FUNCTIONAL MORPHOLOGY OF RAPTOR HINDLIMBS: IMPLICATIONS FOR RESOURCE PARTITIONING

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ABSTRACT.—Prey capture in owls and hawks is largely dependent on the biomechanics of the hindlimbs, and both limb size and grip forces potentially determine the size of prey that can be captured and the extent of possible resource partitioning among sympatric species. Morphological study of six species of sympatric raptors—the owls *Otus asio*, *Strix varia*, and *Bubo virginianus*; and the hawks commonly considered their diurnal ''ecological equivalents,'' *Falco sparverius*, *Buteo lineatus*, and *Buteo jamaicensis*—revealed that, in both groups, talon closure is effected by two discrete mechanisms that function together in a potentially additive or alternative fashion. Grip force measurements obtained from live owls and hawks using ''hydraulic'' perches showed that grip force increases exponentially with body size and that owls produce greater forces than hawks. That finding is consistent with the distinctive osteology and myology of their hindlimbs and with their hunting behavior. These data provide some understanding of the different demands of diurnal and nocturnal hunting as well as the mechanism of coexistence for those six species in eastern woodlands. *Received 3 August 2001, accepted 8 July 2002.*

RESUMEN.—La captura de presas por parte de búhos y halcones depende en gran medida de la biomecánica de las extremidades posteriores. Tanto el tamaño como la fuerza de las extremidades pueden determinar la dimensión de la presa que puede capturarse y el grado de la posible partición de recursos entre especies simpátricas. El estudio morfológico de seis especies simpátricas de rapaces—los búhos *Otus asio*, *Strix varia*, y *Bubo virginianus*; y los halcones normalmente considerados sus ''equivalentes ecológicos'' diurnos, *Falco sparverius*, *Buteo lineatus*, y *Buteo jamaicensis*—reveló que en ambos grupos, el cierre de la garra se efectúa por medio de dos mecanismos discretos que funcionan juntos, probablemente de una manera aditiva o alternativa. Medidas de la fuerza de asimiento obtenidas de búhos y halcones vivos que utilizan perchas ''hidráulicas'' mostraron que la fuerza de asimiento aumenta exponencialmente con el tamaño del cuerpo y que los búhos producen mayores fuerzas que los halcones. Este hallazgo es consistente con la osteología y miología distintiva de sus extremidades posteriores y con su conducta de caza. Estos datos proporcionan cierto entendimiento de las diferentes demandas de caza diurna y nocturna, así como el mecanismo de coexistencia entre estas seis especies en los bosques del este.

SPECIES DIVERSITY OF a community may often be increased by the evolution of resource partitioning among sympatric species. A potential example of this phenomenon is seen in the coexistence of three species of owls (Strigiformes) and three species of hawks (Falconides) in the eastern woodlands of North America. These raptors include Great Horned Owl (*Bubo virginianus*) Barred Owl (*Strix varia*), Eastern Screech-Owl (*Otus asio*), Red-tailed Hawk (*Buteo jamaicensis*), Red-shouldered Hawk (*Buteo lineatus*), and American Kestrel (*Falco sparverius*). The species of these two groups are often referred to as ''ecological equivalents'' (perhaps erroneously) due to similarities in anatomy, habitat use, hunting style, and general prey types (Table 1) (Bent 1937, 1938; Voous 1988; but see Marti and Kochert 1995). What might account for the coexistence of these wide-ranging raptors? Although hawks and owls are not closely related (Sibley and Ahlquist 1990), both of these groups are termed ''raptors'' because of their highly efficient predatory characteristics. These, in turn, are largely dependent on their use of powerful hindlimbs to subdue prey. Despite the previous functional work on raptor force production, there have been no

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TABLE 1. This table includes body mass, body length, and wingspan of the six sympatric raptors considered in this study. All values were taken from the literature (Clark 1987, Earhart and Johnson 1970, Eckert 1987, and Henny and VanCamp 1979; see Johnsgard 1988).

Species	Mass (g)	Length (cm)	Wingspan (cm)
Bubo virginianus	985–2503	47–65	124–158
Strix varia	468–1051	41–61	96–114
Otus asio	140–210	18–26	48–62
Buteo jamaicensis	710–1550	45–55	110–132
Buteo lineatus	460–930	38–47	94–107
Falco sparverius	97–150	22–27	52–61

studies that have concentrated on the functional limitations on prey selection in a number of sympatric species (Csermely et al. 1998, Csermely and Gaibani 1998, Goslow 1967). Therefore, to understand the ecology and coexistence of the different raptors it may be helpful to investigate the function and capacities of their hindlimbs and talons and how they are used during hunting.

Basic raptor form and function.—Although the gross morphology of the different groups of raptors is similar, the digit arrangement differs between Falconides and Strigiformes. Hawks are anisodactylous, meaning that digits 2, 3, and 4 face anteriorly and digit 1 faces posteri-

FIG. 1. Lateral view of the left hindlimb of *Buteo jamaicensis* based on Orosz et al. (1992). Musculature nomenclature is based on Baumel et al. (1979). (A) Posterolateral view of the bones. (B) Posterolateral view of the bones and muscles. The flexor hallucis longus tendon has been pulled posteriorly along the distal portion of the tarsometatarsus to show the vinculum. (C) Anterolateral view of the intertarsal joint.

orly. Owls are zygodactylous: two toes face anteriorly and two toes face posteriorly. In owls, digit 1 and 4 face backwards.

