

ADAPTIVE MECHANISMS OF THE RAPTOR PELVIC LIMB

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THIS study presents some adaptations in the pelvic limb of six North American raptorial species. Bock and von Wahlert (1965) point out the term "adaptation" needs to be defined when used. I studied evolutionary adaptations as I am interested in those structural features that enable raptors to sustain a predatory role within a given environment. I am not concerned with evolutionary pathways. In this regard, I studied closely related and diverse species having similar habits. I investigated the raptorial species from both orders and four of the five families in North America (the nonpredaceous New World vultures, the Cathartidae, were omitted). The species studied were the Cooper's Hawk (*Accipiter cooperii*), Red-tailed Hawk (*Buteo jamaicensis*), Prairie Falcon (*Falco mexicanus*), Sparrow Hawk (*Falco sparverius*), Screech Owl (*Otus asio*), Burrowing Owl (*Speotyto cunicularia*), and the Barn Owl (*Tyto alba*). I compared the raptors to one another, as well as to a generalized nonraptorial species. A "generalized" species is difficult to define, but one that does not use its legs and feet for any particular activity other than walking or standing seems appropriate. I selected the domestic pigeon (*Columba livia*).

The functional aspects of the anatomy of the birds of prey have been little studied. Garrod (1875) described the vinculum connecting the tendons of the flexor digitorum longus and flexor hallucis longus for several genera of Falconiformes. Subsequent workers (Shufeldt, 1887; Hudson, 1937; Ruggeberg, 1960) further discussed the fusion of these tendons. Shufeldt (1909) presented a very general account of the osteology of several species including *A. cooperii*, *B. jamaicensis*, and *F. mexicanus*. Peczely (1964) compared the thoracic vertebrae of several genera of raptors including *Buteo*, *Accipiter*, and *Falco*. Where possible, he related anatomical differences to the habits of the birds. Studies of the pelvic region of various genera of Falconiformes and Strigiformes were made by Hudson (1937, 1948) and Berlin (1963).

Accurate determination of muscle forces has long presented a problem to morphologists. Present knowledge of muscle structure and physiology limit severely the traditional techniques of comparing muscle volumes and weights (for a review, see Gans and Bock, 1965). Eccles and Sherrington (1930) demonstrated the dangers of using the weight (and thus volume) of muscles as an indication of tension. They showed that though the medial gastrocnemius of the cat weighs 2½ to 3 times as much as the soleus, it develops about 6 times as much tetanic tension

TABLE 1
SPECIES, NUMBER, WEIGHT AND ANESTHESIA LEVEL USED FOR LENGTH-TENSION
ANALYSES

Species	Number and sex	Body weight (g) ¹	Total pentobarbital (mg)
<i>A. cooperii</i>	1 ♀	393	10.5
<i>B. jamaicensis</i>	1 ♀	1546	15
<i>C. livia</i>	2 ♀	—	40 mg/kg ²
<i>F. sparverius</i>	8 ♀ ; 2 ♂	—	30 mg/kg ²
<i>O. asio</i>	1 ♂	124	4
<i>F. mexicanus</i>	1 ♂	503	12
<i>S. canicularia</i>	1 ♂	101	4
<i>T. alba</i>	1 ♂	35	7.5

¹ Body weight recorded after removal of the reproductive organs and digestive tract.

² Average number of mg given per kg of body weight.

when stimulated. I have similar data (MS) for a large series of pelvic limb muscles of *F. sparverius*. In accordance, I stimulated each muscle under study and recorded the tension produced. It is hoped further use of this technique for certain kinds of functional morphological problems will prove rewarding.

METHODS

As muscle can develop different active tensions at different lengths (Evans and Hill, 1914), it must be stimulated over a range of lengths to determine its tension parameters. To this end I anesthetized the bird, ventilated its lungs, and surgically isolated and stimulated select leg muscles. The birds were anesthetized intravenously with pentobarbital sodium as a 1% solution. I injected doses of ½ to 1 mg/5 min until plucking of the breast feathers produced no overt movements. I administered further amounts as required throughout the experiment (Table 1).

After anesthetization I surgically isolated the trachea and prepared it for cannulation. To assure adequate lung ventilation I opened the abdominal cavity, punctured the ventral and posterior thoracic air sacs, and passed a mixture of 60% O₂, 39% N₂, and 1% CO₂ through the lungs via the tracheal cannula. Gas flow was adjusted to a level that prevented the bird from breathing actively. Before entering the bird, the gas mixture was humidified to 100% and brought to a temperature of 38° C by passing it through a Plexiglas cylinder into which water at 38° was sprayed continually.

I surgically isolated select tibiotarsal muscles but left the origins intact. Damage to blood supply was minimal and I took care not to cut the fibers of closely adjoining muscles. I maintained the temperature of the exposed leg relatively constant with the aid of a heat lamp and intermittently bathed the preparation with warm (38° C) saline. I measured intermuscular temperatures with a thermocouple at 5–10 minute intervals.

I stimulated each muscle directly with a grid of silver electrodes leading from a Grass Model SD5 stimulator. Supramaximal stimuli every 15–20 seconds produced brief tetani. I delivered impulses of 0.5 msec duration at frequencies of 60–180

pulses/second and voltages of 10–80 V depending on the muscle investigated. For each muscle, I took care to insure a combination of voltage and frequency that would result in maximum muscle response (Joyce et al., 1969). I noted the action of each muscle by observing limb movements following stimulation.

