Anatomy and Histochemistry of Spread-Wing Posture in Birds. I. Wing Drying Posture in the Double-Crested Cormorant, *Phalacrocorax auritus*

RON A. MEYERS*
Department of Zoology, Weber State University, Ogden, Utah 84408-2505

ABSTRACT   Spread-wing postures of birds often have been studied with respect to the function of behavior, but ignored with regard to the mechanism by which the birds accomplish posture. The double-crested cormorant, *Phalacrocorax auritus,* was used as a model for this study of spread-wing posture. Those muscles capable of positioning and maintaining the wing in extension and protraction were assayed histochemically for the presence of slow (postural) muscle fibers. Within the forelimb of *Phalacrocorax,* Mm. coracobrachialis cranialis, pectoralis thoracicus (cranial portion), deltoideus minor, triceps scapularis, and extensor metacarpi radialis pars dorsalis and ventralis were found to contain populations of slow-twitch or slow-tonic muscle fibers. These slow fibers in the above muscles are considered to function during spread-wing posture in this species. J Morphol *233*:67–76, 1997.   © 1997 Wiley-Liss, Inc.

Birds and mammals possess specializations of the musculoskeletal system to reduce the cost of a variety of behaviors. For example, the horse passive stay apparatus (Dyce et al., '87) and albatross shoulder lock (Pennycuick, '82) reduce the overall need for muscle contraction during long-term standing and soaring, respectively. Slow-contracting muscle fibers are specialized for sustained contraction and high fatigue resistance (Goldspink, '77), and can be found in muscles associated with posture. Slow fibers are more efficient at postural (isometric) contractions due to the longer interactions between actin and myosin and the resulting decreased cost of ATP. Within birds, slow fibers have been described as making up a deep layer of the pectoralis muscle of turkey vultures (*Cathartes aura;* Rosser and George, '86a) and white pelicans (*Pelecas erythrorhynchos;* Rosser et al., '94) as a specialization for maintaining wing posture during soaring flight. These fibers have been hypothesized to be present in the pectoralis of all gliding and soaring species (Pennycuick, '72, '82; Meyers, '93). In addition, a suite of slow shoulder muscles function to keep the avian wing in a folded position (Meyers, '92). Both spread-wing and folded-wing behaviors present relatively long-term mechanical events that are made "less-expensive" by the presence of slow-muscle fiber types. Whereas slow-muscle specializations have been described for mammal limbs (which must bear weight constantly when the animal is standing; e.g., see Armstrong, '80; Hermanson et al., '91; Suzuki, '91; Petrie et al., '93), such modifications in the avian forelimb are less often encountered. In part this is due to the fact that in contrast to the mammalian forelimb, the avian wing does not normally bear weight when at rest.

The spread-wing posture of cormorants and other birds is one behavior that could be facilitated by the reduced energetic cost of slow muscle fibers. Although this behavior is believed to function in drying the wings of cormorants (Hennemann, '84, '88; see Simmons, '86, for review), the actual means by which these birds hold the wings spread to perform this behavior has not been addressed. The double-crested cormorant, *Phalacrocorax auritus,* was selected for this study because it represents a readily obtainable species that illustrates the spread-wing posture (Bent, '22). Previous studies on cormorant forelimb morphology (Owre, '67; Livezey, '92) have not commented on pos-