The raptor limb is constructed of three primary bones that, along with the muscles, act in a leverage system. The bones include the femur, tibiotarsus, and the most distal element, the tarsometatarsus (Fig. 1). Associated with these bones are three major muscles responsible for talon closure (Goslow 1967). These include the tibialis cranialis, flexor digitorum longus, and flexor hallucis longus (Fig. 1). Other muscles that are also responsible for talon flexion include the flexor perforatus and perforans muscles. These are small muscles that insert on specific talons and function to flex only one talon (Goslow 1967, Hudson 1937).

Our early studies of owls suggested that raptors are able to close the talons by two different methods (Conroy et al. 1997). One involves contraction of the flexor muscles located on the posterior side of the tibiotarsus. A second more indirect method of talon closure results from contraction of the tibialis cranialis located on the anterior side of the tibiotarsus. If the tibialis cranialis is contracted, the talons will close due to the tautness of the flexor tendons. Therefore, it was necessary to determine if this dual (or ''fail-soft'') mechanism of talon closure operated in all the raptor hindlimbs under study.

The flexor digitorum longus is a deep muscle that lies along the posterior side of the tibiotarsus under the flexor hallucis longus (Fig. 1). It originates along the proximal, posterior side of the tibiotarsus and the lateral surface of the fibula and inserts via tendons that run along the posterior side of the tarsometatarsus onto the proximal base of the claw of digits 2, 3, and 4. Its primary action is to flex digits 2, 3, and 4, but it also flexes digit 1 due to a connection with the tendon of the flexor hallucis longus (Goslow 1972, Hudson 1937, Orosz et al. 1992).

The flexor hallucis longus is a muscle that is superficial to the flexor digitorum longus on the posterior side of the tibiotarsus (Fig. 1). It originates from the posterolateral side of the femoral shaft and from the intercondyloid region of the femur. The flexor hallucis longus inserts onto the proximal base of the digit 1 claw. Its primary action is to flex digit 1 (hallux). Secondarily, it flexes the other three digits because it is attached to the flexor digitorum longus tendon by a vinculum along the distal portion of the tarsometatarsus (Goslow 1972, Hudson 1937, Orosz et al. 1992).

The third muscle to consider in talon closure is the tibialis cranialis, a superficial muscle that lies along the anterior side of the tibiotarsus (Fig. 1). It originates from the anterior side of the tibial crest and the lateral condyle of the femur and inserts onto the distal apex of the external condyle of the tarsometatarsus. Its primary action is to flex the tarsometatarsus, thus pulling it towards the body (Goslow 1972, Hudson 1937, Orosz et al. 1992).

The output or force production of a muscle during muscle contraction is directly proportional to the cross-sectional area of that muscle (Schmidt-Nielsen 1990). In cases where *in vivo* and *in vitro* studies that directly measure force production during contraction can not be performed, cross-sectional area of the muscle provides a means for understanding and approximating potential force production. Other characteristics associated with the morphology of a given muscle can affect the force that it can generate. For example, the angle of pinnation of a pinnate muscle may affect the force of contraction. As the angle of pinnation increases, the force of contraction for a given muscle begins to decrease (Gans and Gaunt 1991, Lieber 1992, Richmond 1998). Specifically, Richmond (1998) writes that force will be decreased by 10% at angles that are >25°. Another characteristic of muscles subjected to high force regimes is the presence of sesamoids or calcified central tendons. Sesamoids may allow for more precise and controlled movement of the digits (Rack and Ross 1984). Ossified tendons have been found in the hindlimb muscles of woodcreepers that experience large forces during vertical climbing (Bledsoe et al. 1993). Ossified tendons have also been found in certain flexors in various falcon species but not in accipiter species (Harcourt-Brown 2001).

To understand the forces produced by a functional unit like the raptor hindlimb, the nature of the lever system must be understood. A lever system is composed of an in-force, that is produced by a muscle contraction, and a resultant outforce, the magnitude of which is dependent on the ratio of the length of the in-lever and out-lever. An in-lever is defined as the straight-line distance between the two attachment points of a muscle. The out-lever is the distance between the insertion of the muscle and the point of movement of the element of interest. In the case of raptor limbs, the in-lever of the flexor hallucis longus is the length of the tarsometatarsus and the hallux and the out-lever is the length of the chord of the hallux claw. The outforce multiplied by the out-lever is equivalent to the inforce multiplied by the in-lever. The mechanical advantage of a system is defined as the ratio of the outforce to the inforce. A higher mechanical advantage indicates higher relative outforce. The velocity ratio is a ratio of the out-lever to the in-lever, or l_o/l_I (Vogel 1988). In other words, as the length of the out-lever increases there is an increase in the amount of distance that the out-lever must travel in the same amount of time. Therefore, the velocity of the out-lever is increased while its outforce decreases. A system can be maximized either for increased force or increased velocity.

