

Comparison of Wing Morphology in Three Birds of Prey: Correlations With Differences in Flight Behavior

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ABSTRACT Flight is the overriding characteristic of birds that has influenced most of their morphological, physiological, and behavioral features. Flight adaptations are essential for survival in the wide variety of environments that birds occupy. Therefore, locomotor structure, including skeletal and muscular characteristics, is adapted to reflect the flight style necessitated by different ecological niches. Red-tailed hawks (*Buteo jamaicensis*) soar to locate their prey, Cooper's hawks (*Accipiter cooperii*) actively chase down avian prey, and ospreys (*Pandion haliaetus*) soar and hover to locate fish. In this study, wing ratios, proportions of skeletal elements, and relative sizes of selected flight muscles were compared among these species. Oxidative and glycolytic enzyme activities of several muscles were also analyzed via assays for citrate synthase (CS) and for lactate dehydrogenase (LDH). It was found that structural characteristics of these three raptors differ in ways consistent with prevailing aerodynamic models. The similarity of enzymatic activities among different muscles of the three species shows low physiological differentiation and suggests that wing architecture may play a greater role in determining flight styles for these birds. *J. Morphol.* 267:612–622, 2006.

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Due to the high energetic costs of flight and its importance in survival, it is assumed that locomotor structure, including skeletal and muscular characteristics, is adapted to meet the demands of a flying animal's environment and ecological niche (Norberg, 1981; Dial, 1992a). Previous investigations of avian wing myology have largely been restricted to the structure and function of the thoracic and shoulder musculature used in level flapping flight, in takeoff, and in landing (e.g., Dial et al., 1991). Relatively less attention has been paid to the roles of the brachial and antebrachial musculature.

The largest muscle in the avian forelimb is the pectoralis, which produces most of the force needed during downstroke. As the primary wing depressor, the pectoralis is the most widely studied of the forelimb muscles. Other brachial and antebrachial muscles, however, are important in determining the position and detailed functioning of the wing (Dial, 1992a). Previous studies of these muscles have focused on their roles in takeoff and landing after level flapping flight (e.g., Dial, 1992a,b; Tobalske et al.,

1997); their roles in adjusting the wing during complicated maneuvering remain largely unknown.

Because birds use their wings in a variety of ways during different flying maneuvers, one would expect their flight muscles to have diverse functional properties relative to force recruitment and fatigability. Different species, however, may be adapted to emphasize certain aspects of flight, e.g., speed versus stamina and maneuverability versus stability. Thus, one would expect to find differences in musculoskeletal design among birds that are adapted for different flying styles (for review, see Norberg, 1981, 1985).

Three raptor species, red-tailed hawks (*Buteo jamaicensis*), Cooper's hawks (*Accipiter cooperii*), and ospreys (*Pandion haliaetus*), are all members of the Family Accipitridae (Sibley et al., 1988; Sibley and Ahlquist, 1990), but display strikingly different locomotor styles in their hunting behavior. Red-tailed hawks commonly locate their prey (usually small mammals) from a perch or by soaring and stooping (Toland, 1986; Johnsgard, 1990). Although they must make adjustments in wing angle to compensate for changes in wind currents and direction, their usual locomotor pattern does not call upon them to make frequent large rotational movements of the forearm and hand.

Cooper's hawks are swift fliers that actively chase down their prey (generally small birds) through woodlands, often requiring a high degree of maneuverability as they avoid tree trunks and branches (Toland, 1986; Johnsgard, 1990). This locomotor style demands fast, large adjustments in wing angle, often involving rotational elements.

Ospreys capture fish at shallow depths. They often hover while searching the water below. After an aerial dive of 5–70 m, ospreys must overcome the drag exerted by water in order to take off again (Grubb, 1975; Toland, 1986; Poole, 1989; Johnsgard,

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1990). Both hovering and water takeoffs in ospreys require large and powerful rotational movements of the wing, including forearm and wrist rotation.

The aim of this study was to determine whether variation in locomotor behavior among these species is reflected in biomechanical differences among them. The possible biomechanical/functional adaptations considered included wing skeletal proportions, relative force generated by selected muscles, and relative oxidative-glycolytic capacity of the muscles. The skeletal measurements were used to determine variation in aspect ratios and the ratios of different wing elements, and to compare them with known species in order to test whether these raptors fit prevailing views on the functional significance of wing and skeletal proportions in birds (Norberg, 1985). Differences in muscle size were assumed to reflect variation in the potential force that muscles can produce (e.g., Peters and Aulner, 2000). Larger muscles can presumably produce greater maximum force, and may be more versatile in function depending on fiber composition and differential recruitment of muscle units. Therefore, we examined enzymatic differences among selected wing muscles in an effort to see whether intrinsic differences in oxidative and glycolytic metabolism might also influence locomotor behaviors. Thus, a descriptive comparison of wing morphology was done to examine the degree to which differences in foraging flight behavior among the raptors is based on biomechanical factors.

MATERIALS AND METHODS

Due to the threatened and protected nature of these species, live experimentation could not be done. However, a great deal of information about forelimb structure and function can be obtained from study of fresh specimens. Carcasses of red-tailed hawks ($n = 7$) and Cooper's hawks ($n = 7$) were obtained from the Carolina Raptor Center (CRC), Huntersville, NC, while osprey ($n = 7$) specimens were obtained from both CRC ($n = 4$) and the Audubon Center for Birds of Prey, Maitland, FL ($n = 3$). Carcasses of healthy specimens that were killed or were euthanized due to severe injury were used in this study. Only birds of adult size that showed no signs of emaciation or other trauma-induced muscle abnormalities were used. All were frozen immediately after death and stored for no more than 2 weeks before use to preserve as much of the structural and biochemical integrity of the muscles as possible.

Skeletal and Wing Measurements

This study compared both skeletal and muscular elements among the three species. Measurements made directly on undissected wings included wingspan, total wing area, arm-wing area, and hand-wing area. Carcasses were positioned with wings displayed in a mid-flight position, then photographed (see below). A ruler was clearly placed in each photograph in order to allow for size calibration. Wingspan was obtained by measuring the distance from the midline of the body to the tip of the longest primary, then doubling this number. Areas of different portions of the wing were obtained by blocking the sections off into simple geometric shapes and calculating their areas individually. These were then summed to get handwing, armwing, or total wing areas.