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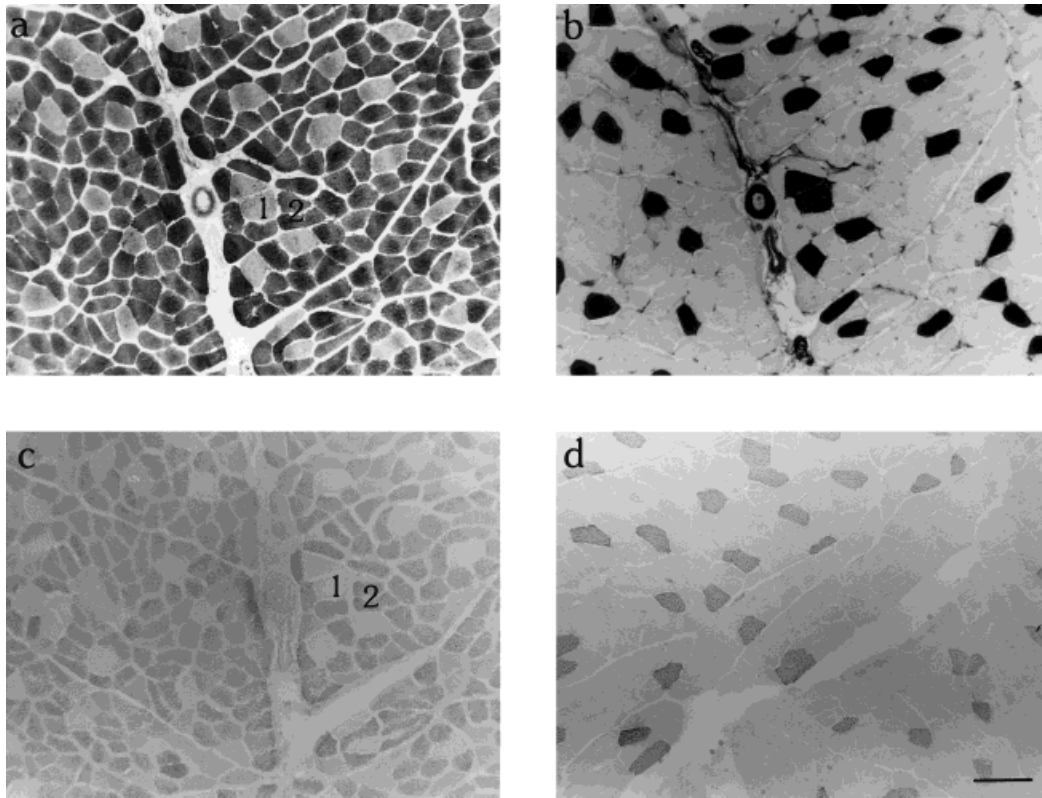*Correspondence to: Ron A. Meyers, Department of Zoology, Weber State University, Ogden, UT 84408-2505.

Fig. 1. *Phalacrocorax auritus.* Serial sections of ATPase histochemistry of M. extensor metacarpi radialis. **a:** Alkaline preincubation (pH 10.4). **b:** Acidic preincubation (pH 4.2). **c:** Anti-fast antibody (MY32). **d:** Anti-slow antibody (S58). 1, slow-twitch fiber; 2, fast-twitch fiber. The positive (dark) reaction in acidic preincubation corresponds with positive anti-slow antibody reaction and that positive reaction in alkaline preincubation corresponds with anti-fast antibody reaction product. Note that in d an adjacent area of fibers is shown. Scale = 100 µm.

sible muscle function during spread-wing posture. The goal of this study is to examine those forelimb muscles of *Phalacrocorax auritus* capable of positioning the spread wing, and to assess which muscles contain slow-contracting (postural) fibers.

MATERIALS AND METHODS

Two individuals of *Phalacrocorax auritus* (obtained from the Louisiana State University Museum of Zoology and North Carolina State Museum of Natural History) were dissected to identify which muscles were biomechanically suited to function during spread-wing posture. Dissections were illustrated with a Holbein camera lucida. Nomenclature follows that of Meyers ('93) for the muscles and *Nomina Anatomica Avium* (Baumel and Witmer, '93) for the skeleton. Fresh muscle samples from three birds were

