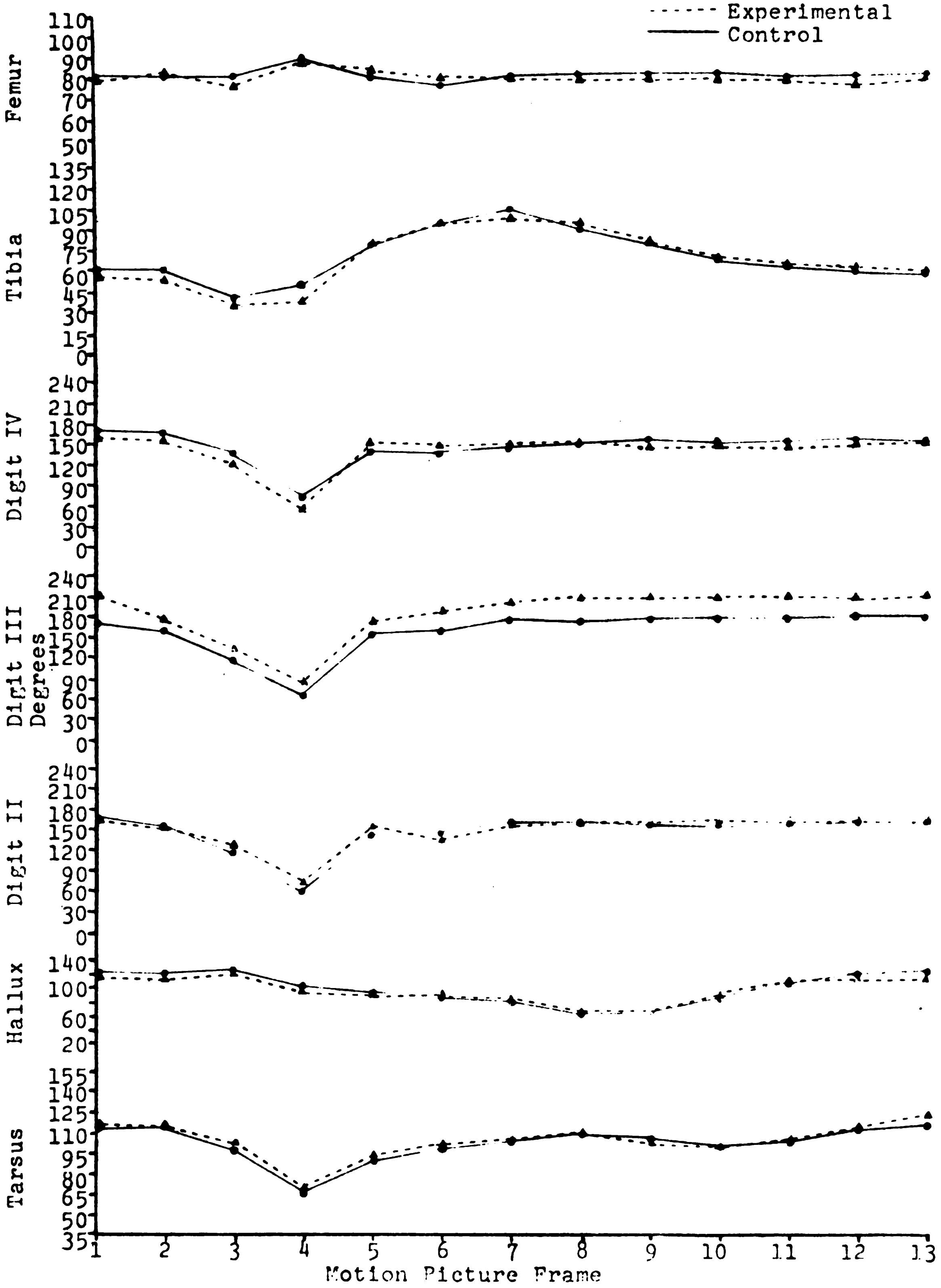

Figure 22. The locomotor pattern of Coturnix following severance of M. flexor perforans et perforatus digiti III.