Keel length, humerus length, and ulna length were measured directly after dissection and removal of soft tissue. Humerus length was measured between the articular surfaces of the caput humeri and the condylus ventralis. Ulna length was measured between the olecranon and the condylus ventralis ulnae. Keel length was measured between apex carinae to the point where it could no longer be distinguished from the rest of the sternum. Hand length was measured from the articular surface between the radius and carpometacarpus to the tip of the longest primary. Alula length was measured from the base of the first digit (phalanx digiti alulae) to the tip of the longest of the alular remiges.

Aspect ratio was calculated by dividing the square of the wingspan by the total wing area (Norberg, 1979; Kerlinger, 1989). Total wing area comprised the sum of the areas of both wings plus the area of body between the wings. Wing loading was determined by dividing the body mass by the total wing area (Hartman, 1961; Kerlinger, 1989).

Muscle Measurements

Ideally, an analysis of the functional properties of muscle would measure actual forces, speeds of contraction, and fatigability (e.g., Peters and Nishikawa, 1999). These can only be measured directly in live specimens. Due to the protected status of the species in this study, we used some indirect indicators of muscle force and metabolic properties that could be obtained from fresh carcasses.

Individual flight muscles (nomenclature according to Baumel et al., 1993) were analyzed in two different ways. Videos of live specimens taken at the CRC along with still photos were used to determine the natural wing positions at midflight. Wings of the freshly thawed specimens were then set at the mean shoulder, elbow, and wrist angles at midflight for their species (Cooper's hawk: $S = 54.0^\circ \pm 3.2^\circ$, $E = 112.3^\circ \pm 6.4^\circ$, $W = 154.1^\circ \pm 2.8^\circ$ [$n = 3$]; red-tailed hawk: $S = 51.7^\circ \pm 2.4^\circ$, $E = 102.3^\circ \pm 8.1^\circ$, $W = 145.7^\circ \pm 5.8^\circ$ [$n = 5$]; osprey: $S = 59.0^\circ \pm 5.0^\circ$, $E = 123.0^\circ \pm 4.0^\circ$, $W = 148.5^\circ \pm 1.5^\circ$ [$n = 3$]). With the wings in midflight position, the muscle lengths from origin to insertion were measured. Muscles were then removed and weighed. Muscle mass divided by length was used to estimate mean whole muscle cross-section of individual muscles (e.g., Chadwell et al., 2002). This cross-section was used as an indicator of maximum potential force production. The estimated cross-sections are meant for comparisons among species only and do not imply actual force measurements. It should be noted that force estimates (by cross-section) are oversimplifications that are limited by the assumption of equivalent angles of pinnation, and also do not take into account changes in force production during normal lengthening or shortening contractions.

One goal of our study was to establish whether, in addition to any proportional differences in force, physiological differences existed between muscles in the raptor species. For instance, if the rotator muscles of the forearm were larger in ospreys or Cooper's hawks than in red-tailed hawks, were they also more resistant to fatigue? Muscle fiber typing per se does not provide us with truly quantitative comparisons. Because, for example, oxidative capacity can differ within fiber type, we felt a better functional comparison would be the more quantitative enzymatic analysis. To estimate relative oxidative and glycolytic capacity among the muscles under study and compare them across species, enzymatic activity in selected whole muscles was analyzed via assays for citrate synthase (CS) and for lactate dehydrogenase (LDH), using standard spectrophotometric methods (Lutz et al., 1998). Use of whole muscles can also be a confounding factor in such comparisons if, for example, enzymatic levels differ from one part of the muscle to another. In order to test this, we took multiple samples of the large pectoralis and found no significant differences in either oxidative or glycolytic activities among regions.

Cross-sectional areas of a total of 12 brachial and antebrachial muscles were estimated (Table 1, Figs. 1–4). A subset of five muscles was then processed for analysis of CS and LDH activities. Each muscle was homogenized in a 2-mM EDTA/KCl solution (pH 7.4). One ml of muscle homogenate was then added to 2.5

TABLE 1. Selected muscles from the thorax, shoulder, brachium, and antebrachium

Muscle	Function
Coracobrachialis cranialis	Protraction of the brachium
Deltoides minor	Protraction, elevation, dorsal rotation of the brachium
Tensor propatagialis pars longa	Tensor of propatagium; flexion of antebrachium
Tensor propatagialis pars brevis	Tensor of propatagium; flexion of antebrachium
Brachialis	Flexion of antebrachium
Pronator superficialis	Pronation of antebrachium
Pronator profundus	Pronation of antebrachium
Supinator	Supination of antebrachium
Pectoralis	Depression and ventral rotation of brachium
Supracoracoideus	Elevation, dorsal rotation of brachium
Latissimus dorsi pars cranialis	Elevation of brachium
Ectepicondylo-ulnaris	Supination of antebrachium

ml 20 mM Tris buffer (pH 6.9) and sonicated. It was then centrifuged at 8,000g for 10 min and the supernatant stored for use in the assays. The muscles thus treated were: pectoralis, tensor propatagialis pars brevis, supracoracoideus, supinator, and pronator superficialis. These muscles were chosen for enzymatic analysis because they had the greatest differences in cross-section among species and were representative of the range of forelimb functions. Because of the pectoralis' large size, plugs of tissue ~1 cm³ were taken from a total of four sites, two each from the cranialateral and caudomedial aspects of both sternobrachial (cranial) and thoracobrachial (caudal) heads. CS and LDH activities of the pectoralis and gastrocnemius from Japanese quail (*Coturnix japonica*) (n = 3) were also analyzed for comparative purposes.

Data Analysis

Potential relative force production of individual muscles was compared by converting cross-sectional surface area of each muscle into a percentage of total body mass. These proportional data were tested for normality. Since they were normally distributed,

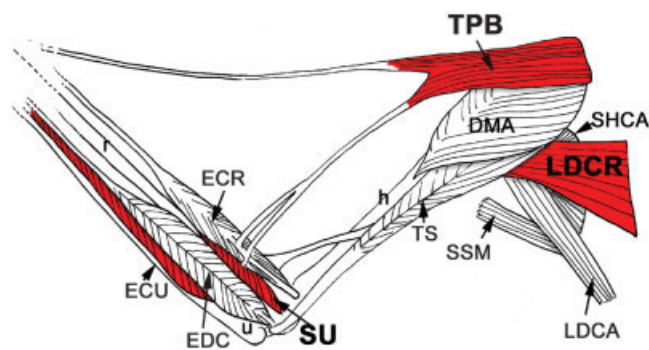


Fig. 1. The superficial dorsal musculature of a red-tailed hawk wing. The muscles we studied are indicated in red; other muscles are included for orientation. h, humerus; r, radius; u, ulna; DMA, deltoideus major; ECR, extensor carpi radialis; ECU, extensor carpi ulnaris; EDC, extensor digitorum communis; LDCA, latissimus dorsi pars caudalis; LDCR, latissimus dorsi pars cranialis; SHCA, scapulohumeralis caudalis; SSM, serratus superficialis pars metapatagialis; SU, supinator; TPB, tensor propatagialis pars brevis; TS, triceps brachii (scapulotriceps).