obtained via shooting in the Cape Fear River, North Carolina, under possession of valid state and federal permits. Muscle samples were immediately removed mid-belly, quick-frozen by immersion into isopentane cooled to about $-150°C$ in liquid nitrogen, and stored at $-70°C$. Transverse serial sections (10–12 µm thickness) were cut on a freezing cryostat at $-20°C$ and mounted on glass slides for staining. Histochemical staining for myosin ATPase followed the protocol of Staron et al. ('83), which permits the differentiation of slow-twitch, fast-twitch, and slow-tonic fibers (Hikida, '87) (see Figs. 1, 2). Hikida ('87) has shown that pectoralis, biventer cervicis, and cranial latissimus dorsi muscles from rock doves (pigeons; *Columba livia*) consist of fast-twitch, mixed fast-twitch/slow-twitch, and slow-tonic muscle fibers, respectively. In the present study, these
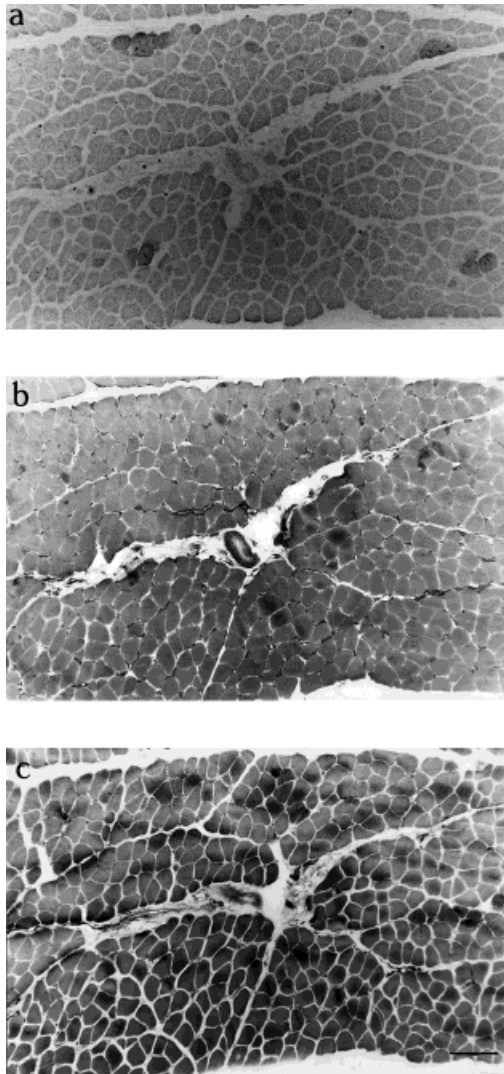
Fig. 2. *Phalacrocorax auritus.* Serial sections of ATPase histochemistry of M. latissimus dorsi cranialis to illustrate slow-tonic staining profile. **a:** Alkaline preincubation (pH 10.4). **b:** Acidic preincubation (pH 4.2). **c:** S58—anti-slow antibody. Note that both ATPase reactions have a moderate staining intensity, unlike the slow-twitch reaction. Scale = 100 μm.

pigeon muscles were run concurrently as controls for examples of the three fiber types (Meyers, '92). Routine staining procedures for oxidative capacity (nicotinamide adenine dinucleotide diaphorase-NADH; Novikoff et al., '61) were also used.

Additional serial sections were stained with antibodies to fast and slow myosin fol-

lowing the procedure described in Hermanson and Cobb ('92). The anti-fast antibody MY32 (Sigma Chemical Co., St. Louis, MO) labels histochemically defined type II fibers in mammals and birds, whereas the anti-slow antibody S58 (Dr. Frank Stockdale, Stanford University Medical School, CA) labels type I fibers in mammals and both type I and tonic fibers in birds. Frozen serial sections were obtained in the same manner as for the histochemistry. Sections were allowed to reach room temperature, covered with 2% normal goat serum, and incubated in a humidified chamber at 4°C for 30 min. The normal goat serum was removed and the primary antibody applied to the tissue and incubated for 16 h in a humid chamber at 4°C. After rinsing 10 min in 0.05 M phosphate-buffered solution (PBS) with 0.85% NaCl, the sections were incubated in a goat anti-mouse antibody for 10 min to recognize the primary antibody, and the PBS rinse repeated. Finally, sections were then reacted with a strepavadin enzyme conjugate for 5 min and the PBS rinse repeated. Staining was performed with a substrate chromagen for 15 min. The second antibody, enzyme conjugate, and substrate chromagen are from a commercially available staining kit (Zymed Laboratories, South San Francisco, CA).