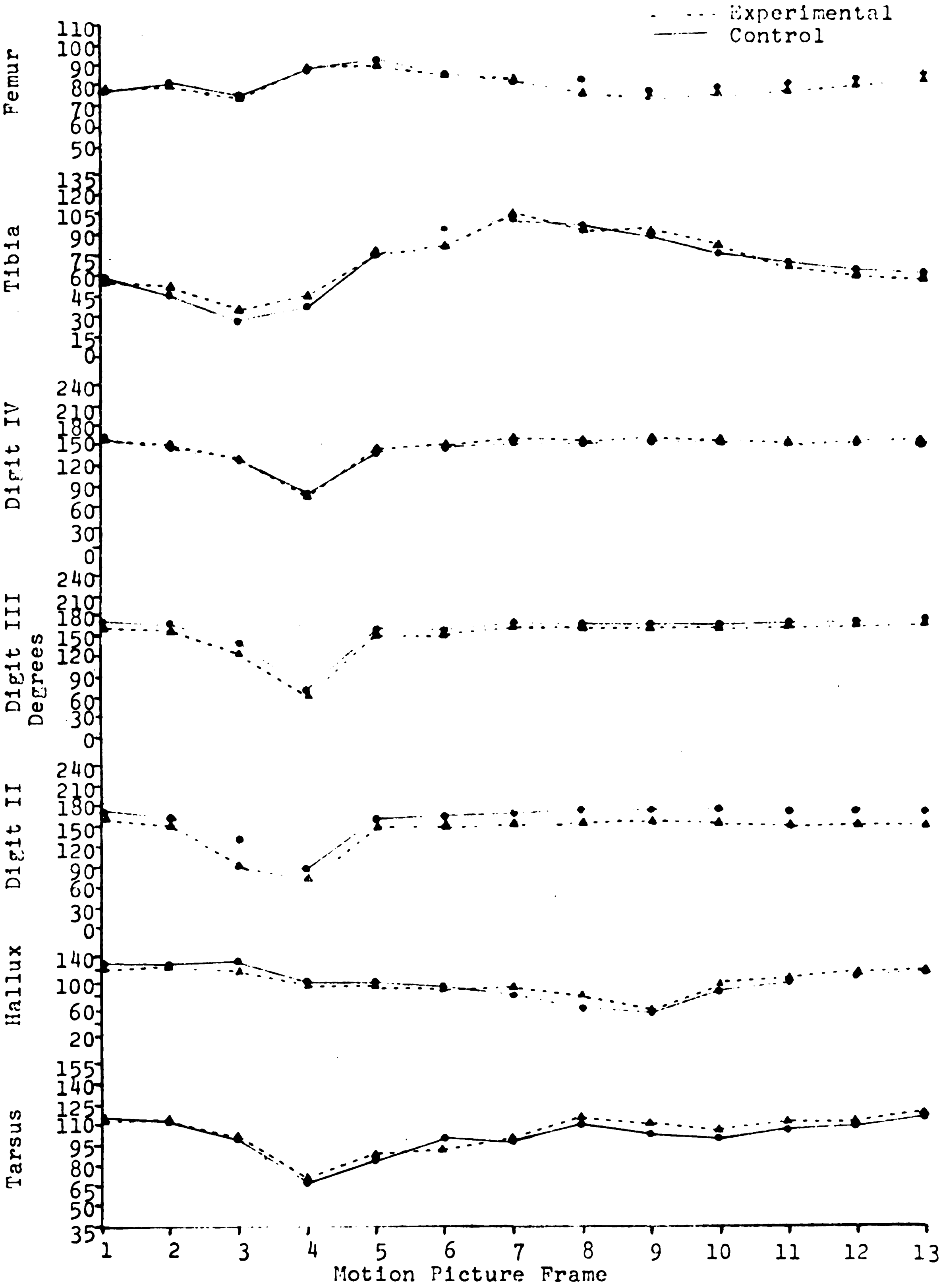

Figure 23. The locomotor pattern of Coturnix following severance of M. flexor perforatus digiti II.