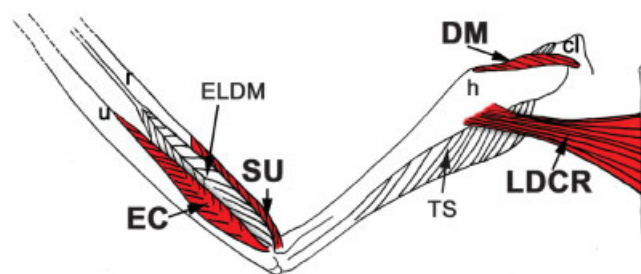


Fig. 2. Deep dorsal muscles of a red-tailed hawk wing. Muscles in our study indicated in red: cl, clavicle; h, humerus; r, radius; u, ulna; DM, deltoideus minor; EC, ectepicondylo-ulnaris; ELDM, extensor longus digiti majoris; LDCR, latissimus dorsi pars cranialis; SU, supinator; TS, triceps brachii (scapulotriceps).

we then compared them among species using one-way analysis of variance (ANOVA). Muscles were also grouped according to function (e.g., dorsal rotators, elevators, etc.), their cross-sectional surface areas totaled, and converted into percentage of body mass. All percentage values were found to be normally distributed, and so could also be compared using one-way ANOVA. Due to multiple comparisons, the sequential Bonferroni adjustment (Rice, 1989) was used to maintain an experiment-wise error rate of 5%.

Individual skeletal elements were analyzed using analysis of covariance (ANCOVA) with body length as the covariate. Body length was measured from the cranial surface of the first thoracic vertebrae to the caudal surface of the synsacrum immediately before the first caudal vertebrae. Cervical and caudal vertebrae were excluded from body length measurement, as these may vary greatly in number between avian species. ANCOVA was also used to compare handwing and armwing areas, but body mass was used as the covariate for these measurements.

Enzymatic assays were analyzed using one-way ANOVA and pair-wise comparisons were examined with Fisher's PLSD test. No significant differences were found among the regions of the pectoralis that we sampled in any of the species, so we were able to combine these data and report single mean values \pm standard error (SE) for CS and LDH activities in the pectoralis muscles.

RESULTS

Body Measurements

Body mass and body length were compared among species using one-way ANOVA. Body mass was not significantly different between osprey and red-tailed hawk; both, however, had significantly greater body mass than the Cooper's hawk (Table 2). Body length as measured in this study did not differ significantly between osprey and red-tailed hawk ($P = 0.636$), but did vary significantly between Cooper's hawk and osprey ($P = 0.015$) and Cooper's hawk and red-tailed hawk ($P = 0.049$) (Table 2).

Individual skeletal elements of the wing (humerus length, ulna length, and hand length) all varied significantly among species, even when overall differences in body size were taken into account using the ANCOVA analysis. These results showed that for most comparisons, osprey skeletal elements were relatively longer than those of the red-tailed hawk, which in turn were longer than those of the Cooper's hawk (Table 2). The keel of the red-tailed hawk was significantly relatively shorter than either of the

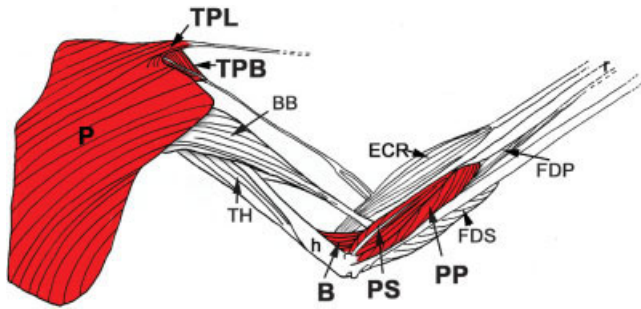


Fig. 3. Superficial ventral musculature of a red-tailed hawk wing. Muscles in our study indicated in red: h, humerus; r, radius; B, brachialis; BB, biceps brachii; ECR, extensor carpi radialis; FDP, flexor digitorum profundus; FDS, flexor digitorum superficialis; P, pectoralis; PP, pronator profundus; PS, pronator superficialis; TH, triceps brachii (humerothorax); TPB, tensor propatagialis pars brevis; TPL, tensor propatagialis pars longa.

other species ($P < 0.0001$), while the red-tailed hawk alula was significantly longer ($P = 0.001$) (Table 2).

Aspect ratios differed significantly, with the osprey displaying a significantly higher aspect ratio than either of the other two species ($P = 0.0089$) (Table 2). Although wing loading averaged highest in the osprey, the differences were not significant between the three species (Table 2).

Handwing area and armwing area were analyzed using ANCOVA with body mass as the covariate (Table 2). Significant differences were found in handwing area, with Cooper's hawk having smaller handwing area for its body mass than either of the other two species ($P = 0.005$). The osprey appeared to have relatively the smallest armwing area for its body mass, but high variability produced insignificant differences.

Handwing area was also analyzed using armwing area as a covariate in order to get a sense of proportion between the two (Table 2). No significant differences were found, although differences between osprey and Cooper's hawk approached significance ($P = 0.0615$), as did differences between osprey and red-tailed hawk ($P = 0.0514$). So the trend, although insignificant, was osprey > red-tailed hawk > Cooper's hawk, reflecting the relatively large handwing of the osprey.

Muscle Cross-Sectional Area

Of the 12 individual muscles analyzed (Table 1, Figs. 1–4), eight showed significant differences between two or more species (Table 3). In five of these (pectoralis, pronator superficialis, supracoracoideus, supinator, and tensor propatagialis pars brevis), the Cooper's hawk had significantly larger cross-sectional surface area per gram of body mass than either of the other two species. The greatest difference was in the pectoralis, where the Cooper's hawk

averaged 1.75 times greater than the osprey, and 2.4 times greater than the red-tailed hawk. The other muscles where cross-sectional area in the Cooper's hawk was the biggest ranged from about 1.3–2.0 times larger than the other two species. Of the other three significantly different results, the osprey had greater cross-sectional areas for two muscles than the other two species (brachialis, 1.4 times greater, and coracobrachialis cranialis, 1.5 times greater), and was the same as the Cooper's hawk for one (pronator profundus, at nearly 2.0 times larger than red-tailed hawk). In all cases where there were significant differences, the red-tailed hawk displayed the smallest cross-sectional areas for its body size (Table 3).