The dimensions of an organism change in accordance with changes in mass. As the body mass of an animal increases, the limb dimensions usually change to support the increased weight. If the animal maintains the same proportions despite a change in body mass, then the increase in body mass results in an isometric change of the other body proportions. For example, a 1 unit change in the body length will result in a 2 unit change surface area and a 3 unit change in mass. Isometric change can be quantified in a graph as an exponent of 0.33, for a length versus mass graph, or 0.67, for an area versus mass graph. If the exponent is significantly greater or less than those decimals, the change is considered allometric (Schmidt-Nielsen 1984).

Building on available information on raptor anatomy and function and on the above physical principles, we have attempted to understand the functional morphology and forces generated in the hindlimbs and talons of six sympatric raptors in the hope that data ac-

quired might provide some insight into the differential exploitation of available resources.

METHODS

General.—Three *Falco sparverius*, 3 *Buteo lineatus*, 4 *Buteo jamaicensis*, 10 *Otus asio*, 17 *Strix varia*, and 12 *Bubo virginianus* carcasses were obtained from rehabilitation and educational institutions. Birds were weighed and sexed. A leg was removed from the body and mass was determined. The leg was skinned and hydration was maintained using an avian ringer solution. All muscular nomenclature follows Baumel et al. (1979).

Mechanism.—The hindlimbs of all six species were manipulated to determine how the talons could be closed. The flexor digitorum longus and the flexor hallucis longus were pulled to simulate their contraction, a test of the known method of talon closure. A second test consisted of holding the tendons of the two flexor muscles taut while the tibialis cranialis was pulled on in order to mimic the effects of the tibialis cranialis contraction during talon closure.

Morphology.—The muscles and tendons were removed from the bones of the hindlimb, and the bones were cleaned in an Alconox® and Terg-A-Zyme® solution or by dermestid beetles. The length and width at midshaft of each bone was determined to the nearest 0.1 mm using vernier calipers. Those measurements, along with qualitative measurements, were used to describe the relative robustness of each bone.

The flexor digitorum longus, flexor hallucis longus, and tibialis cranialis were removed and the cross-sectional area of each muscle was calculated. The muscles studied were pinnate muscles and therefore the physiological cross-sectional area was determined using the physiological cross-sectional area formula $Acs = (Mm \times \cos q)/(r \times Lm)$ where Mm is muscle mass, q is angle of pinnation, r is muscle density, and Lm is mean fascicle length (Calow and Alexander 1973).

The mass of each muscle was found to the nearest 0.1 g without the removal of sesamoid bones. The density was found by placing the muscle in a graduated cylinder filled with avian ringer solution and dividing the mass by the volume displaced. The angle of pinnation was found by placing a protractor along the central tendon and measuring the angle of an individual fiber to the nearest 0.5°. Ten measurements on each muscle were taken, and the average of those was used as an estimate of angle of pinnation. Fascicle length was measured to the nearest 0.1 mm using vernier calipers. Again, 10 measurements were taken along the length of the muscle and averaged. Finally, muscles were examined for the presence of sesamoids.

Force measurements.—Eighteen hawks and 16 owls were tested for maximum and grip-force production. Male and female birds of each species were tested.

Force measurements were taken using hydraulic perches. Five threaded steel pipes with holes drilled in them were used. The pipe diameters were 0.95 cm (3/8 inches), 1.27 cm (1/2 inches), 1.91 cm (3/4 inches), 2.54 cm (1 inch), and 5.08 cm (2 inches). Each pipe was sprayed with foam adhesive and open cell foam was wrapped around the pipe. The foam was wrapped with duct tape. The perch then was dipped in PlasticDip® in order to seal the system and make it water tight. One end was capped and the other end was fitted with a T-junction. The top of the T-junction was also capped while the other end was left open in order to connect to a pressure transducer. Each pipe was then filled with water. Multiple circumferences were measured on each perch and the average was found. The mean circumference of perch 1 was 7.78 cm, perch 2 was 11.11 cm, perch 3 was 16.39 cm, perch 4 was 19.45 cm, and perch 5 was 21.75 cm. Force measurements were taken using a 30 mV pressure transducer connected to the open end of the T-junction. Pressure changes were recorded by the transducer and sent to an amplifier and then to a BioPac® system. The BioPac® was connected to an IBM Thinkpad 380XD running ACKNOWLEDGE 3.2.5 software.

Testing took place in the laboratory, at rehabilitation centers, and at falconers' homes. Prior to testing a bird, perches were calibrated. A beaded chain was wrapped around the perch and then around pulleys on either side of the perch. A wooden dowel held the chain apart right under the pulleys. Standard masses were hung from the chain to calibrate the perch.

Birds were tested on perches appropriate for their foot size. Each bird was forced to grip in one of several ways depending on the size or temperament of the bird. They were either pushed backward at the keel, pushed at the knees in order to push the bird off balance, or pulled backward by the jesses.

A zero voltage point was determined prior to putting the a bird on the perch. Each voltage peak that was due to a grip by a bird was recorded and converted to force units. The grip force was calculated by subtracting the weight of the bird from the maximum outforce: Grip Force = Maximum Outforce − Weight.