The literature on the classification of fiber types (especially of avian muscle fibers) is not in uniform agreement (Gollnick and Hodgson, '86; Torrella et al., '93). One scheme recognizes fiber subtypes on the basis of ATPase reactivity and utilizes type I and type II designations (Pette and Staron, '90). The other scheme uses metabolic enzymes in addition to ATPase and identifies fibers as SO (slow, oxidative), FOG (fast, oxidative, glycolytic), and FG (fast, glycolytic) (Pette and Staron, '90). As Pette and Staron ('90) indicate, these two classification schemes are not interchangeable. The fiber type nomenclature of Hikida ('87) and Meyers ('92), where avian fibers are defined as fast-twitch, slow-twitch, or slow-tonic, is used here.

Black and white photographs of entire muscle cross sections were used to count individual muscle fibers. Ratios of slow and fast fibers were taken and the standard error of the mean from three specimens was calculated.

RESULTS

Cormorants exhibit a full spread-wing posture (Simmons, '86), with the wing outstretched in extension and protracted (Fig. 3). In this position, the wing is extended at
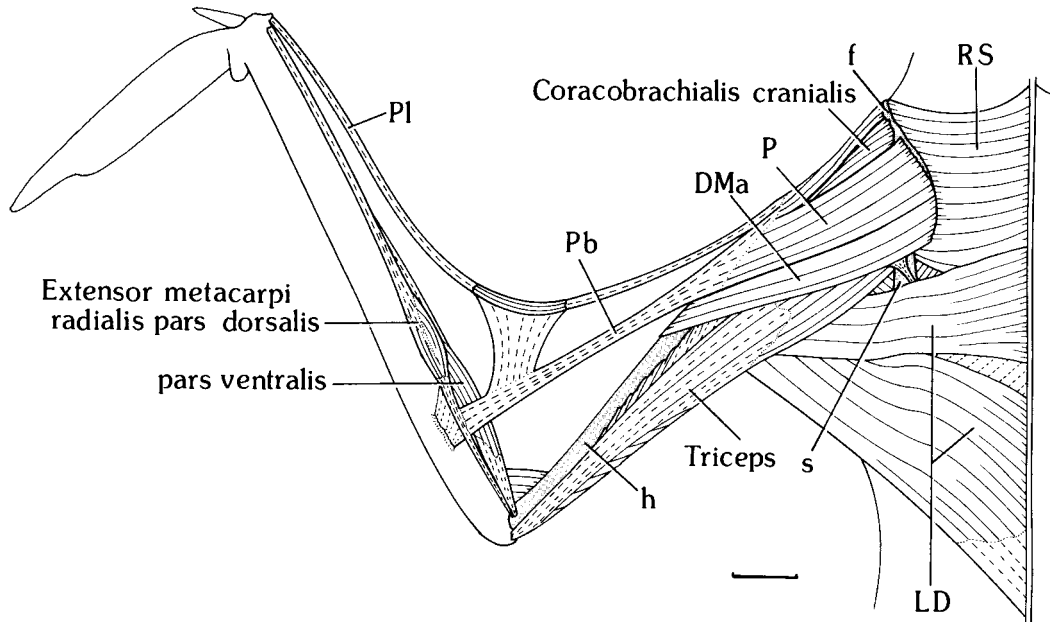
Fig. 3. *Phalacrocorax auritus.* Dorsal view of the left forelimb of the double-crested cormorant. DMa, deltoideus major; f, furcula; h, humerus; LD, latissimus dorsi cranialis and caudalis; P, propatagialis; Pb, propatagialis brevis tendon; Pl, propatagialis longus tendon; RS, rhomboideus superficialis; s, scapula. Scale = 1 cm.

the wrist and elbow joints and protracted at the shoulder. Dissections revealed no locking mechanism, but five muscles positioned to produce this posture in *Phalacrocorax:* M. extensor metacarpi radialis dorsalis and ventralis at the carpal joint, M. triceps scapularis at the elbow joint, and Mm. coracobrachialis cranialis, pectoralis thoracicus (cranial fascicles), and deltoideus minor at the shoulder joint. A description of the gross morphology of these muscles and their histochemical characterization follows. For a complete description of the forelimb myology of *Phalacrocorax auritus,* see Owre ('67). All muscles examined show a moderate to strong intensity for NADH. Avian slow-twitch and slow-tonic fibers do not show a high reactivity for NADH (Torrella et al., '93). In all cases, the anti-slow and anti-fast antibodies corresponded with the histochemical identification for slow (twitch and tonic) and fast fibers, respectively (see Figs. 1 and 2).