The same trends were apparent among the muscles grouped by function (Table 4). Out of nine functional groups, the Cooper's hawk had significantly larger cross-sectional surface area per gram of body mass than either of the other two species in four of them: the humeral depressors, dorsal and ventral rotators of the humerus, and patagial tensors. In three, Cooper's hawk and osprey were both significantly larger than the red-tailed hawk (although not different from each other): the humeral elevators, forearm pronators, and wing flexors. In one group (humeral protractors), the osprey was significantly larger than the other two species. In all cases where significant differences were found, the red-tailed hawk again displayed the smallest cross-sectional areas for its body size (Table 4).

Muscle Enzyme Analysis

Table 5 shows the results of our enzymatic assay for CS, and Table 6 the results of the LDH assay. For comparative purposes, we included previously reported values from the literature on some other birds and mammals (see notations in tables). In addition, the results from our assays of the pectoralis and gastrocnemius of the Japanese quail are included.

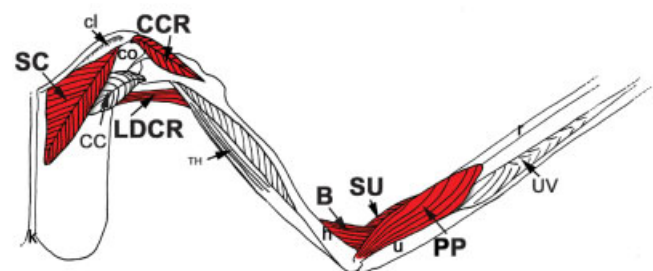


Fig. 4. Deep ventral musculature of a red-tailed hawk wing. Muscles in our study indicated in red: cl, clavicle; co, coracoid; h, humerus; k, keel; r, radius; u, ulna; B, brachialis; CC, coracobrachialis caudalis; CCR, coracobrachialis cranialis; LDCR, latissimus dorsi pars cranialis; PP, pronator profundus; SC, supracoracoideus; SU, supinator; TH, triceps brachii (humerothorax); UV, ulnometacarpalis ventralis.

TABLE 2. Body measurements and skeletal elements (mean \pm SE)*

	Cooper's hawk	Osprey	Red-tailed hawk
Body mass (g)	496.5 \pm 50.1 ¹	1137.7 \pm 55.1 ²	1135.7 \pm 102.8 ²
Body length (cm)	9.5 \pm 0.4 ¹	10.9 \pm 0.2 ²	11.2 \pm 0.6 ²
Humerus (cm)	7.3 \pm 0.3 ¹	13.8 \pm 0.3 ²	11.2 \pm 0.4 ³
(% Body length)	77.0 \pm 1.7 ¹	126.6 \pm 0.6 ²	100.8 \pm 4.3 ³
Ulna (cm)	8.2 \pm 0.2 ¹	18.2 \pm 0.3 ²	13.4 \pm 0.3 ³
(% Body length)	86.4 \pm 2.8 ¹	167.2 \pm 1.7 ²	120.0 \pm 5.4 ³
Hand (carpus + longest primary feather) (cm)	23.0 \pm 0.2 ¹	47.2 \pm 1.9 ²	40.1 \pm 0.6 ³
(% Body length)	259.0 \pm 9.0 ¹	422.8 \pm 19.3 ²	359.4 \pm 14.8 ³
Alula (cm)	10.1 \pm 0.4 ¹	12.1 \pm 0.4 ¹	12.9 \pm 0.4 ²
(% Body length)	106.6 \pm 2.8 ¹	111.6 \pm 4.6 ¹	116.1 \pm 6.7 ²
Keel (cm)	6.2 \pm 0.2 ¹	7.4 \pm 0.1 ¹	6.1 \pm 0.4 ²
(% Body length)	65.8 \pm 0.4 ¹	67.9 \pm 1.3 ¹	54.6 \pm 2.1 ²
Aspect Ratio	6.4 \pm 0.3 ¹	9.3 \pm 0.8 ²	7.0 \pm 0.4 ¹
		7.2 ^b	6.3 ^a
	2.2 ^c	3.0 ^c	5.2 ^b
			5.8 ^d
Wing loading (g/cm ²)	0.5 \pm 0.1	0.6 \pm 0.1	0.5 \pm 0.1
		0.96 ^e	0.46 ^a
		0.56 ^b	0.52 ^b
			0.59 ^d
Handwing Area (cm ²)	135.6 \pm 2.8 ¹	527.1 \pm 61.2 ²	417.7 \pm 16.6 ²
(% Body mass)	35.8 \pm 4.0	42.6 \pm 4.9	42.0 \pm 3.7
Armwing Area (cm ²)	207.9 \pm 11.9	492.4 \pm 45.9	487.7 \pm 27.6
(% Body mass)	54.9 \pm 6.0	39.6 \pm 3.4	48.2 \pm 2.4
Handwing area/armwing area	0.7 \pm 0.04	1.1 \pm 0.1	0.9 \pm 0.1
		0.8 ^e	

*Although wing elements are shown in percent of body length or body mass for easy visual comparison, the statistical significance of the differences was determined in an ANCOVA using body length or body mass as the covariate. Results with the same numerical notation are not significantly different from each other. For aspect ratio and wing loading, results from previous studies are shown as noted.

^aMueller et al. (2004).

^bKerlinger (1989).

^cHartman (1961).

^dSavile (1957).

^eKirmse (1998).

CS assays revealed significant differences between species in two of the five muscles analyzed (Table 5). In the supinator, Cooper's hawk had the highest level of enzyme activity, having about 1.7 times the activity

compared to osprey and over twice the activity of the red-tailed hawk. In the pronator superficialis, Cooper's hawk had significantly higher levels of oxidative activity, about 1.9 times greater than red-tailed hawk.