RESULTS

Mechanism.—From manipulations of the leg it was found that the six species studied had the same ''fail-soft'' or dual mechanism that we had noted in our preliminary studies with owls. Therefore the foot can be closed in two different ways, either directly by contracting the flexor muscles along the posterior of the ti-
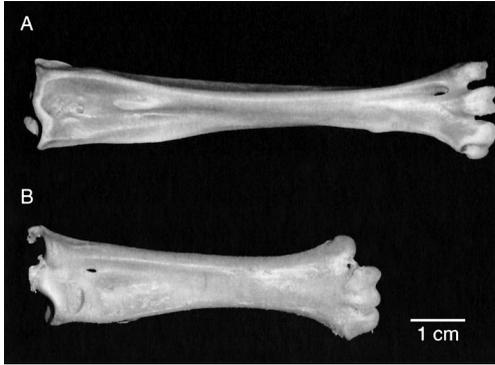
FIG. 2.   These two bones are the tarsometatarsus of a similarly-sized hawk and owl. (A) *Buteo jamaicensis*. (B) *Bubo virginianus*.

biotarsus or indirectly by contracting the tibialis cranialis which flexes the intertarsal joint thus pulling the tendons taut on the posterior side of the limb and closing the foot.

Osteology.—Bone characteristics were compared between similarly sized raptors. The lengths of the different leg bones differed in similarly sized raptors. The length of the tarsometatarsus was significantly longer in hawks than owls (Fig. 2, Table 2). This is also demonstrated by the ratios of the lengths of different bones in the hindlimb. In each case, the femur and the tibiotarsus were relatively shorter in hawks (Table 2). Increased robusticity of owl bones could be seen in the general shape of the tarsometatarsus and its articulation with the tibiotarsus and the phalanges. In hawks, the shape of the tarsometatarsus was triangular in cross-section whereas the owl bone was broad and flat. At the intertarsal joint, the condyles of the tibiotarsus appeared smaller in the diurnal raptors than in a similarly sized owl. The distal portion of the tarsometatarsus was more rounded in owls, a condition related to their zygodactylous feet which would allow digit 4

to rotate to the posterior side of the limb more easily. Finally, the articulations with the phalanges, or the trochlea of the tarsometatarsus, were more deeply grooved and larger in the owls indicating that the individual digits are larger in owls than hawks (see Fig. 2).

A length-to-width ratio quantified the robusticity of the bones. The higher the ratio, the more gracile or less robust the bone. There was a trend of gracility seen in the hawk tarsometatarsus. The length-to-width ratio of the tarsometatarsus was significantly greater for each hawk than the comparable owl (Table 3, Fig. 2).

Musculature.—The flexor digitorum longus is a deep muscle that lies along the posterior side of the tibiotarsus. It flexes digits 2, 3 and 4, and to a lesser degree, digit 1. Within the owls studied, the flexor digitorum longus was the larger of the two flexor muscles and its area was significantly greater than that of the hawks (ANOVA, $F = 10.90$, df = 1 and 48, $P < 0.01$). The cross-sectional area of the this muscle is smaller in hawks, but the scaling exponent (when plotted logarithmically) is significantly higher in hawks ($b_{owl} = 0.835$, $b_{hawk} = 1.188$, $t = 2.02$, df = 46, $P < 0.02$; Fig. 3A).

The flexor hallucis longus is a deep muscle located on the posterior side of the tibiotarsus. Its primary action is to flex digit 1. Secondarily, it flexes the other three digits because it is attached to the flexor digitorum longus tendon by a viniculum. In hawks, the flexor hallucis longus is the largest muscle in cross-sectional area, and it is larger in hawks than in owls (ANOVA, $F = 4.66$, df = 1 and 48, $P < 0.05$). When the log of muscle cross-sectional area is graphed against the log of body mass, the slopes are allometric for both hawks and owls and are not statistically different ($b_{hawk} = 0.92$, $b_{owl} = 0.85$; $t = 0.45$, df = 46, $P > 0.5$; Fig. 3B).

The tibialis cranialis is a superficial muscle that lies along the anterior side of the tibiotar-

TABLE 2.   Mean lengths (centimeters) ±1 SE of leg bones of sympatric raptors. Ratios were found by dividing each bone length into the length of the tarsometatarsus.

Species	Femur	Tibiotarsus	Tarsometatarsus	Ratios
B. virginianus	7.69 ± 0.099	11.86 ± 0.151	6.20 ± 0.063	1.24:1.91:1.00
B. jamaicensis	8.36 ± 0.256	10.96 ± 0.390	8.44 ± 0.032	0.99:1.30:1.00
S. varia	6.97 ± 0.030	10.34 ± 0.076	5.77 ± 0.036	1.21:1.79:1.00
B. lineatus	6.44 ± 0.120	9.21 ± 0.144	7.73 ± 0.083	0.83:1.19:1.00
O. asio	3.72 ± 0.40	5.28 ± 0.114	3.21 ± 0.073	1.16:1.64:1.00
F. sparverius	3.39 ± 0.143	4.93 ± 0.056	3.67 ± 0.044	0.92:1.34:1.00

TABLE 3. Length/width measurements for each of the three bones that constitute the avian hindlimb. The values are listed as the mean ±1 SE.