M. extensor metacarpi radialis (EMR)

M. extensor metacarpi radialis is made up of two bellies in *Phalacrocorax auritus:* pars ventralis and pars dorsalis. EMR lies on the cranial surface of the antebrachium and

arises from the Processus supracondylaris dorsalis of the humerus. The ventral belly is the more proximal of the two, arises via mixed tendinous and fleshy fibers, and extends for about one-third the length of the ulna. The pars dorsalis has a long, thin tendon of origin, and the belly becomes fleshy at a point distal to the attachment of the aponeurosis of the propatagial sling to EMR (Fig. 3). It is fusiform in shape like the ventral belly, but smaller.

About three-fourths toward the insertion, the two tendons join. The tendon of EMR rides over the cranial aspect of the wrist joint and inserts onto the Proc. extensorius of the carpometacarpus.

EMR functions to extend the wrist and hand, assisting the automatic flexion-extension mechanism of the avian wing skeleton (Fisher, '57; Vazquez, '94). Both bellies contain a mixture of slow-twitch and fast-twitch fibers, although the dorsal belly possesses more slow fibers (29%) compared to the proximal belly (5.8%) (Fig. 4; Table 1).

M. coracobrachialis cranialis (CBC)

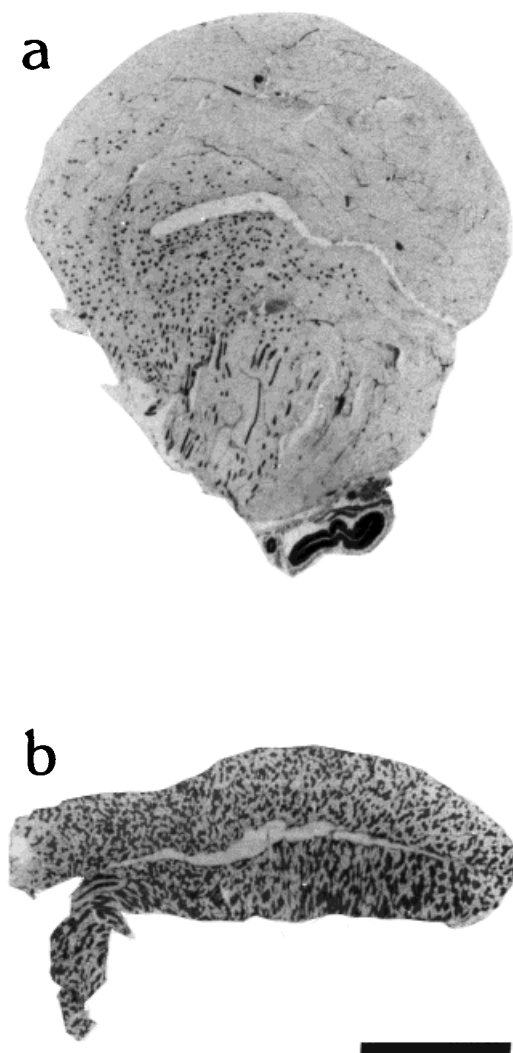M. coracobrachialis cranialis arises from the Processus acrocoracoideus of the cora-

CBC crosses the cranial surface of the shoulder joint, and is in a position to protract the humerus. Histochemistry showed CBC contains an average of 31% slow-twitch fibers (Table 1). The majority of slow fibers are located on the ventro-cranial edge of the muscle (Fig. 6a).