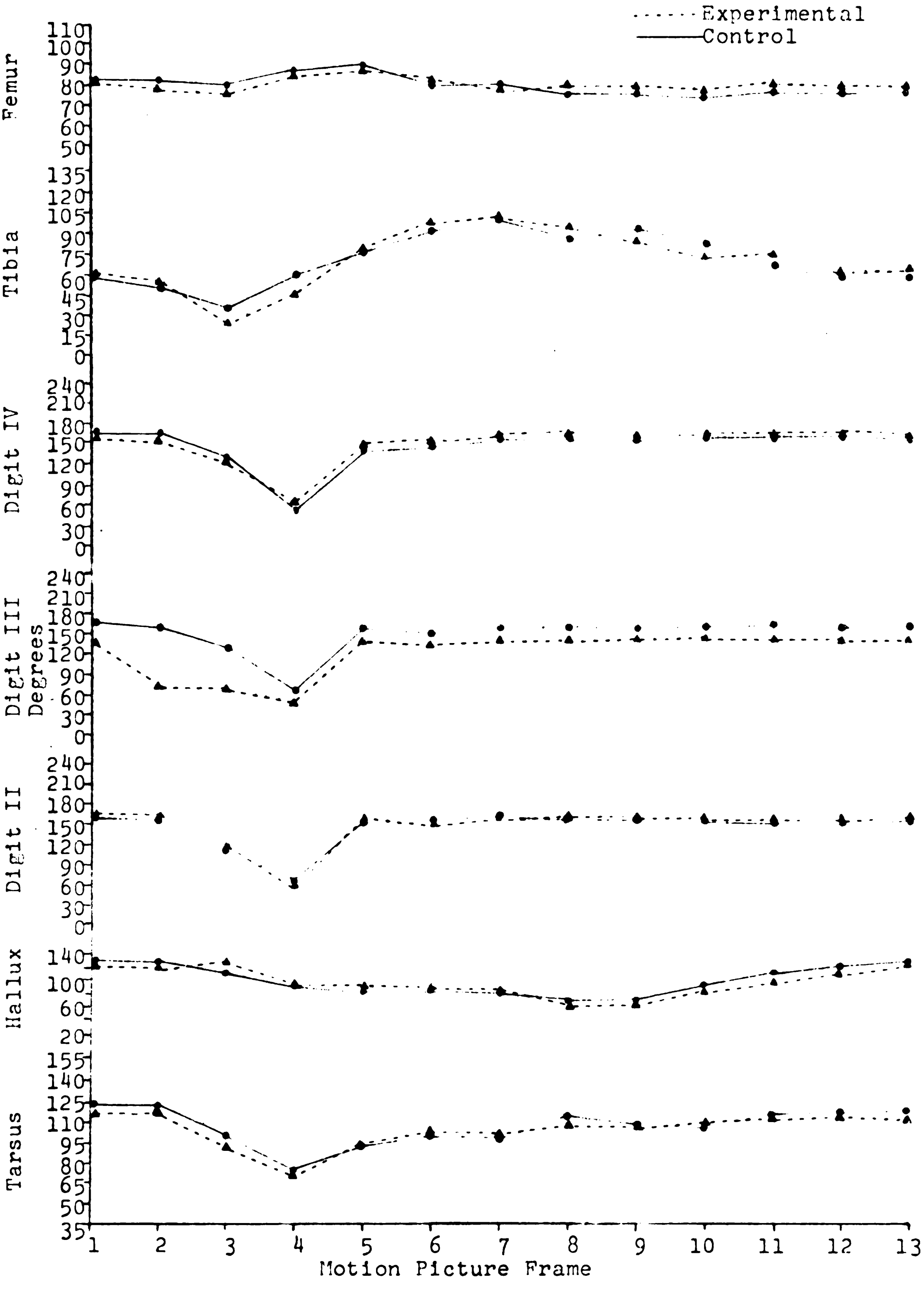

Figure 24. The locomotor pattern of Coturnix following severance of M. flexor perforatus digiti III.