Species	Femur	Tibiotarsus	Tarsometatarsus
B. virginianus	10.22 ± 0.103	16.46 ± 0.355	6.59 ± 0.170
B. jamaicensis	11.00 ± 0.345	17.16 ± 0.681	13.94 ± 1.462
S. varia	12.33 ± 0.244	19.84 ± 0.326	8.67 ± 0.134
B. lineatus	10.63 ± 0.109	15.58 ± 1.135	11.29 ± 0.394
O. asio	12.78 ± 0.238	18.27 ± 0.459	9.85 ± 0.276
F. sparverius	10.88 ± 0.252	17.18 ± 0.562	14.53 ± 0.216

sus. The primary action is to flex the tarsometatarsus that indirectly causes the digits to flex if the muscles along the posterior side of the limb are held taut. Owls and hawks possess a tibialis cranialis of similar cross-sectional area (Fig. 3C) ($t = 0.121$, df = 46, $P > 0.9$).

The total cross-sectional area of the three muscles was not significantly different in the hawks and owls although there was a trend for owls to have slightly more total muscle cross-

sectional area than the equivalently sized hawks (ANOVA, $F = 2.65$, df = 1 and 48, $P = 0.11$; Fig. 3D). The slopes from the mass and combined cross-sectional area plot were not statistically different ($t = 0.19$, df = 46, $P > 0.5$).

Characteristics of each muscle were also compared to understand the different functional capabilities of falconiform and strigiform hindlimbs. Fascicle lengths were similar in
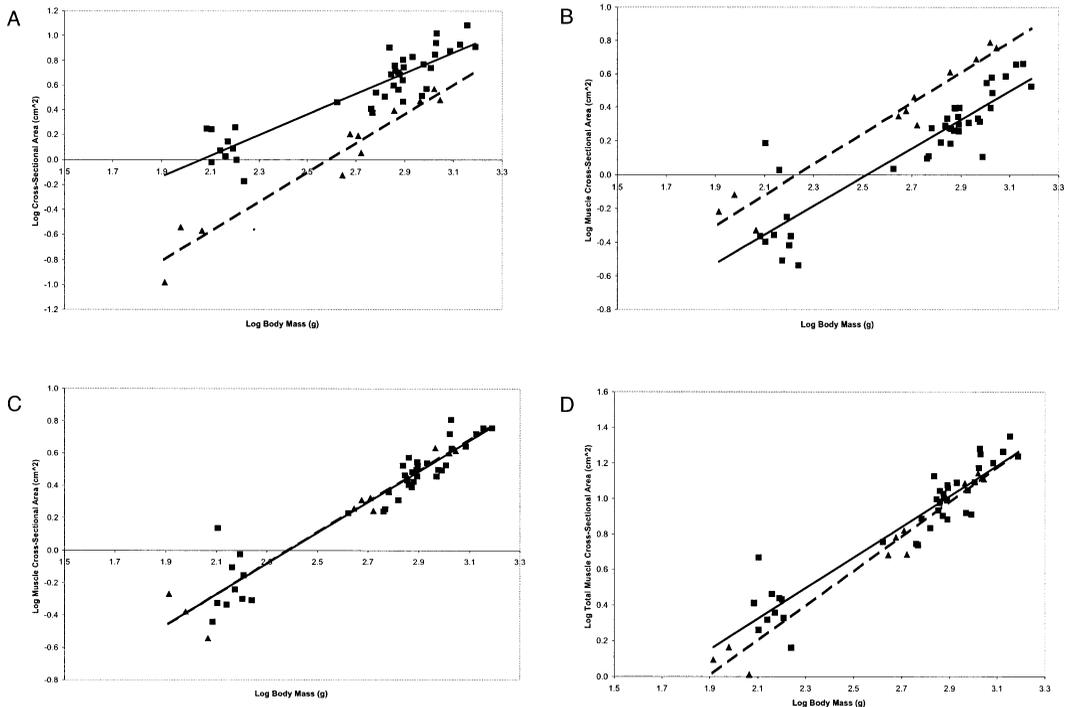
FIG. 3. Log transformed graphs of muscle cross-sectional areas and body mass. Squares designate owls and triangles designate hawks. The solid line designates the owls and the dashed line represents the hawks. (A) Flexor digitorum longus, owls: $y = 0.84x - 1.72$, $R^2 = 0.82$; hawks: $y = 1.19x - 3.07$, $R^2 = 0.95$. (B) Flexor hallucis longus, owls: $y = 0.85x - 2.15$, $R^2 = 0.81$; hawks: $y = 0.92x - 2.06$, $R^2 = 0.95$. (C) Tibialis cranialis, owl best-fit regression line: $y = 0.95x - 2.27$, $R^2 = 0.91$; hawks best-fit regression line: $y = 0.96x - 2.30$, $R^2 = 0.94$. (D) Total hindlimb musculature, owls: $y = 0.86x - 1.48$, $R^2 = 0.88$; hawks: $y = 0.98x - 1.85$, $R^2 = 0.97$.

TABLE 4. Average fascicle length and angle of pinnation for each of the three muscles examined. The values listed are means ±1 SE.