M. triceps scapularis (TS)

M. triceps scapularis is an extensor of the forearm and arises from the scapula via an L-shaped tendon. One leg of the "L" attaches to the connective tissue over the glenoid joint capsule, adjacent to the scapula, whereas the other attaches to the dorsal scapular surface just caudal to the glenoid. About one-fourth of its length distally, the belly of TS is joined by a connective tissue band (the humeral anchor) extending from the humerus. This connective tissue band attaches to the humerus deep to the insertion of M. deltoideus major (see George and Berger, '66, for a discussion).

TS passes within a groove (Sulcus scapulotricipitalis) below the dorsal epicondyle of the humerus and inserts onto the olecranon of the ulna (Fig. 3). There is some blending of fibers between scapular and humeral heads of the triceps.

TS assists in the opening of the wing (extension). By virtue of the linkage between elbow and wrist (Fisher, '57; Vazquez, '94), contraction of the triceps and extension of the elbow also result in wrist extension. Histochemistry revealed TS possesses slow-twitch fibers (459 and 964 fibers in two specimens) along the cranio-ventral aspect of the muscle (Fig. 6b).

M. pectoralis thoracicus (PT)

M. pectoralis thoracicus is the largest muscle of the avian flight apparatus and functions in the propulsive downstroke during flight. It takes its origin from the sternal body, the ventro-lateral edge of the sternal keel, and from the lateral surface of the furcula. Most fascicles of this complex muscle converge onto the Crista deltopectoralis (deltopectoral crest) of the humerus; some deep fascicles insert onto the tendon of origin of the humeral head of the biceps. In *Phalacrocorax auritus,* the furcula is highly bowed cranially, and fascicles of the pectoralis arise from its entire length. Those fibers arising from the dorsal-most aspect of the furcula extend caudally to the humerus and insert roughly perpendicular to the principal insertion on the deltopectoral crest. This band of

Fig. 4. *Phalacrocorax auritus.* Whole muscle sections of 4.2 preincubation ATPase histochemistry showing distribution of fast- and slow-twitch fibers in M. extensor metacarpi radialis pars dorsalis **(a)** and M. extensor metacarpi radialis pars ventralis **(b)**. Cranial is to the left, dorsal to the top. Scale = 200 μm.

coid, lateral to the coracoid-furcular articulation, and adjacent to the Lig. acrocoracohumerale. It is a relatively thick, parallel-fibered muscle, oval in cross section and fleshy throughout. CBC crosses over the dorso-cranial aspect of the shoulder joint and inserts onto the Impressio coracobrachialis on the cranial surface of the humerus, proximal to the insertion of M. pectoralis (Fig. 5).

TABLE 1. Numbers and percentages of slow-twitch fibers in a representative mid-belly cross section from selected muscles in the cormorant, Phalacrocorax auritus

Muscle	Specimen	No. of Fibers		% Slow fibers	Mean slow % ± SE
		Slow	Fast		
M. deltoideus minor[1]	1	4,136	823	83	89 ± 8.5
	2	4,406	208	95	
M. coracobrachialis cranialis	1	2,538	6,515	28	
	2	5,176	11,022	32	31 ± 0.38
	3	6,585	13,551	33	
M. extensor metacarpi radialis					
pars dorsalis	1	918	2,922	24	29 ± 5.3
	2	1,479	2,209	40	
	3	975	3,016	24	
pars ventralis	1	1,024	17,013	5.7	5.8 ± 0.88
	2	312	3,922	7.0	
	3	604	12,178	4.7	

[1]Slow fibers are slow-tonic.

fascicles, lying just ventral to M. coracobrachialis cranialis, is fleshy throughout, and is positioned over the dorsal surface of the shoulder (Fig. 5).