TABLE 3. Cross-sectional surface areas for selected muscles (% body mass; mean \pm SE)*

	Cooper's hawk	Osprey	Red-tailed hawk
<i>Brachialis</i>	0.010 \pm 0.001 ¹	0.014 \pm 0.001 ²	0.008 \pm 0.001 ¹
<i>Coracobrachialis cranialis</i>	0.019 \pm 0.001 ¹	0.031 \pm 0.003 ²	0.018 \pm 0.001 ¹
<i>Deltoideus minor</i>	0.002 \pm 0.001	0.006 \pm 0.001	0.004 \pm 0.001
<i>Ectepicondylor-ulnaris</i>	0.014 \pm 0.002	0.015 \pm 0.002	0.012 \pm 0.001
<i>Latissimus dorsi pars cranialis</i>	0.010 \pm 0.001	0.010 \pm 0.001	0.008 \pm 0.001
<i>Pectoralis</i>	1.10 \pm 0.10 ¹	0.630 \pm 0.05 ²	0.450 \pm 0.04 ³
<i>Pronator profundus</i>	0.038 \pm 0.001 ¹	0.041 \pm 0.006 ¹	0.022 \pm 0.001 ²
<i>Pronator superficialis</i>	0.019 \pm 0.001 ¹	0.014 \pm 0.001 ²	0.010 \pm 0.001 ³
<i>Supracoracoideus</i>	0.058 \pm 0.005 ¹	0.046 \pm 0.002 ²	0.032 \pm 0.001 ³
<i>Supinator</i>	0.010 \pm 0.001 ¹	0.005 \pm 0.001 ²	0.006 \pm 0.000 ²
<i>Tensor propatagialis pars brevis</i>	0.039 \pm 0.003 ¹	0.027 \pm 0.003 ²	0.020 \pm 0.001 ³
<i>Tensor propatagialis pars longa</i>	0.022 \pm 0.003	0.021 \pm 0.005	0.018 \pm 0.002

*Results with the same numerical notation were not significantly different from each other.

TABLE 4. Cross-sectional surface areas of functional muscle groups (% body mass; mean \pm SE)*

	Cooper's hawk	Osprey	Red-tailed hawk
Humeral depressors (<i>Pectoralis</i>)	1.10 \pm 0.10 ¹	0.63 \pm 0.05 ²	0.45 \pm 0.04 ³
Humeral elevators (<i>Latissimus dorsi pars cranialis</i> , <i>supracoracoideus</i> , <i>deltoideus minor</i>)	0.07 \pm 0.010 ¹	0.06 \pm 0.003 ¹	0.04 \pm 0.001 ²
Dorsal rotators of the humerus (<i>Supracoracoideus</i> , <i>deltoideus minor</i>)	0.06 \pm 0.005 ¹	0.05 \pm 0.002 ²	0.04 \pm 0.001 ³
Ventral rotators of the humerus (<i>Pectoralis</i>)	1.10 \pm 0.10 ¹	0.63 \pm 0.05 ²	0.45 \pm 0.04 ³
Humeral protractors (<i>Coracobrachialis cranialis</i> , <i>deltoideus minor</i>)	0.02 \pm 0.002 ¹	0.04 \pm 0.003 ²	0.02 \pm 0.001 ¹
Antebrachial pronators (<i>Pronator superficialis</i> , <i>pronator profundus</i>)	0.06 \pm 0.001 ¹	0.05 \pm 0.006 ¹	0.03 \pm 0.002 ²
Antebrachial supinators (<i>Supinator</i> , <i>ectepicondyloulnaris</i>)	0.02 \pm 0.002	0.02 \pm 0.002	0.02 \pm 0.001
Propatagial tensors (<i>Tensor propatagialis pars brevis</i> , <i>tensor propatagialis pars longa</i>)	0.06 \pm 0.003 ¹	0.05 \pm 0.008 ^{1,2}	0.04 \pm 0.003 ²
Wing flexors (<i>Brachialis</i> , <i>tensor propatagialis pars brevis</i> , <i>tensor propatagialis pars longa</i>)	0.08 \pm 0.004 ¹	0.06 \pm 0.008 ¹	0.05 \pm 0.003 ²

*Results with the same numerical notation are not significantly different from each other.

LDH assays found differences between raptor species in three of the five muscles analyzed (Table 6). In two of them, Cooper's hawk had the highest LDH activity, and in one red-tailed hawk was the highest. In the tensor propatagialis pars brevis, Cooper's hawk had significantly higher levels of glycolytic enzymes than either osprey ($P = 0.0231$) or red-tailed hawk ($P = 0.0347$) (>5 times higher), and in the supinator, Cooper's hawk showed significantly higher levels than osprey ($P = 0.0008$) ($\sim 6\times$) or red-tailed hawk ($P = 0.0064$) ($\sim 5\times$), while red-tailed hawk showed higher levels than osprey ($P = 0.0221$) ($\sim 2\times$). In the supracoracoideus, red-tailed hawk had significantly higher levels of enzyme activity (>2 times higher) than either osprey ($P = 0.0007$) or Cooper's hawk ($P = 0.0003$), while osprey had higher levels than Cooper's hawk ($P = 0.0252$).

In summary, CS activity was highest in the pronators and supinators of the Cooper's hawk. LDH activity was also highest in these muscles, as well as the propatagial flexor. LDH activity was also unusually high in the red-tailed hawk supracoracoideus. All other muscles showed no significant differences.

DISCUSSION

Cooper's hawks are primarily avivores. Observations suggest that they take their prey on the wing, after actively chasing it down up to 60% of the time (Toland, 1986). These chases take place in woodlands and dense underbrush, which requires Cooper's hawks to make rapid changes to wing position in order to avoid collisions with obstacles. Cooper's hawks must also be able to accelerate quickly and change direction in order to overtake their prey.

Ospreys are piscivores that specialize in hunting species that occur at shallow depths. They often locate schools of fish by soaring over the waterways. In up to 44% of hunts (Toland, 1986), ospreys target their prey while briefly hovering. After diving, the osprey must then be able to lift itself and its prey clear of the water. Both hovering and getting out of

the water require large rotational movements of the wings, including large degrees of supination and pronation.

Red-tailed hawks are generalist predators, although their primary prey items are small mammals. They locate prey either from perches or from soaring flight, during which relatively small wing adjustments are required. As they swoop down to take prey, they approach using level flight. In the last few seconds before striking, they elevate the wings and rotate the body forward to bring their feet into position to grasp prey (Goslow, 1971). This ventral rotation of the body is thought to be controlled by the pectoralis (Dobbins, 1992). These behavioral differences suggest that Cooper's hawks and ospreys use more frequent and more forceful rotational movements of the wing than is typical of red-tailed hawks.