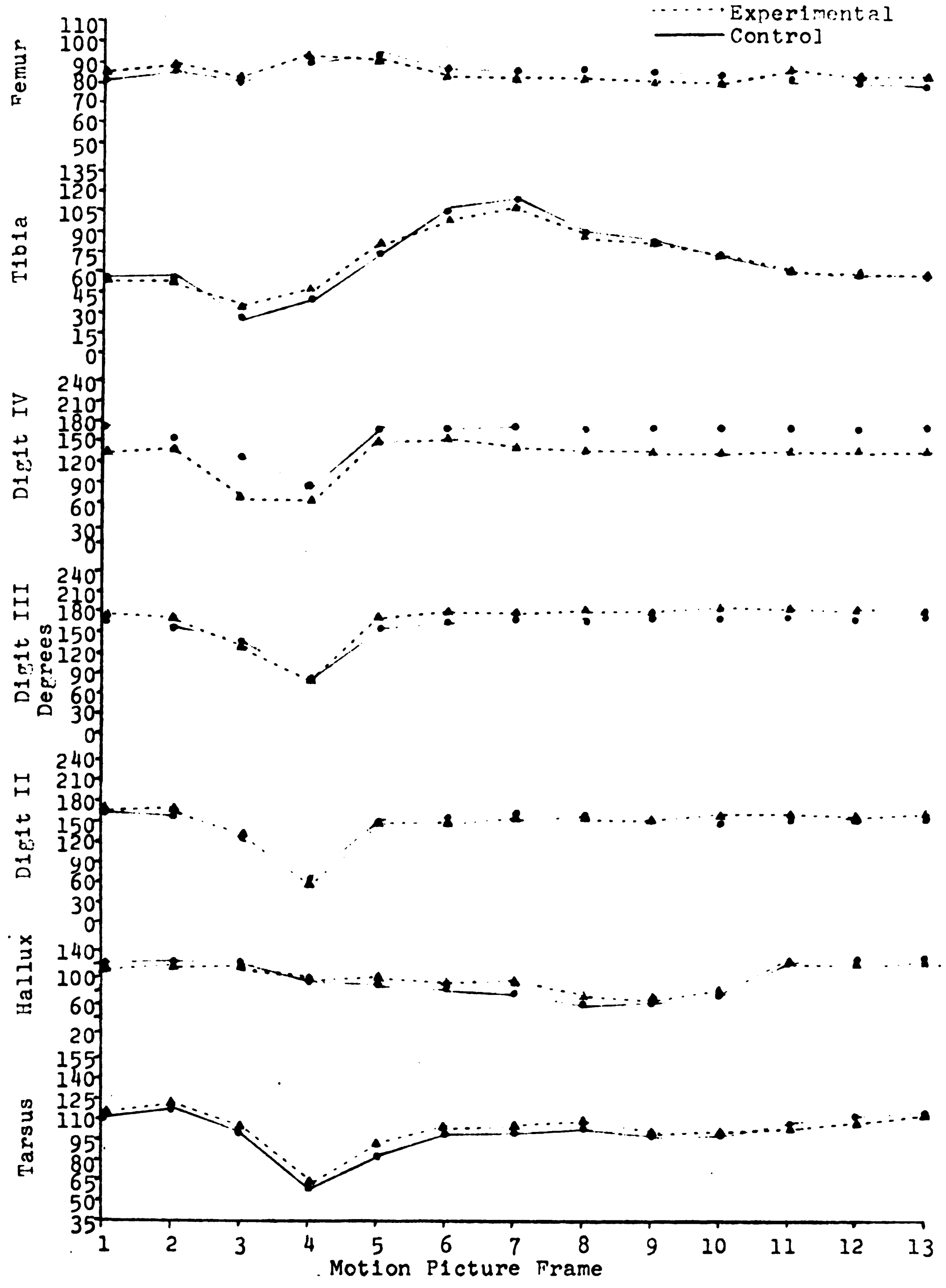

Figure 25. The locomotor pattern of Coturnix following severance of M. flexor perforatus digiti IV.