	Mean fascicle length (cm)			Mean angle of pinnation (degrees)		
Species	Tibialis cranialis	Flexor digitorum longus	Flexor hallucis longus	Tibialis cranialis	Flexor digitorum longus	Flexor hallucis longus
B. virginianus	2.41 ± 0.148	2.06 ± 0.125	2.59 ± 0.150	<10	<10	<10
B. jamaicensis	2.89 ± 0.1.64	2.58 ± 0.108	2.65 ± 0.216	28.94 ± 1.906	24.83 ± 2.408	29.43 ± 4.475
S. varia	2.12 ± 0.073	1.97 ± 0.771	2.12 ± 0.084	<10	<10	<10
B. lineatus	2.27 ± 0.168	2.48 ± 0.273	1.87 ± 0.187	23.80 ± 1.470	19.23 ± 1.420	24.05 ± 2.860
O. asio	1.57 ± 0.129	1.20 ± 0.085	1.34 ± 0.088	<10	<10	<10
F. sparverius	1.10 ± 0.132	0.76 ± 0.047	0.95 ± 0.054	21.80 ± 1.250	17.08 ± 1.620	20.66 ± 2.270

hawks and owls. However, angle of pinnation, a predictor of potential force production, was greater in hawks than owls, suggesting a greater force potential for owls. The angle of pinnation of strigiform muscles was <10° whereas the angle of pinnation of falconiform muscles ranged from 14 to 35° (Table 4).

Sesamoids, which are ossifications of tendons found in areas of high stress, were not found in hawks except in the flexor hallucis longus in the American Kestrel. There, they are relatively short calcifications located in the proximal third of the muscle. Well-developed sesamoids that spanned the length of each muscle were found in all three of the muscles studied in each of the three owls.

The anatomical study indicated that owl hindlimbs may be exerting greater muscular forces due to small angles of pinnation, the presence of sesamoids in muscles, the short length of the tarsometatarsus, and robusticity of the tarsometatarsus. That finding was tested using live birds and hydraulic perches.

Force measurements.—The grip force of each species was found to be significantly different from every other species (one-way repeated measures ANOVA, $F = 88.41$, df = 32 and 80, $P < 0.001$; multiple range test for means, $P <$

0.05). In each comparison of equivalently sized owls and hawks, owls had a greater maximal outforce and a greater grip force (Table 5, Fig. 4A and B). The total maximal outforce and grip force production of each group of raptors was found to increase nonlinearly with mass (for logged data, see Fig. 4A and B). The increase in force production within each group was similar to the increase in total muscle cross-sectional area (compare Figs. 4 and 3B; $b_{hawk\ force} = 0.97$, $b_{hawk\ muscle} = 0.98$, $b_{owl\ force} = 0.85$, $b_{owl\ muscle} = 0.86$).

DISCUSSION

Although hindlimbs of Falconides and Strigiformes are very similar in that both use the same mechanism to close the talons, the two groups possess significant differences in morphology, force production, and hunting behavior. In particular, differences in the flexor musculature and limb dimensions seem to explain many of the differences in force production in those birds.

Both owls and hawks appear to use the same dual or ''fail-soft'' mechanism to close the talons. ''Fail-soft'' is an engineering term: in fail-soft systems a failure in the function of a part of the system does not result in ''immediate or

TABLE 5. Experimental data from the species studied including their mass and the two output variables.

	Mass (g)		Outforce (N)		Grip force (N)	
Species	Mean ± 1 SE	Range	Mean ± 1 SE	Range	Mean ± 1 SE	Range
B. virginianus	1397.3 ± 38.2	1277–1600	144.10 ± 22.95	97.7–291.8	130.40 ± 22.81	83.2–277.7
S. varia	783.3 ± 28.6	732–861	53.00 ± 8.50	42.5–78.4	45.32 ± 8.24	35.4–70.0
O. asio	150.8 ± 6.7	135–166	20.42 ± 4.17	10.2–30.5	18.94 ± 4.20	8.6–29.0
B. jamaicensis	1357.6 ± 61.7	1112–1509	85.33 ± 12.71	45.4–133.8	72.32 ± 12.89	32.3–122.6
B. lineatus	624.0 ± 83.0	497–780	40.56 ± 5.48	29.8–47.6	34.42 ± 5.26	23.9–40.0
F. sparverius	122.1 ± 6.2	90–140	8.93 ± 1.65	2.8–17.7	7.73 ± 1.62	1.7–16.3
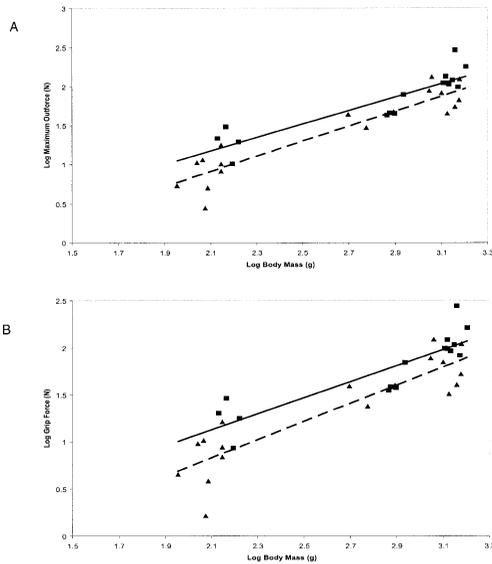
FIG. 4. Log-transformed graphs of hindlimb force production and body mass. Squares designate the owls and triangles designate the hawks. (A) Maximum outforce, owls: $y = 0.85x − 0.66$, $R^2 = 0.77$; hawks: $y = 0.97x − 1.20$, $R^2 = 0.80$. (B) Grip force, owls: $y = 0.86x − 0.64$, $R^2 = 0.81$; hawks: $y = 0.97x − 1.12$, $R^2 = 0.86$.