In preparing to measure muscle force, I first measured the length of the muscle before cutting the tendon of insertion. I clamped a solderless terminal onto the tendon and then connected it to a Grass FTIZ tension transducer that recorded on a Beckman RB Dynograph. I maintained the sensitivity of the dynograph at index 10. I fixed the transducer on an adjustable jack that could be raised and lowered in 1-mm intervals. The head of the femur was firmly fixed to the table to facilitate near isometric recording. Each muscle tested was first shortened to a length at which it developed little tension when stimulated. I then stretched it 1 mm and stimulated, stretched it a second mm and stimulated again until I reached a length at which no further active tension could be produced. During the original measurement of muscle length, I maintained the digits in an extended position, and held the coxofemoral, femorotibial, and intertarsal joints at 90°.

In addition to the birds used for tension measurements, I made fresh dissections of the following birds (numbers studied in parentheses): *A. cooperii* (2), *B. jamaicensis* (2), *C. livia* (2), *F. mexicanus* (1), *F. peregrinus* (1), *F. sparverius* (5), *O. asio* (1), *S. canicularia* (1), and *T. alba* (2). I described the muscles and measured their appropriate moment arms and tendon excursions.

For many muscles the effective moment arm changes as the angle of the joint changes. In these instances I measured the moment arm at increments from full joint flexion to full extension. I laid the specimen on a plastic sheet upon which was drawn a circle divided into 360°. Placing the pivot of the joint over the center of the circle, I moved the distal limb segment and measured the moment arm at 10° intervals. I made the measurements twice for each muscle and used the average.

I determined the passive excursion of a tendon that occurs with change in the angle of the joint by moving the joint through 30° and noted the distance moved. I did this three times for each muscle and used the average. I made all measurements to the nearest 0.1 mm using dividers and vernier calipers.

MYOLOGY

I selected for analysis 16 major flexor and extensor muscles of the tibiotarsus and digits; space limits this report to only 3 of these muscles, the tibialis anterior, flexor hallucis longus, and flexor digitorum longus (see Goslow, 1967, for a similar treatment of the remaining 13 muscles).

The following muscle descriptions are based on two specimens of the Red-tailed Hawk (*Buteo jamaicensis*). The patterns found in the other species are discussed in relation to *B. jamaicensis* as a standard.

M. tibialis anterior (tib. ant.).—This muscle is located on the anterior border of the tibiotarsus (Figure 1). It originates by two heads, the larger arising from the anterior side of the tibial crest and also from a line down the medial surface of the shaft of the tibia. The other head arises by a tendon from the distal apex of the external condyle and passes distally between the head of the fibula and the lateral apex of the tibial crest. The heads fuse and pass distally becoming a strong tendon that passes under a fibrous loop near the distal end of the tibiotarsus. The tendon passes between the condyles of the tibiotarsus and inserts on a tubercle located on the anterior surface of the tarsometatarsus.

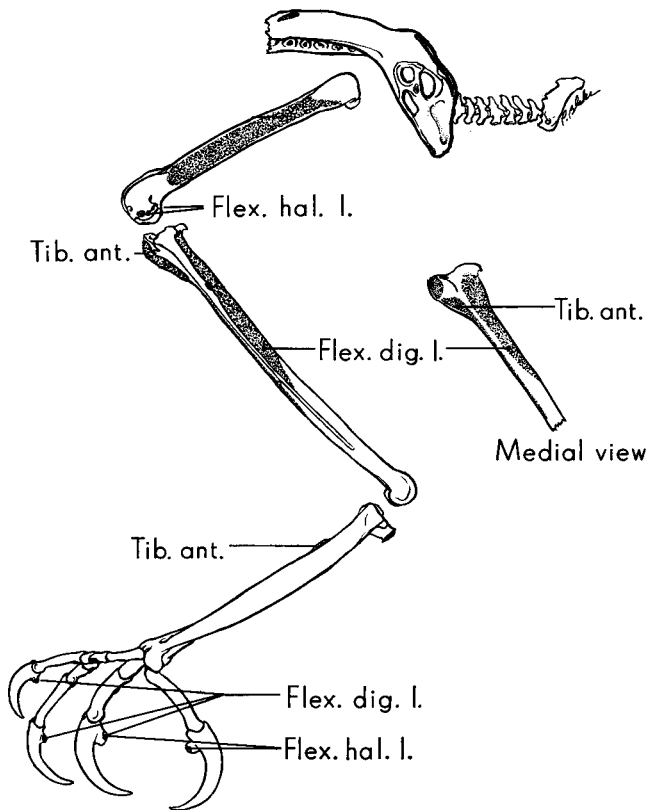


Figure 1. Lateral view of the left pelvic limb bones of *B. jamaicensis*, showing principal areas of muscle origin and insertion.

Action: Flexion of the tarsometatarsus.

M. flexor digitorum longus (flex. dig. 1.).—This deep muscle is large and rises from an extensive area of the posterolateral, posteromesial, and posterior surfaces of the tibiotarsus (Figure 1). Its tendon passes through the tibial cartilage and courses distally along the posterior sulcus of the tarsometatarsus. Just above the bases of the digits the tendon divides into three branches, one of which passes to each of the foretoes. These course ventral to the phalanges, perforating the superficial flexors of the digits, to insert on the base of the unguinal phalanges. Distally along the tarsometatarsus, this muscle tendon fuses with the tendon of the flexor hallucis longus by way of a strong tendinous vinculum. Thus independent movement of the two tendons is lost.