The cranial (dorsal) fascicles of the pectoralis are in a position, if activated separately from the rest of the muscle, to assist protrac-

tion of the humerus. In one individual, the free dorsal edge of this region possesses a small pocket (approximately 100) of slow-twitch fibers within an otherwise completely fast-twitch pectoralis. These are the only slow fibers found in the pectoralis of *Phalacrocorax auritus.*
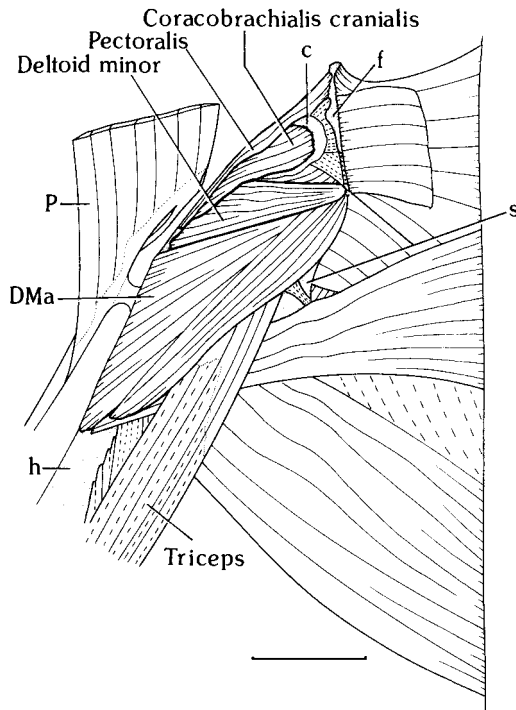

Fig. 5. *Phalacrocorax auritus.* Dorsal view of the left shoulder of the double-crested cormorant. M. propatagialis cut and reflected. c, coracoid. Other abbreviations as in Figure 3. Scale = 1 cm.
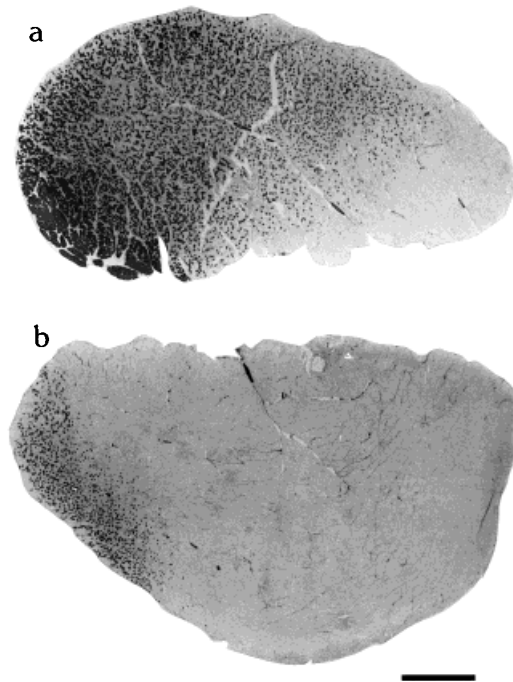

Fig. 6. *Phalacrocorax auritus.* Whole muscle sections of 4.2 preincubation ATPase histochemistry showing distribution of fast- and slow-twitch fibers in M. coracobrachialis cranialis (**a**) and M. triceps scapularis (**b**). Cranial is to the left, dorsal to the top. Scale = 200 μm.

M. deltoideus minor (DMi)

M. deltoideus minor lies on the dorsal aspect of the shoulder joint, cranial to M. deltoideus major. The two muscles together have the appearance of cranial and caudal portions of a single muscle layer. This thin, fleshy muscle lies just caudal to M. coracobrachialis cranialis (Fig. 5). DMi arises from the acromion of the scapula cranially to the origin of M. deltoideus major. It passes directly over the surface of the shoulder joint; however, it lies cranial to the actual point of rotation. DMi inserts onto the dorsal side of the deltopectoral crest of the humerus, proximal to the insertion of the dorsal fascicles of the pectoralis (see above).

Although small and thin, DMi is in a position to protract the humerus. It may also be able to maintain the slight dorsally adducted wing. Histochemically, DMi is almost entirely comprised of slow-tonic fibers (89%) with a smaller proportion of fast-twitch fibers (11%; Table 1) (see Figure 2 for tonic staining profile).