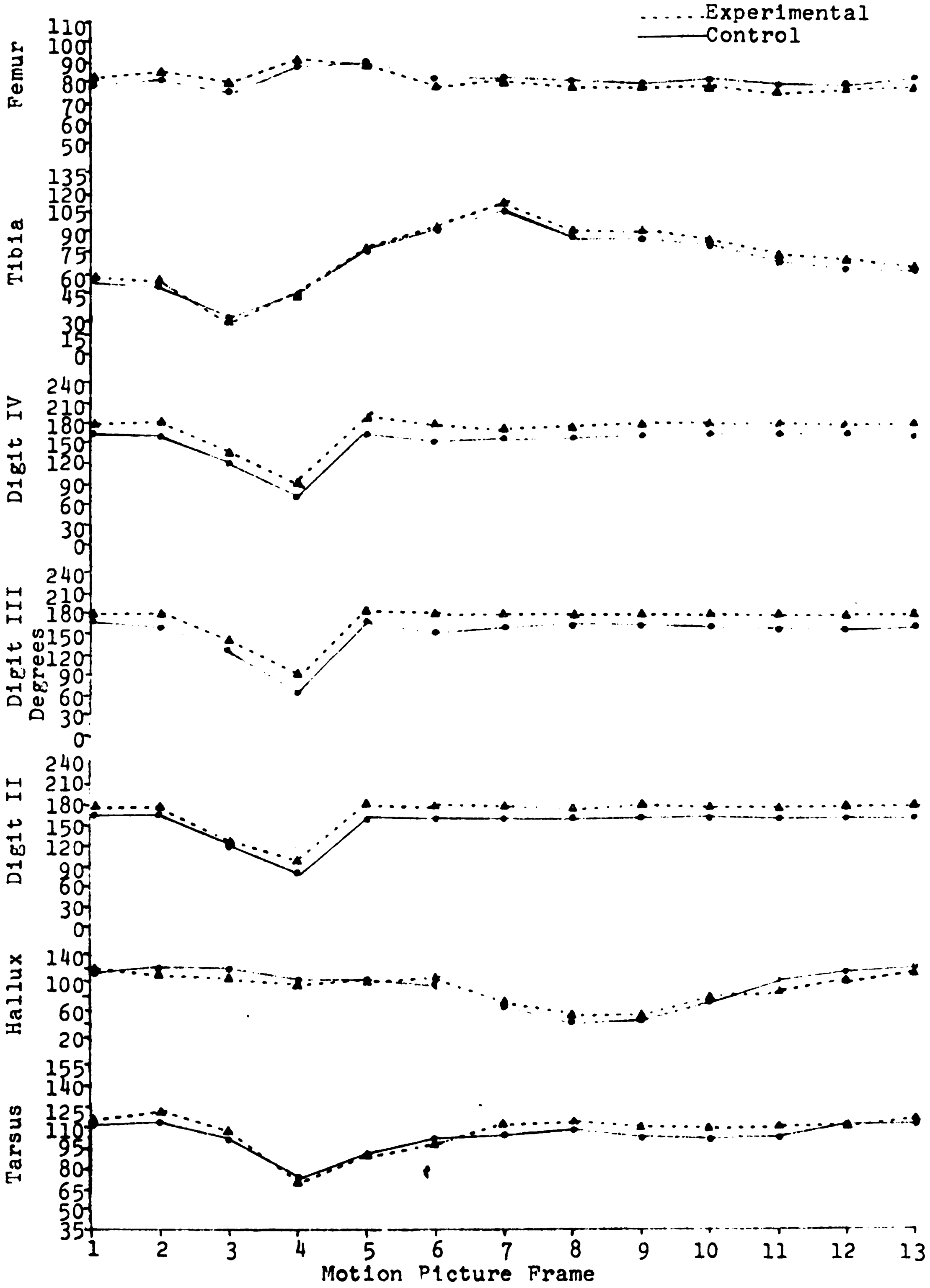

Figure 26. The locomotor pattern of Coturnix following severance of M. flexor digitorum longus.