significant disruption of operations or in degrading output quality'' (Morris 1992). That implies that the system has alternative or back-up components. That dual mechanism is of special interest because it represents a convergent evolutionary adaptation because those two different groups of raptors are not closely related (Sibley and Ahlquist 1990). It is possible that the tendon-locking mechanism used by many species of birds for perching (Quinn and Baumel 1990) has evolved into that special dual mechanism of talon closure described here. To test the importance of the tibialis cranialis to talon closure, the relative proportions of the tibialis cranialis should be compared in raptorial and nonraptorial birds. It is still not well understood if the two different mechanisms are used alternatively or additively although from examining videos of *O. asio* and *B. jamaicensis* hunting and by observing falconry birds, it would appear to be additive. The birds first grasp the prey, by what would appear to be the flexor muscles because the limb is extended. Then, the bird will flex the joint between the tibiotarsus and the tarsometatarsus, effectively bending over the prey, indicating that the tibi-

alis cranialis is active. There are several advantages to having a dual talon-closure mechanism. First, if there is some injury to either of the digital flexors, the digits could still be closed by flexing the lower leg; once the digital flexors were taut, the digits would flex by indirect means. Secondly, the tibialis cranialis potentially lengthens the digital flexors during its contraction allowing forces above isometric tension to be developed in the digital flexors. Lastly, the additive effect of the tibialis cranialis in foot closure during the pinning phase would drive the talons further into the prey animal and thus increase the gripping ability. Although the work to date is consistent with an additive or ''fail-soft'' system, confirmation of that mechanism must await studies of muscle activation patterns.

The digit pattern in Strigiformes is zygodactylous or symmetrical. Payne (1962) proposed that a symmetrical grip reduced the chance of prey escape by maximizing the area of the foot and therefore limiting the paths of escape by a prey animal. Thus, having a symmetrical grip may allow owls to subdue larger prey with a greater success than similarly sized hawks.

The hindlimbs studied reinforce our perception that the two groups use different hunting styles. The differences are associated with the reciprocal relationship between speed and force in different types of lever systems. The distinctive morphology of Strigidae appears to be associated with an especially forceful grip whereas the hindlimbs of Falconides seem adapted for high-velocity movements. This is seen in the differences in tarsometatarsus length between the two groups (Fig. 2, Table 2). The owl tarsometatarsus is relatively short and wide with large condyles for attachment to the digit. The hawk tarsometatarsus is relatively long and gracile. When comparing the limb bone ratios of the two groups, there is a distinct trend for hawks to have a relatively longer tarsometatarsus (Table 2). If the tarsometatarsus is considered the out-lever of the hindlimb, then the increased length of the hawk tarsometatarsus would indicate an enhanced ability for rapid movement whereas the owl would have a lever system that favors high force production. This also would be consistent with the differences in angle of pinnation and presence of sesamoids in owls. Further study of the lever systems of the raptor hindlimbs could explain how

the total hindlimb muscle cross-sectional area is similar in the two groups, but the grip force is different. One possible explanation is that the out-lever includes a length associated with the digit. The chord of the digit would also add to the out-lever for the muscles examined in this study. The chord was not considered here because of its constant change as the talons flex during an attack. Preliminary data indicate similar toe lengths between owls and hawks.

The differences found in the cross-sectional areas of the flexor digitorum longus and the flexor hallucis longus are associated with the different digit arrangements in the two groups of raptors as well as aspects of their hunting behavior (Fig. 3A and B). Hawks have a relatively larger flexor hallucis longus; owls have a relatively larger flexor digitorum longus. This trend was also noted by Goslow (1972). To hunt effectively, hawks must have a larger muscle controlling the hallux. Otherwise a prey animal would be able to escape the bird's grip. During hunting, hawks also use the hallux to grab at the prey if the prey is not subdued immediately. Strigids, however, with their symmetrical toe arrangement do not need as large a flexor hallucis longus muscle because one of the digits flexed by the flexor digitorum longus can be moved posteriorly.

From examination of the muscles, it was found that strigiform muscles are well adapted for greater force production or are experiencing greater stresses during contraction than the same muscles in hawks. Generally, the hawks studied did not have sesamoids in the hindlimb musculature except in the case of the American Kestrel, whereas all the strigiform hindlimb muscles examined had well developed sesamoids that spanned the entire length of the muscle. Various falcons have been found to have intratendinous ossifications in the flexor hallucis longus similar to what was found in this study in the American Kestrel (Harcourt-Brown 2001). The presence of an ossified tendon in the flexor hallucis longus in *Falco* spp. may be due to a higher velocity attack than accipiters (Goslow 1972, Harcourt-Brown 2001). Rack and Ross (1984) postulated that ossification might increase the precision of movement of the digits, a possible advantage for the nocturnal-hunting owls. That would allow owls to have greater control over the individual digits during foot closure. Although the function of

avian sesamoids has not been adequately determined, there seems to be a trend towards finding ossified tendons in muscles that are overcoming large forces as demonstrated by Bledsoe et al. (1993) in woodcreepers.