Action: The flexor digitorum longus is a flexor of the unguinal phalanges (talons) of the foretoes, but its fusion with the tendon of the flexor hallucis longus lets it contribute to the flexion of the talon of digit I. Some flexion of the entire digit results from tension applied to the tendon of the flexor digitorum longus.

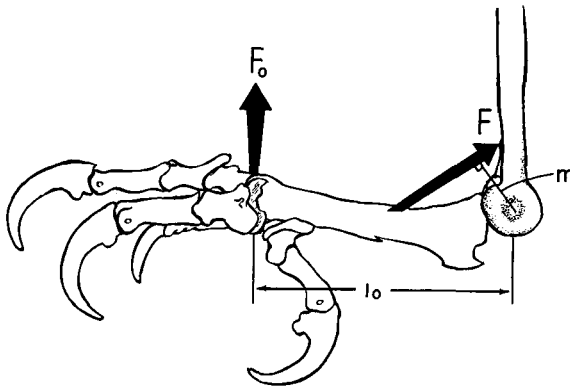


Figure 2. Representation of the method followed in the analysis of inforces and outforces of bone-muscle systems used in this study. F , initial force; F_o , outforce; l_o , out lever; m , moment arm.

M. flexor hallucis longus (flex. hal. 1.).—This large muscle rises by two heads, a small anterior head and a larger posterior one. The anterior head rises from the posterolateral side of the femoral shaft just proximal to the external condyle. The posterior head rises from the intercondyloid region of the femur, and the two heads fuse almost immediately. The muscle's belly extends the length of the tibiotarsus before forming a strong tendon that passes through the tibial cartilage and continues distally along the sulcus of the tarsometatarsus. At the distal end of the tarsometatarsus the tendon passes between the first and second metatarsals. After sending a stout branch to the tendon of the flexor digitorum longus leading to digit II, it courses distally to insert on the base of the unguinal phalanx of the hallux. As noted above, the tendons of the flexor hallucis longus and the flexor digitorum longus are closely fused at the level of the tarsometatarsus.

Action: The flexor hallucis longus is a strong flexor of the unguinal phalanges (talons) of digits I and II, but its fusion with the main tendon of the flexor digitorum longus permits it to flex the talons of the digits III and IV as well. Some flexion of the entire digit results from tension applied to the tendon of the flexor hallucis longus.

MECHANICS

I determined the tetanic tensions of the three muscles, and these tensions, coupled with osteological measurements, provided the basis for analysis. Using the method of torque analysis I calculated the approximate forces produced by certain bone-muscle systems. I ignored the forces of friction (probably negligible) and the restrictive forces imposed upon joints by ligaments and muscle masses (assumed relatively small). Forces of gravitation and inertia (not negligible, but less than for heavier animals) were also ignored and loading, where applicable, was considered symmetrical.

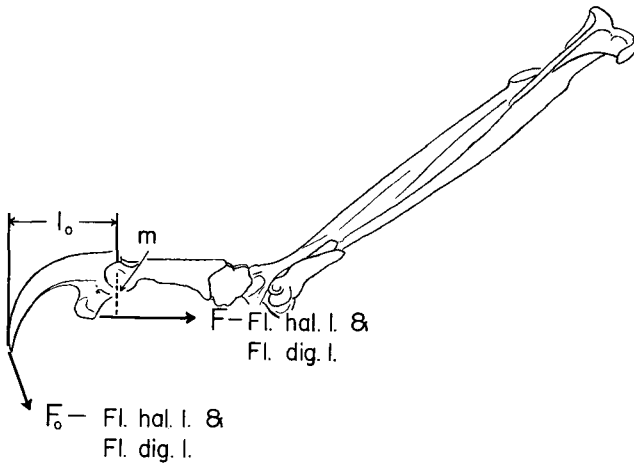


Figure 3. Points of measurement for the inforce and outforce calculations of the flexor hallucis longus and flexor digitorum longus. F , initial force; F_o , outforce; l_o , out lever; m , moment arm.

Torque is the effect of a force on an object with respect to a center of rotation. For skeletal elements the center of rotation is an anatomical joint. The magnitude of a torque is equal to the product of the magnitude of the force and its moment arm. The length of the moment arm is the perpendicular drawn from the center of rotation to the vector line of the force. Torques are expressed in units of force and length. In this study the unit used is the gramweight-centimeter. The vector line of the force produced by the muscle is the inforce, while the vector line of the force produced at the end of the bone affected is the outforce.

Consider Figure 2. The outforce (F_o) may be determined by solving for F_o in the equation $(F_o)(l_o) = (F)(m)$, where F is the original inforce; m is the moment arm; l is the lever arm of the outforce; and F_o is the outforce at right angles to the direction of movement. The outforce (F_o) was computed with knowledge of the physiological force produced by the muscle (F), coupled with measurements of the moment arm (m) and outlever (l_o).