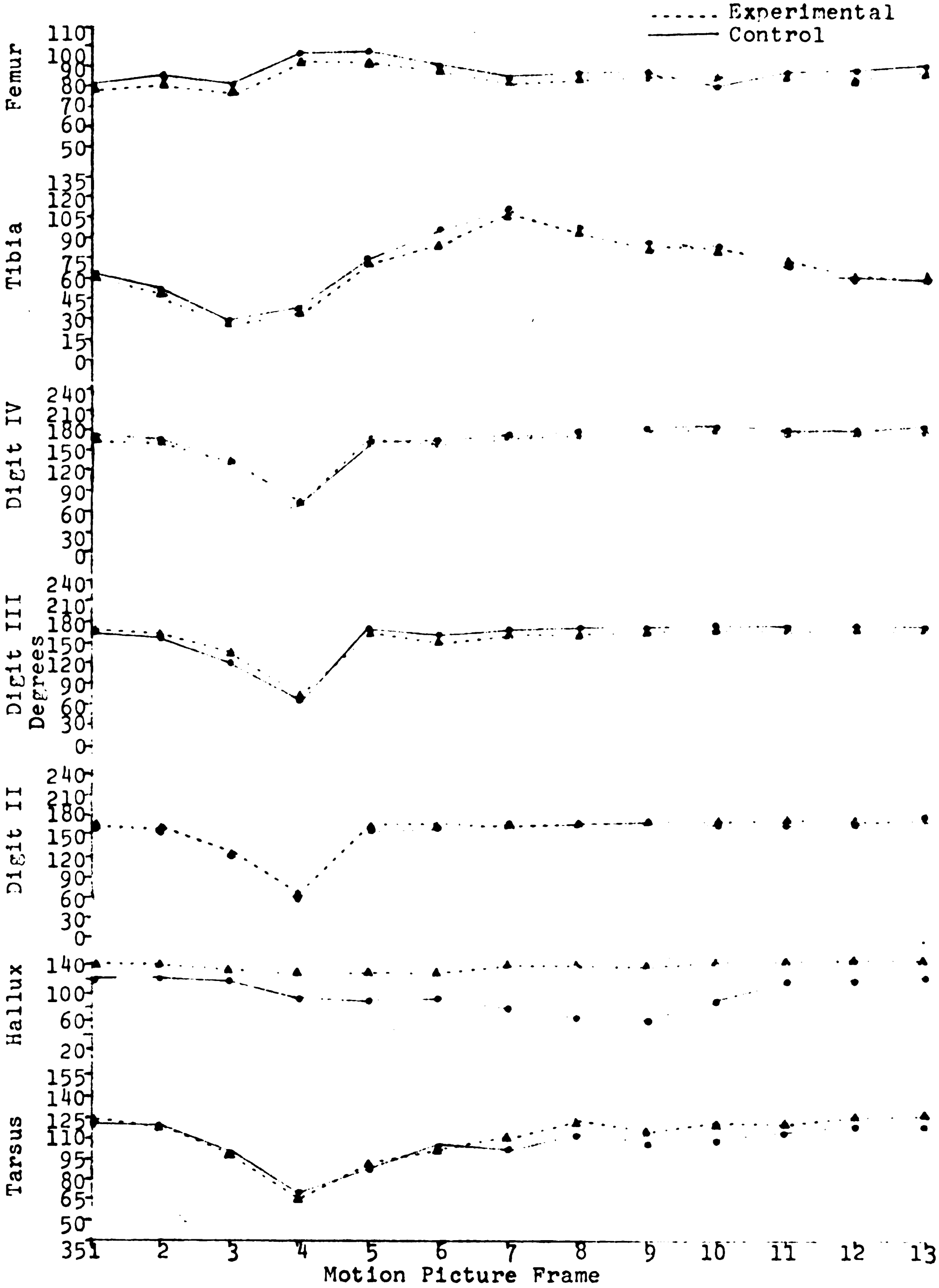

Figure 27. The locomotor pattern of Coturnix following severance of M. flexor hallucis longus.