Body Measurements

Aspect ratio (ratio of wing length to wing width) and wing loading (body mass divided by wing area) are the classic descriptors of the variation of wing design among bird species. Additionally, the proportion of various skeletal elements and the overall shape of the wing have been correlated with the flight style of different species in a number of studies (e.g., Norberg, 1979). It is important to note that differences in feather proportion may in some cases be more important than that of skeletal elements; i.e., long versus short primaries on carpi of the same length may result in highly different wing shapes (Norberg, 1979). For this reason, we chose to measure the length of the hand from wrist joint to tip of the longest primary, rather than measuring the length of the carpus alone.

Previous studies have shown that short, rounded, elliptical wings that maximize thrust are found in birds that need to accelerate quickly and make sudden lateral movements, such as birds that capture their prey through pursuit (Kirmse, 1998; Lockwood

TABLE 5. Citrate synthase activity of selected muscles (mean $\mu\text{g} \pm \text{SE}$)^{*}

	Cooper's hawk (n = 5)	Osprey (n = 5)	Red-tailed hawk (n = 5)	Japanese quail (n = 3)	Coot (high altitude) ^a	Coot (sea level) ^a	Grey seal ^b	Harbor seal ^b	Fur seal ^b	Rat ^b
<i>Pectoralis</i>	12.0 \pm 1.6	10.3 \pm 0.9	12.1 \pm 1.2	1.7 \pm 0.4	125	121	—	<i>Pinnipedia</i>	17.0 \pm 1.2	<i>Rodentia</i>
<i>Pronator</i>	10.6 \pm 1.9 ¹	9.7 \pm 1.6 ^{1,2}	5.6 \pm 1.3 ²	—	—	—	—	—	—	—
<i>superficialis</i>										
<i>Supracoracoideus</i>	11.02 \pm 2.10	7.43 \pm 2.03	11.96 \pm 3.27	—	—	—	—	—	—	—
<i>Supinator</i>	21.8 \pm 3.0 ¹	13.2 \pm 1.6 ²	9.4 \pm 2.6 ²	—	—	—	—	—	—	—
<i>Tensor</i>	8.2 \pm 0.8	9.0 \pm 1.6	7.8 \pm 1.3	—	—	—	—	—	—	—
<i>propatagialis</i>										
<i>pars brevis</i>	—	—	—	2.9 \pm 0.8	—	—	—	—	—	—
<i>Gastrocnemius</i>	—	—	—	—	65.2	59.0	—	—	—	15.7 \pm 1.5
<i>Extensor</i>	—	—	—	—	—	—	—	—	—	—
<i>digitorum</i>										
<i>longus</i>										
<i>Tibialis anterior</i>	—	—	—	—	67.0	62.2	—	—	—	—
<i>Plantaris</i>	—	—	—	—	69.4	61.0	—	—	—	—
<i>Longissimus dorsi</i>	—	—	—	—	—	—	7.4 \pm 0.7	24.5 \pm 2.2	12.1 \pm 0.1	—

^{*}Results for the three raptor species with the same numerical notation are not significantly different from each other.

¹León-Velarde et al. (1993).

²Reed et al. (1994).

TABLE 6. Lactate dehydrogenase activity of selected muscles (mean $\mu\text{g} \pm \text{SE}$)^{*}

	Cooper's hawk (n = 3)	Osprey (n = 3)	Red-tailed hawk (n = 3)	Japanese quail	Coot (high altitude) ^a	Coot (sea level) ^a	Grey seal ^b	Harbor seal ^b	Fur seal ^b	Rat ^b
<i>Pectoralis</i>	12680.1 \pm 2029.9	10064.2 \pm 1118.2	7506.1 \pm 1337.9	3241.0 \pm 1458.8	2348	2890	—	<i>Pinnipedia</i>	1128.4 \pm 206.3	<i>Rodentia</i>
<i>Pronator</i>	25037.1 \pm 1067.1	9761.3 \pm 1760.6	13845.0 \pm 3284.5	—	—	—	—	—	—	—
<i>superficialis</i>										
<i>Supracoracoideus</i>	10769.0 \pm 3101.1 ¹	12989.8 \pm 419.8 ³	29278.0 \pm 62.0 ²	—	—	—	—	—	—	—
<i>Supinator</i>	30,792.1 \pm 8431.2 ¹	5025.0 \pm 15.0 ³	11,102.2 \pm 687.8 ²	—	—	—	—	—	—	—
<i>Tensor</i>	47855.0 \pm 4315.8 ¹	6690.0 \pm 1290.3 ²	9170.3 \pm 4213.2 ²	—	—	—	—	—	—	—
<i>propatagialis</i>										
<i>pars brevis</i>	—	—	—	7951.7 \pm 2835.2	—	—	—	—	—	—
<i>Gastrocnemius</i>	—	—	—	—	2936	3250	—	—	—	810.0 \pm 144.0
<i>Extensor</i>	—	—	—	—	—	—	—	—	—	—
<i>digitorum</i>										
<i>longus</i>										
<i>Tibialis anterior</i>	—	—	—	—	3280	3780	—	—	—	—
<i>Plantaris</i>	—	—	—	—	2900	2013	—	—	—	—
<i>Longissimus dorsi</i>	—	—	—	—	—	—	538.4 \pm 47.3	788.5 \pm 62.0	969.65 \pm 39.7	—

^{*}Results for the three raptor species with the same numerical notation are not significantly different from each other.

¹León-Velarde et al. (1993).

²Reed et al. (1994).

et al., 1998). Because pressure is uniformly distributed across this wing type, it also gives high maneuverability (Savile, 1957). The handwing is generally short when compared to the armwing (Norberg, 1979; Kirmse, 1998). These wings have a low aspect ratio and low wing loading (Norberg, 1979, 1985).

Birds that use static soaring (i.e., soaring in low velocity wind), tend to have a broad wing designed to minimize drag and maximize lift (Lockwood et al., 1998). The handwing is generally short but broad (Kirmse, 1998), while the armwing is long and broad to maximize the lift provided by the secondary feathers (Norberg, 1979, 1981, 1985). The alula is the tuft of feathers supported by the phalanx digiti alulae, the only free digit found on the wing. These feathers act as a spoiler, which helps control the passage of air over the wing during flight. Previous studies (Savile, 1957) have found that the alula is more pronounced in soaring birds. Low aspect ratio and low to medium wing loading are also typical of soaring wings (Savile, 1957; Norberg, 1981, 1985).