I measured the outforce at a point along the bone or segment where I thought it to be the most important. For example I measured the outforce for the tibialis anterior (Figure 2) at the tarsal region, but I could have measured it at the end of the talons. This would have lengthened the outlever (l_o) and thus reduced the magnitude of the outforce. I considered the probable functional relationships before I determined the outforce used. This method is somewhat arbitrary, but using the same loca-

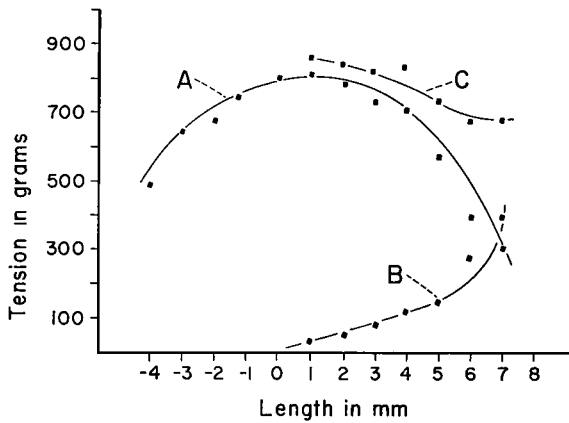


Figure 4. Length-tension relationships of the tibialis anterior of *F. sparverius*. A, active tension; B, passive tension; C, total tension.

tion of the outforce for all species in analyzing a given bone-muscle system introduced no errors. Figure 3 illustrates the position of the inforce, moment arm, and outforce for the flexor digitorum longus and flexor hallucis longus.

Mechanical treatment of the flexors of the digits is difficult. Dempster (1961) discusses the problem with respect to analysis of the human digit. Tension of the tendon of the talon flexor for example, results in the application of forces to the intermediate phalanges of the digit as well as to the talon. Thus intradigital forces result from a flexion force applied to the distal phalanx or phalanges, as well as from contacts between phalanges. To simplify analysis the segments of the digit proximal to the insertion of these tendons were treated as if they were rigid structures.

RESULTS

The active force produced by a muscle when stimulated reaches a maximum at some particular muscle length (Evans and Hill, 1914). This length, at which active isometric tension is greatest, has been termed the "reference length" of the muscle. When the muscle is either shortened or lengthened beyond its reference length, the active tension that it can develop diminishes.

Figure 4 shows the length-tension relationship for the tibialis anterior muscle of a Sparrow Hawk. The numeral "0" along the abscissa of the graph represents the length of the muscle in the leg of the bird when the femorotibial and intertarsal joints are at a 90° angle. Muscle lengths longer and shorter than the "0" length are shown by positive and nega-

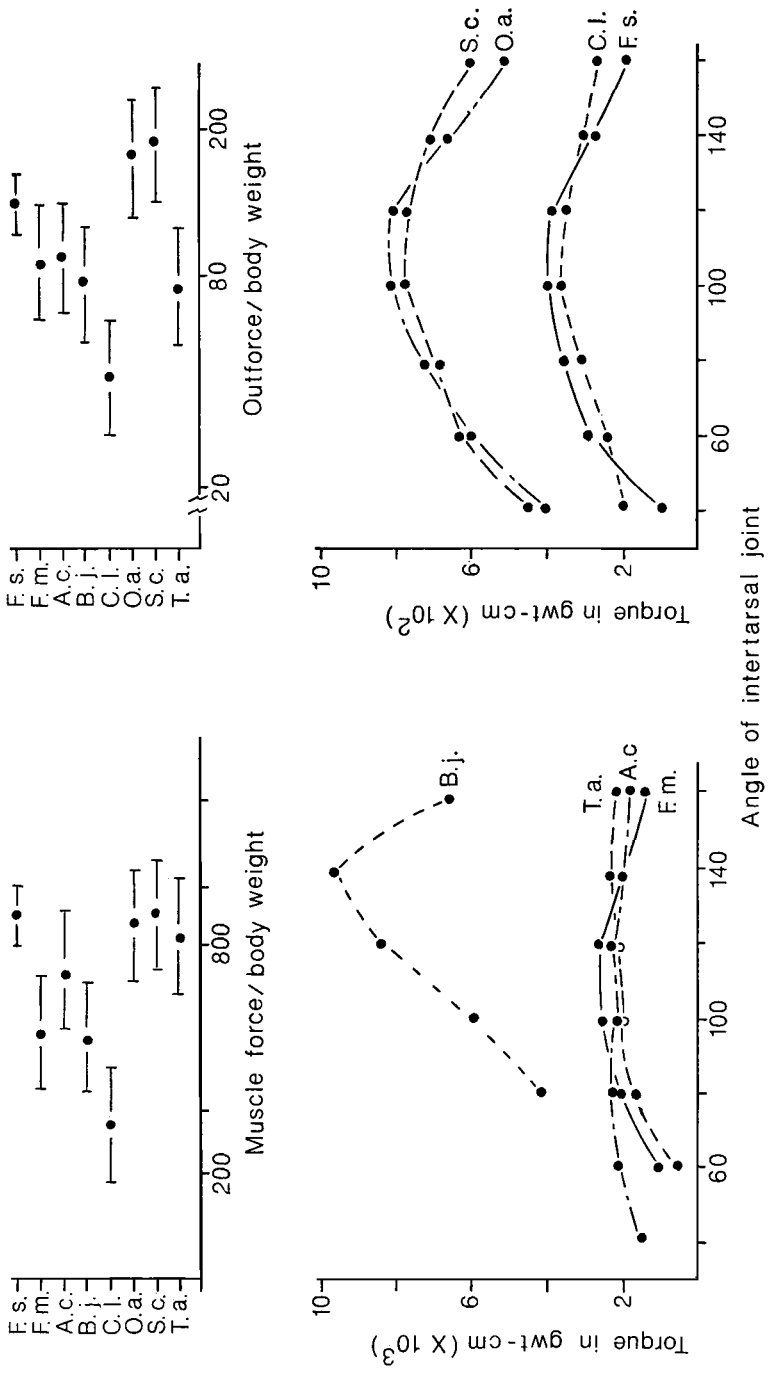


Figure 5. Muscle forces and torque of the tibialis anterior muscle. Top right: maximum resultant outforces of the bone-muscle system. Bottom: torque plotted against change in the angle of the intertarsal joint. See text for further explanation.

tive numerals. The figure illustrates the amount of active tension the muscle develops at different lengths (A) as well as the amount of passive tension (B) and the total tension (C) developed. The active tension is a result of the isometric tension developed at stimulation. The stretch of inert elastic material (connective tissue) in the muscle produces the passive tension (Banus and Zetlin, 1938). The total tension is a combination of both these components and is the tension considered most important to this study.