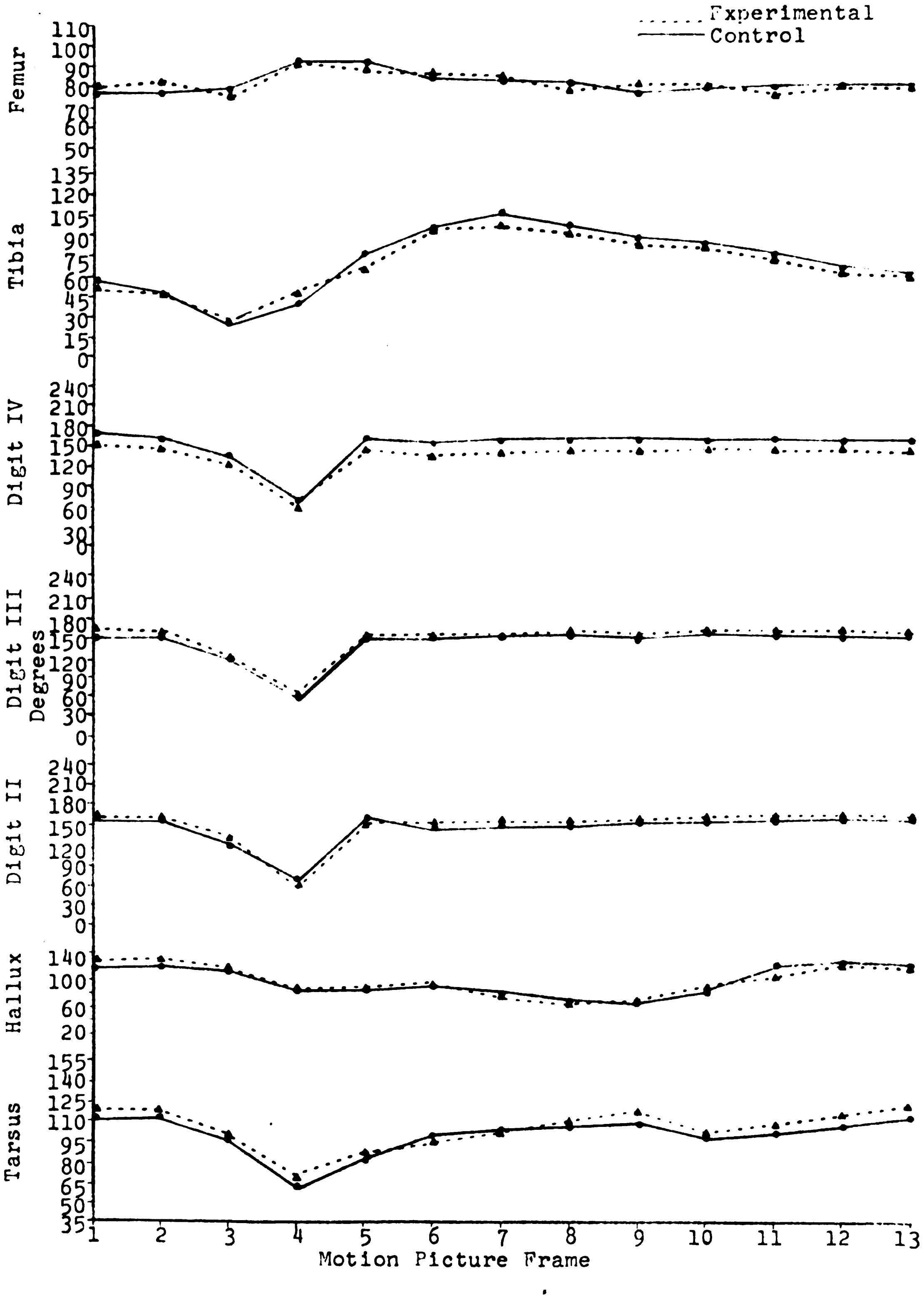

Figure 28. The locomotor pattern of Coturnix following severance of M. extensor brevis digiti IV.