Hovering fliers must compensate for high inertial forces. In order to decrease the amount of inertia that must be overcome, the highest mass of the wing is located as proximally as possible, while the lighter-mass handwing is greatly elongated (Norberg, 1979, 1981, 1985). These wings have a high aspect ratio, and wing loading may be increased over that of birds of the same weight (Savile, 1957; Norberg, 1981). These features are also consistent with the high aspect ratio wings typical of birds that soar in high velocity wind (i.e., dynamic soarers) (Savile, 1957; Norberg, 1985).

Measurements of aspect ratio and wing loading have been only sparsely reported for raptorial birds (Kerlinger, 1989; Mueller et al., 2004). In this study, the Cooper's hawk was found to demonstrate the characteristics associated with the elliptical wing. Their wing was relatively short overall, particularly the handwing portion formed by the carpus and primary feathers. All individual skeletal elements were significantly shorter than in the other birds, and the handwing area was one-third or less of that in the other two species. The aspect ratio was significantly smaller than that found in the osprey, although wing loading did not differ significantly among any of the species.

While the handwing and armwing elements of the red-tailed hawk were longer than those of the Cooper's hawk, their aspect ratios were not significantly different. Thus, although the bony elements of the wing were relatively longer in red-tailed hawks than in Cooper's hawks, their long secondary feathers and large handwing area produce a very broad average wing chord, resulting in a relatively low aspect ratio. In addition, the alula was significantly longer than that of either of the other species. This design fits the pattern previously described for static soaring birds.

Observations of the osprey correlate with previous studies of hovering and dynamic soaring birds (Norberg, 1985). All wing skeletal elements were significantly longer than those found in the other two species. The wing had a significantly higher aspect ratio than both other species, indicating a long but narrow wing useful in both hovering and flying or soaring in high velocity winds.

In addition to the traditional wing elements, keel length was also measured for the three species in this study. The keel length of the red-tailed hawk was significantly shorter than that of either of the other two species, which may reflect its proportionally smaller pectoralis.

Previous reports of aspect ratio in these species have varied greatly, from 3.00 (Hartman, 1961) to 7.2 (Kerlinger, 1989) in the osprey alone. These discrepancies probably reflect different means of calculating aspect ratio as well as different means of obtaining measurements. Our results for the osprey most closely matched those obtained by Kerlinger (1989), although our mean ratio was higher (9.3) (Table 2). For the red-tailed hawk, our results agree with those obtained by Mueller et al. (2004).

Reports of wing loading in the literature are far more consistent than those of aspect ratio, and agreed with the findings of this study (Hartman, 1961; Kerlinger, 1989; Mueller et al., 2004). Wing loading did not differ significantly among the three species, despite differences in structural proportions and aspect ratio.

Muscle Cross-Sectional Area

Large muscle size may reflect an increased maximum force potential, but it is also important to note that it may reflect a larger pool of muscle fibers from which to recruit different populations needed for different functions (e.g., Herring et al., 1979). The pectoralis, in particular, is a complex muscle comprising two major subdivisions, the thoracobrachialis and the sternobrachialis (Fisher, 1946; Rosser and George, 1986b; Meyers, 1991; Meyers and Mathias, 1997). These are complexly pinnate compartments and, depending on the pattern of recruitment, can produce depression of the wing over a wide range of protracted, midline, and retracted angles. So in addition to greater overall force, the large pectoralis in particular may produce forceful movements over a diversity of wing trajectories, perhaps allowing for the high maneuverability of Cooper's hawks. The pectoralis was second largest in the osprey, and again this may reflect both the need for a powerful downstroke to elevate the body from the water after a dive, as well as the need for complex movements both in hovering and in clearing the water, both of which require strong depression combined with protraction or retraction of the humerus. The red-tailed hawk displayed the smallest pectoralis of the three species. As a soaring hunter, the

red-tailed hawk would not typically make complicated adjustments over a large range of wing positions; adjustments that are made are far more subtle, and probably do not depend on the recruitment of large numbers of muscle fibers to perform.

The wing flexors allow folding of the wing at the elbow, which will change the instantaneous aspect ratio and control the balance between lift and drag to effect maneuvering (Brown, 1952; Tucker, 1987, 1992; Pennycuik et al., 1992; Warrick and Dial, 1998). Propatagial tensors regulate both the stiffness and the shape of the leading edge of the wing, adjusting wing camber and lift generation (Brown et al., 1994; Brown and Cogley, 1996). Due to the insertion of their tendons on the antebrachium and carpus, they can also act in conjunction with other muscles as wing flexors (Brown et al., 1994). Both wing flexors and propatagial tensors were relatively large in the Cooper's hawk, perhaps allowing it to make the maneuvers needed to successfully navigate the complicated architecture of its woodland habitat while in pursuit of prey. Although the forearm supinators as a group were not significantly different from the other species studied, *M. supinator* itself was significantly larger in the Cooper's hawk, suggesting that it may play an important role in adjusting wing position during flight. The antagonistic pronators were also large in the Cooper's hawk. Osprey had equally large pronators that may be particularly important, as ospreys must powerfully flick their long handwing (leading edge down, trailing edge up) as they hover and as they exit the water after a dive.

A trend was observed in osprey functional muscle groups and individual muscles, in which this species was intermediate in size between the Cooper's hawk and the red-tailed hawk, or else was equal to the Cooper's hawk but still significantly larger than the red-tailed hawk. This trend held for all functional groups except for humeral protractors, which were significantly larger in the osprey than in either of the other species. Observations of ospreys taking off from the water after a dive indicate that the wings must be lifted cranially in order to get them free from the water and in position for the first downstroke of flight, perhaps explaining the need for strong humeral protractors. Equally as large in the osprey as in the Cooper's hawk were the humeral elevators, antebrachial pronators, and wing flexors. All would aid both in positioning the wing for take-off from the water, and in the hovering flight that precedes a dive.

The results reflect the fact that, for different reasons, both Cooper's hawks and ospreys are using powerful and diverse movements of the wing in a variety of planes that includes frequent rotation of the handwing and the armwing. Because red-tailed hawks spend much of their time soaring, there is less demand for the diverse and forceful movements of the wings that characterize the hunting styles of

the other two species. This may explain why they displayed the weakest relative force potential in 8 out of 12 individual muscles and in 8 out of 9 functional groups where significant differences occurred.