After I determined length-tension curves for the three pelvic limb muscles, I measured the length change of each muscle as the affected joint was moved. The length of the muscle (and thus its tension), coupled with its moment arm (measured from dissection data) determine the amount of torque possible around a joint at any given time.

A factor contributing to torque, which has been more or less ignored up to this point, is the number of motor units within the muscle that are activated at the time of contraction. In the living organism a variable number of motor units are activated within a muscle to produce a smooth movement (Mollet, 1966). The torque data presented in this investigation are based upon muscle forces derived at maximal stimulation, and the forces derived by this method are probably higher than those the living bird actually develops during normal movements. In other words, the forces measured were actual forces of the muscles but only *potential* forces for the organism. A basic assumption of this study is that a direct relationship exists between maximal "potential" force measured and the actual force developed in the organism.

Figures 5 through 7 present muscle force data. The upper graphs of each figure show maximum muscle forces and resultant outforces of the bone-muscle system; the lower graphs present torque or turning forces. The upper graphs will be discussed first.

The upper left-hand graphs express the maximum muscle force developed by a muscle as a percentage of the bird's body weight (intestinal tract and reproductive organs removed). The right-hand graphs express the maximum outforce produced as a percentage of the bird's body weight. The two graphs show the relative development of a particular muscle and the relative muscle force and (or) skeletal components in determining the effectiveness of a particular lever system.

I determined length-tension curves for each of the three pelvic muscles of 10 Sparrow Hawks. It cannot be assumed that the amount of variation found in these 10 muscles is equal to that found in the muscles of the other species. Intraspecific differences are probably not great, particularly as the coefficient of variation for the muscles of the Sparrow Hawk were relatively high—they ranged from 9 to 18. Gans (1963)

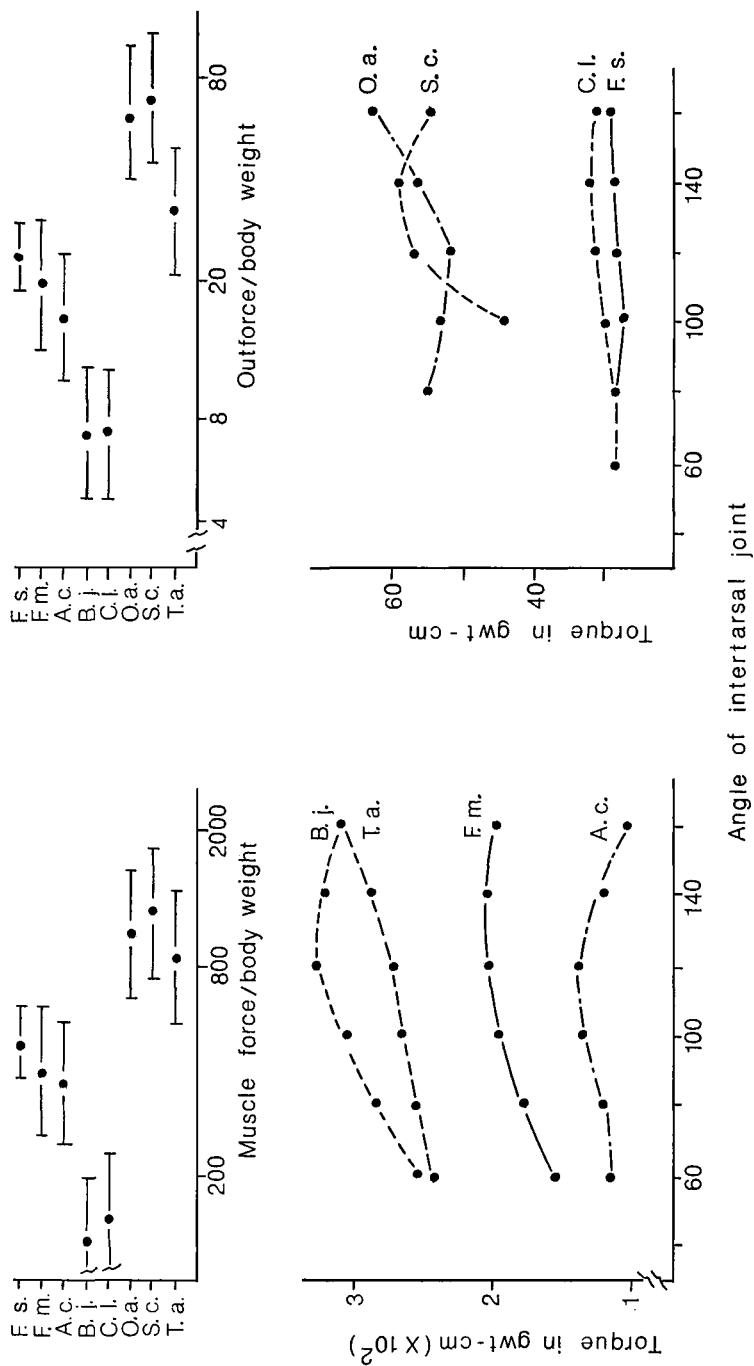


Figure 6. Muscle forces and torque of the flexor digitorum longus muscle. Top left: maximum muscle forces. Top right: maximum resultant outforces of the bone-muscle system. Bottom: torque plotted against change in the angle of the intertarsal joint. See text for further explanation.