All of the muscles studied were pinnate muscles. Pinnate muscles, unlike parallel-fiber muscles, have a central tendon with fascicles that come off the tendon at an angle. The pinnation angle differs in hawks and owls. A higher angle of pinnation results in a smaller cross-sectional area and may be associated with a decrease in force production (Richmond 1998). The net force of contraction is also reduced because the muscle fiber is oriented away from the direction of contraction. In all of the muscles examined, hawks had larger angles of pinnation than owls, which would suggest that their hindlimb muscles are unable to produce the same force as those of owls during muscle contraction. Angle of pinnation is not the only characteristic of muscles that may affect force production. The type of fibers found in a muscle also affects the force production (e.g. Romey et al. 1999, Sokoloff et al. 1998). Force production during muscle contraction will also be affected depending on whether the muscle has been stretched and where on the force-velocity curve the muscle is working (Biewener 1998).

Force produced by talons during talon closure and hunting behavior of each group may be related to the time at which they are hunting. Owls hunt during dusk and dawn when the light levels are low. If an owl attacks and misses a prey animal, it may be at a strong disadvantage when it comes to following up on the attack. Although their hearing is acute, owls might not be able to chase down an animal using visual cues in the dark especially if there are abundant obstacles at ground level. Instead they are more likely to return to their perch to locate the animal. Payne (1962) noted in Barn Owls that if the result of a prey strike was unsuccessful, the Barn Owl would fly back up into the air and strike at the mouse again, even if the mouse was close enough to the original strike location to be grabbed by an extension of the limb. P. D. Weigl (pers. obs.) has often noted this behavior while observing hunting in three species of owls. Owls are often sit-and-wait predators that pounce on their prey with great vertical momentum (Goslow 1971). The hunting behavior of Strigiformes is

associated with high force production and other adaptations to limit prey escape.

The hawks of this study are diurnal hunters and thus have the ability to use visual cues during and after an attack. Therefore, if they are unable to subdue prey initially, they are potentially able to chase down their prey visually and catch it. Films of hunting hawks demonstrate that hawks attack more horizontally than owls, thereby using the large hallux to grab at the prey as they pass over the animal. In many instances they will merely stun an animal on the initial attack with the hallux and then return to the animal to subdue it (Goslow 1967).

On the basis of our research to date, it appears that both hawks and owls have the same dual mechanism for closing talons. Morphological differences in the two groups primarily involve the relative cross-sectional areas of the two flexor muscles, the contrasting angles of pinnation, the presence of sesamoids, and the relative length of the tarsometatarsus. Hawks were found to have larger flexor hallucis longus muscles, whereas owls had larger flexor digitorum longus muscles. Overall, total muscle cross-sectional area did not differ in the two groups. Hawks had higher angles of pinnation than owls in muscles examined and sesamoids were not found in hawk muscles. The tarsometatarsus was longer in the hawk species than in similarly sized owl species, indicating that the lever system of hawk limbs may be optimized for speed of movement and not force.

Morphological findings were reinforced by the force values that we measured using live birds. Owls do produce significantly greater force during talon closure than comparably sized hawks. Previous work recording grip forces in Great Horned Owls by Marti (1974) found a value of force production during talon closure that falls in the range found in this study (13,000 g or 127 N, see Table 5). Despite the large force values found in this study, we in no way suggest that these measurements represent the maximal forces exerted by the talons during a prey strike. Instead, the data here provide a conservative estimate of force production by the flexion of the talons in six raptor species under the relatively controlled conditions of the study.

Given the above analysis of the biomechanical capacities and hunting behaviors of these six raptors, how well do those characteristics relate to data on prey-size selection from field studies? Great Horned Owls are capable of taking relatively large mammals such as porcupines (*Ezethizon dorsatum*) and skunks (e.g. *Mephitis mephitis*) as well as large birds such as pheasants and quail (Bent 1938, Earhart and Johnson 1970). Barred Owls prey mainly on medium-sized mammals, including mice and squirrels (*Sciurus* spp.) as well as wetland species of amphibians (Bent 1938, Earhart and Johnson 1970). Eastern Screech-Owls are known to prey on a variety of insects, small birds, and small mammals (Earhart and Johnson 1970). Red-tailed Hawks are recorded as subsisting primarily on rodents and larger mammals such as skunks and rabbits (*Sylvilagus* spp.) as well as some birds (Bent 1937, Fitch et al. 1946). Red-shouldered Hawks, like Barred Owls, subsist mainly on medium-sized mammals such as squirrels and chipmunks (e.g. *Tamias striatus*) but they also prey heavily on wetland species such as frogs and salamanders (Bent 1937, Bosakowski and Smith 1992). The American Kestrel, like the Eastern Screech-Owl, eats mostly insects and small mammals (Bent 1938). Similarly sized raptors take similar species of mammals despite the temporal difference in their hunting behavior. During winter months when other prey species—such as amphibians and some of the small birds—are not available, these six species must subdivide the available mammalian resource base very precisely to continue to coexist.

Both the group and species differences between grip force and hunting behavior of owls and hawks suggest at least a partial basis for resource partitioning in the eastern deciduous forests. The differences also provide evidence that the similarly sized raptors are not simple "ecological equivalents," in agreement with the conclusions of Marti and Kochert (1995). Each raptor studied has a unique force production that would allow for a degree of prey specialization. That prey specialization is also related to the different time at which those birds are hunting. Overall it may be possible for all six of the species to survive in a given area because they have managed to specialize in some part of the available resource base due to their different sizes and different grip strengths.

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