Muscle Enzyme Analysis

Previous studies of avian skeletal muscle fibers have identified several main types: fast twitch glycolytic (FG), fast twitch oxidative-glycolytic (FOG), and slow fibers. FG fibers are characterized by large fiber size, low myoglobin content, and their dependence on anaerobic (glycolytic) respiration. They are highly fatigable, but produce fast, forceful movements. FOG fibers are often smaller in size and contain both oxidative and glycolytic enzymes. They may have less force potential but are more fatigue-resistant than FG fibers. In contrast, slow fibers are highly oxidative and fatigue-resistant, but are also relatively weak. Typically, FG and FOG fibers are found in phasic muscles, while slow fibers are confined to postural muscles (Rosser and George, 1986b; Rosser et al., 1987).

Studies of soaring birds have suggested that slow fibers may be found within the deep layers of the pectoralis, and function to support the body between the wings. These fibers are often confined to the deep layers of the muscle (Fisher, 1946; Rosser and George, 1986b; Meyers, 1991; Meyers and Mathias, 1997) in birds with an undivided pectoralis (including the species of this study). In some birds, e.g., New World vultures and other members of the stork family, these fibers form a distinct head of the pectoralis (Fisher, 1946; Rosser and George, 1986a; Meyers and Mathias, 1997).

CS and LDH activity in vertebrate skeletal muscle have previously been reported for some mammal and avian species (see Tables 5 and 6). CS activity for the three raptor species and the Japanese quail analyzed in this study closely matched results found for mammals (Table 5). The coot, however, perhaps due to its migratory habits, had much higher CS activities. LDH activity of the Japanese quail muscles was similar to that found in previous avian studies, and generally higher than in mammals. The LDH activity levels for the three raptors were much higher than previously reported in mammals, avians, or Japanese quail (Table 6). Although the quail gastrocnemius is similar in LDH activity to some of the raptor muscles, many of our results for raptors were considerably higher. Large standard errors in our data suggest quite a bit of variability, but in the two most variable results (red-tailed hawk tensor propatagialis pars brevis and Cooper's hawk supinator), the differences among species were so great that they still reached statistical significance. The interesting question is why all of the raptors have relatively such high levels of LDH activity. Future comparisons with other birds should clarify how unusual this level of activity is among avians.

No significant differences were found in glycolytic and oxidative enzyme activities of the pectoralis among the three species in this study. This supports the findings of previous studies that suggest that all migratory birds have a pectoralis comprised largely of metabolically diverse FOG fibers and do not differentiate highly from one another in this particular manner, although they do differ in myosin heavy-chain expression (Rosser et al., 1996). However, a study by Rosser and George (1986b) found the presence of slow fibers in the red-tailed hawk pectoralis but not in the sharp-shinned hawk (*Accipiter striatus*), a species closely related to the Cooper's hawk that pursues a similar lifestyle. Although it could be argued that the presence of slow fibers in the red-tailed hawk pectoralis was related to its soaring, these fibers were not found in the pectoralis of other soaring birds tested, and the authors suggested that the lack of evidence of slow fibers in other species was related to their sampling method rather than to the actual absence of such fibers. They concluded that the few slow fibers that were discovered were most likely not of great importance in postural maintenance during soaring. Our study supports this conclusion in that we did not find greater citrate synthase (CS) activity in the red-tailed hawk pectoralis than in the other species.

Cooper's hawks showed high levels of CS activity in the supinator and pronator superficialis. Because chases after prey may require sustained changes of wing orientation, most fibers in these muscles may have high levels of oxidative enzymes in order to provide the endurance needed. In addition, the supinator also displayed high levels of glycolytic enzymes, suggesting that this muscle is composed of metabolically diverse FOG fibers, and may be responding to the need for fast acceleration and changes of wing angle which are required when maneuvering through forests and underbrush. Although ospreys display large amounts of supination and pronation of the wing during hovering and take-off from water, they do not have to sustain these movements for more than a few seconds at a time. This suggests that the muscle fibers responsible for these movements may be skewed less towards oxidative enzymes (lower CS activity than in the Cooper's hawk), perhaps reflecting the need for rapid and powerful rather than enduring motions of the wing.

Red-tailed hawks displayed significantly higher levels of lactate dehydrogenase (LDH) activity in the supracoracoideus than either of the other two species. The supracoracoideus is likely recruited only during takeoff in this bird, as it does little sustained flapping compared to the other two species in this study. Therefore, it may rely on heavily glycolytic fibers in order to make the powerful movements needed to take off, particularly when burdened with prey.

In the Cooper's hawk, the tensor propatagialis pars brevis displayed a higher glycolytic capacity than in the other two species. Previous studies by Rosser et al. (1987) suggested that high levels of fast twitch fibers in this muscle correlate with its role as a wing flexor. If so, this muscle may be more metabolically diverse in the Cooper's hawk than in the other two species, having both endurance and the ability to make the fast, forceful adjustments of wing shape and position required by its flight style.

Overall, relatively few differences were found in enzymatic activity among the muscles compared across species. Most of the significant differences showed that Cooper's hawks have higher levels of activity of both CS and LDH. This may simply attest to their metabolically demanding lifestyle.

Tobalske et al. (1999) considered the role of muscle fiber composition in the flight styles of three passerines. Zebra finches (*Taenopygia guttata*) utilize a flap-bound gait, while budgerigars (*Melopsittacus undulatus*) rely on continuous flapping and ruby-throated hummingbirds (*Archilocus colubris*) hover. All three of these birds have a pectoralis that consists solely of FOG fibers; however, aspect ratio, wing loading, and skeletal proportions differ dramatically among species, leading Tobalske et al. (1999) to conclude that wing architecture may play a bigger role in flight kinematics than muscle fiber types. Our results, showing little difference in enzymatic activity among the flight muscles, lend support to that hypothesis.

The results of this comparative biomechanical/functional analysis are consistent with the prevailing analyses of the relationship between wing architecture and flight style. The Cooper's hawk displayed characteristics consistent with the elliptical wing shape found in birds whose lifestyle requires a high degree of maneuverability, while the red-tailed hawk wing matched previous descriptions of static soarers, and the results for the osprey matched that of both hoverers and dynamic soarers. In addition, our work on the enzymatic differences found in these species supports the previous hypothesis that wing architecture may play a larger role in the diversity of flight styles than does metabolic differences within the muscle fibers. Hence, this study provides further data from previously neglected species, demonstrating that they fit within the theoretical framework already established by investigations using more common and unprotected species.

Although a great deal of supportive data has come from the study of these carcasses, relatively noninvasive techniques such as electromyography or strain gauge implants for examining muscle structure and physiology in the living birds would be a useful avenue of future inquiry.

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