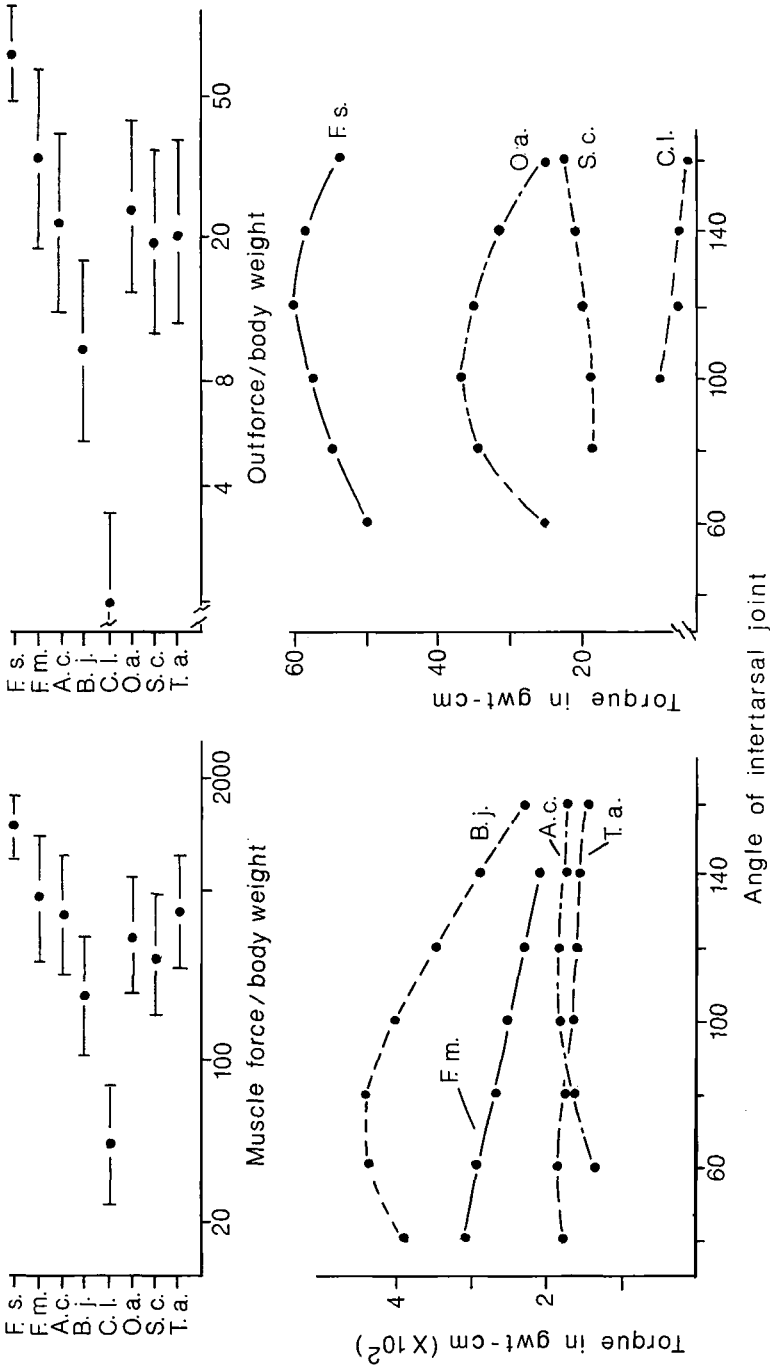


Figure 7. Muscle forces and torque of the flexor hallucis longus muscle. Top left: maximum muscle forces. Top right: maximum resultant outforces of the bone-muscle system. Bottom: torque plotted against change in the angle of the intertarsal joint. See text for further explanation.

pointed out the shortcomings of using a detailed analysis where variability is great; in accordance with this, ranges of variability are noted and used in comparisons.

I could make only one or two measurements for each muscle of the other species under consideration. Statistical techniques employed for comparing these data follow the single specimen methods often used by paleontologists as described by Simpson et al. (1960). I determined the standard deviation (s) and coefficient of variation (V) for each muscle of the Sparrow Hawk and two standard deviations above and below the true mean for this species were plotted. I treated the single measurement made for an individual of another species as though it coincided with the population mean (m). Assuming the value of V in this species to be the same as that for the Sparrow Hawk, I calculated a probable standard deviation ($V = 100 s/m$). The single measurement could represent either the low end of the population distribution or the high end. Since 95 percent of the measurements within a normal population fall within two standard deviations above and two standard deviations below the mean for that measurement, I compared these data as follows: Four calculated standard deviations were established above and below the single point measurement for each species. These are shown as the range lines above and below the points (Figure 5, upper graphs). If the measured point for a second species does not fall within the range established for the first, I assume the muscle force percentages are significantly different. For example, in the upper left-hand graph of Figure 5, a comparison of the measured muscle force of the tibialis anterior of the pigeon with the ranges of the other species indicates a significant difference between these forces in the pigeon and those in all the raptors studied. The horizontal axis of each graph is drawn on a log scale. This was done to maintain the appropriate relationship between the coefficient of variation and the standard deviation, as the absolute size of the means varied from those determined for the Sparrow Hawk.

The lower graphs of each figure show data derived by plotting the torque (moment arm \times force) of a muscle against the angle through which the joint involved rotates. Unless otherwise stated, these data incorporate both the change in moment arm length and the change in the muscle length (thus its force) as the angle of the joint rotates (see METHODS). The left-hand graph plots data for the larger species and the right-hand graph data for the smaller ones. The initials of each genus and species accompany the respective curves. The important thing to note in these figures is the angle(s) of the intertarsal joint at which torque is maximum.

Figure 5 presents data for the major flexor of the tarsometatarsus. The tibialis anterior appears to be significantly more developed in the raptors as a group, with *F. sparverius*, *A. cooperii*, and the three owl species representing the most developed condition. The torque curves for these species illustrate that the tibialis anterior is capable of maintaining maximum effectiveness through a relatively wide range of intertarsal angles.

Figures 6 and 7 illustrate data for the two major flexor muscles of the talons. These muscles affect all of the talons simultaneously but each to a different degree. The effect is dependent on the length of the moment arm involved. To gain an outforce value resembling the actual value produced by the bird, I divided the muscle's force by four before making the outforce calculations. Data are presented for talon II only.

Figure 6 illustrates relatively greater development of the flexor digitorum longus in the three owl species. This muscle appears least well-developed in *B. jamaicensis* and *C. livia*. Combining the outforce data for both these flexors shows a significantly least amount of development of these muscles in *C. livia* as compared to the raptors. A relatively high degree of development is shown in the small raptors *O. asio* and *S. canicularia*.

Recall that the tendons of the flexor digitorum longus and the flexor hallucis longus are fused in the species studied. The muscles have undoubtedly lost their independent action. Figure 6 shows the flexor digitorum longus to be most effective for most species when the intertarsal joint is maximally extended. The curves in Figure 7 for the flexor hallucis longus, however, indicate just the opposite pattern of effectiveness for the larger species and *C. livia*. For the other smaller species maximum effectiveness appears to be at intermediate angles of extension. A division of labor between these two muscles is probable, the flexor digitorum longus functioning with maximum effectiveness when the legs are well extended, and the flexor hallucis longus becoming most effective as the intertarsal angle is closed. Recall that the segments of the digit were extended when the data were recorded. As the digits are flexed, both curves will be shifted to the left thus changing their effectiveness with respect to the intertarsal angle.

DISCUSSION

This study contributes to the interpretations of various adaptations of raptorial birds by determining the relative magnitudes of the outforces of select pelvic limb muscles. Despite the limited number of specimens subjected to muscle analysis in this study, certain morphological trends are evident, and the techniques described here should be useful

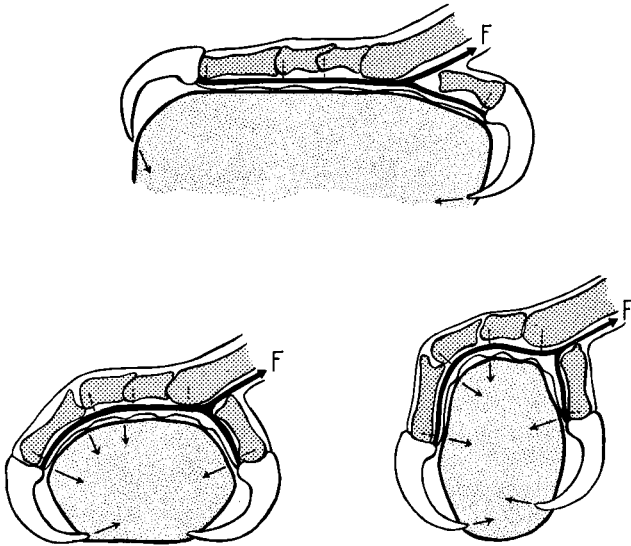


Figure 8. Action of the deep flexor muscles on the hallux and on digit III at the foot of the raptor. The distal phalanges are flexed around the proximal ones as prey size is reduced. This mechanism of conformity to different shapes maximizes contact surface between the digits and a variety of prey. F, force of flexors.

for other similar investigations. Techniques employing electromyography or implants of minute tensiometers in the tendons of muscles might also aid in determining the exact form-function complexes present.

As a group, the raptors have marked development of the tibialis anterior muscle, the flexor of the tarsometatarsus. This muscle's development is undoubtedly correlated with the action of holding struggling prey close to the body at the time of the kill (all raptors considered except *T. alba*). The upper right-hand graph of Figure 5 illustrates relatively low development of the outforce system of the tibialis anterior in *C. livia* and *T. alba*. The loss in outforce in *T. alba* is a result of the relatively long tarsometatarsus in this species as seen in osteological comparisons (Goslow, 1967). This increase in the length of the tarsometatarsus might be correlated with increased velocity of the foot at the time of leg extension or with the amount of vegetation present in the habitat of the raptor and its common prey. An analysis of the attack and strike of *T. alba* (Payne, 1962; Goslow, 1967) revealed the owl thrusts the feet markedly downward just before contact with the prey. An increased velocity of the foot during such a strike would be advantageous.

On the other hand *F. mexicanus* has a relatively short tarsometatarsus

(Goslow, 1967) and marked development of the outforce system of the tibialis anterior (upper right-hand graph, Figure 5). This falcon's short and stout tarsometatarsus may be the result of selective pressure toward strengthening the bone to withstand the stresses encountered at impact with the prey.

Also the raptors show marked development of the two talon flexors. In the owls the more highly developed of the two is the flexor digitorum longus, while in the falcons it is the flexor hallucis longus. In *A. cooperii* and *B. jamaicensis* the two muscles are equivalent. As the talon closes its moment arm increases, thus increasing the outforce at the end of the talon. The presence of ligamentous slings makes these muscles effective for closing the entire digit as well as for closing the talon. Figure 8 shows the basic mechanism. If resistance is met at any point along the ventral surface of the digit, the segments of the digit distal to the point of resistance continue to rotate. This arrangement facilitates maximum contact between prey and digit (reptorial birds) or perch and digit (perching birds). In some species of raptors the talons and digits are relatively long. This is particularly true of accipiters, some of the large falcons, and *T. alba*. If the digits are unusually long and there is not compensatory development of the muscles responsible for flexion, then the relative outforce at the end of the segments is reduced. If, however, these segments are relatively short, the ability to secure prey is probably impaired. Undoubtedly there is some relationship between the size of the digits and the characteristics of the prey involving its weight, its agility, and the relative ease or difficulty of killing it. The relative lengths of the digits vary markedly within some of the species of raptors studied. Within the large falcons, for example, the female's digits are often relatively longer than the male's. In Peale's Falcon (*F. peregrinus pealei*) I have measured individuals in which digit III is as long as the tarsometatarsus. This is not the average condition for Peregrine Falcons, yet it does exist. Whether these marked variations are random or adaptive within particular populations is difficult to ascertain.

Garrod (1875) noted that the vinculum connecting the flexor digitorum longus and the flexor hallucis longus is oriented downward from the tendon of the latter to the former. Thus he speculated when the flexor digitorum longus contracts only the foretoes are closed but when the flexor hallucis longus contracts all of the toes close. The flexor hallucis longus is the more highly developed talon flexor in the falcons, whereas in the other raptors studied, and most perching species (Hudson, 1937; Ruggeberg, 1960), the flexor digitorum longus is the more highly developed. In the latter species, this pattern of development would correlate well with perching habits.

Length-tension data indicate a division of labor between the two flexors; the flexor digitorum longus being more effective at the time of full extension of the leg, and the flexor hallucis longus being more effective at the time of flexion. Films revealed that most raptors close the toes around the prey at contact when the legs are extended (Goslow, 1971). In this situation the flexor of the foredigits (flexor digitorum longus) seems to be the most important flexor of the talons. The large falcons often strike with their legs flexed and feet maximally extended (Goslow, 1971). In many instances, the falcons deliver a glancing strike to the prey. At contact the falcons immediately close their toes, but because of their high speed, contact time with the prey is brief. This appears to limit the degree of piercing and tearing possible with the foretalons, but the speed and direction of movement appear optimum for effectiveness of the hind talon (hallux). These two factors, then, the degree of flexion of the legs and the position of the hallux at impact, appear to be adaptive factors coinciding with maximal development of the flexor hallucis longus of the falcons. Why this muscle is so highly developed in the small falcon (*F. sparverius*) is not clear. Its most commonly employed pattern of attack and strike is quite different from that of the larger falcons. Quite possibly this smaller falcon descended from a larger ancestor adapted for striking in a manner similar to *F. mexicanus*. If this is the case, marked development of the flexor hallucis longus over the flexor digitorum longus in *F. sparverius* would be ancestral and not directly adaptive. Fossil evidence on this subject would be of interest.

Analysis of outforce data for the small superficial flexors of the digits show no major trends or patterns that separate the pigeon from the raptors (Goslow, 1967). Isolated variations are seen but no adaptive significance can be given to them.

The owls as a group normally demonstrate the zygodactylous condition of the digits when perching or standing. This digit orientation is maintained during the strike by *O. asio*, *S. canicularia*, and *T. alba* (Goslow, 1967). Payne (1962) noted this posture in *T. alba* and demonstrated via a series of experiments the symmetrical placement of the eight talons to maximize the area covered by the feet at impact. The adaptive value of such talon positioning by a nocturnal raptor intent upon pinning its prey to the ground is great.

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SUMMARY

A method for the mechanical analysis of bone-muscle systems is presented. Select systems of the pelvic limb of seven species of raptors are compared with a nonraptorial bird, the domestic pigeon (*C. livia*).

The outforce systems of the tibialis anterior (flexor of the tarsometatarsus), flexor digitorum longus, and flexor hallucis longus (deep flexors of the digits) are significantly developed in raptors. Of the two flexors of the digits, the flexor digitorum longus is more highly developed in owls, while in falcons the flexor hallucis longus is stronger. In the Red-tailed Hawk and the Cooper's Hawk they are equal.

Torque data reveal a division of labor between the two flexors of the digits. The flexor digitorum longus is more effective when the leg is fully extended while the flexor hallucis longus is more effective at the time of flexion. Most raptors close their toes around the prey at contact when the leg is extended thus placing the flexor digitorum longus at its most optimum length for tension. But the Prairie Falcon and Peregrine Falcon often strike with the leg in a flexed position thus placing the flexor hallucis longus at its optimum length for tension.

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