DISCUSSION
Muscles involved in wing spreading

The muscles in a position to produce the spread-wing posture in the cormorant (Mm. coracobrachialis cranialis, pectoralis, deltoideus minor, triceps scapularis, and extensor metacarpi radialis) all show populations of slow-contracting fibers. A real problem is understanding how many muscle fibers are needed or required to perform a particular postural role. For example, although the percentage of slow-twitch fibers in EMRd is five times that of EMRv, it has less than a two-fold increase in fiber *number.* Thus, fiber number, total cross-sectional area, and the weight of the limb are all important—maybe more so than relative percentage.

M. triceps scapularis, which functions to extend the elbow, contains a seemingly small number of slow-twitch fibers (an average of 710 from two individuals) relative to total muscle cross-sectional area (Fig. 6b). Although the percentage makes this muscle look as if it is not well suited to maintain wing extension, these slow fibers may be able to perform this function if: 1) the absolute number of fibers is sufficient for the task, and 2) this muscle only needs to assist, and not produce wing extension. When at rest, if wing-closing muscles are not activated, the weight of the wing may produce an open (semi-extended) position. Thus the triceps may only need to assist this weight-driven extension.

The extensor metacarpi radialis complex can function to maintain the wrist in extension. In birds, a bony linkage causes simultaneous flexion and extension of the elbow and wrist (Fisher, '57; Vazquez, '94).

At the shoulder joint, M. coracobrachialis cranialis has the best biomechanical leverage to protract the wing. Simpson ('79) described this muscle as containing some tonic fibers and being a joint stabilizer in the pigeon, whereas Meyers ('92) found it to be entirely fast-twitch in the kestrel. Its role as a joint stabilizer in the pigeon is unclear since it would function in humeral protraction as well. Fisher ('46) indicated that CBC is well developed in vultures; Stegmann ('64) suggested its importance in gliding and soaring species.

The pectoralis is unusual in the cormorant since it extends onto the dorsal (!) surface of the wing. This dorsal "strip" of fascicles adjacent to the coracobrachialis cranialis (Fig. 5) has a small population of slow-twitch fibers in one individual. Most birds possess a uniformly fast-twitch pectoralis muscle (unless a deep belly is present—see Rosser et al., '94). Rosser and George ('86b) described the "deep distal region" of the pectoralis of *P. auritus* as possessing some slow-tonic fibers, although in their figure these fibers stain like the slow-twitch fibers in my study. I did not find any other slow fibers (twitch or tonic) in the cormorant pectoralis except for those described above.

M. deltoideus minor is largely slow-tonic in the cormorant, as it is in the American kestrel (Meyers, '92). In the kestrel it crosses the shoulder joint caudal to the joint, a position better suited for flexion of the shoulder joint. In the cormorant this small muscle may assist in wing protraction since it passes cranially over the shoulder joint. It may also assist in holding the wing slightly adducted toward the dorsal midline, which is the typical posture for cormorant wing-drying. Like the cranial latissimus dorsi and brachialis muscles, this muscle may be relegated to a completely postural role in birds (Simpson, '79; Meyers, '92; Torrella et al., '93).

To definitively assess if these slow muscle fibers are used in spread-wing posture (or any other, for that matter), selective electrophysiological recordings from these fibers or their motor neurons (see Burke, '81) during this behavior is necessary. Short of this,

however, we can compare these data with those from other studies on avian muscle histochemistry. From previous studies, it seems that the presence of slow fibers in avian muscles is clearly associated with posture. Gliding birds such as vultures and pelicans possess a deep, slow layer to the pectoralis (Pennycuick, '82; Rosser and George, '86a; Rosser et al., '94). In addition, tonic muscles at the shoulder and elbow joints function to maintain the closed wing (Meyers, '92). Unfortunately, a good comparative data base on avian wing muscle histochemistry (pectoralis aside) is lacking. Maier's ('83) study of muscle spindle densities also included a histochemical analysis of many fore- and hindlimb muscles in the pigeon. In the forelimb, the flexor carpi ulnaris and supinator muscles were found to possess 5 and 10 percent slow-twitch fibers, respectively. EMR, in the pigeon, showed no slow fibers (Maier, '83). In addition, the EMR and triceps lack any slow muscle fibers in the mallard, *Anas platyrhynchos* (Torrella et al., '96). Many of the same muscles responsible for cormorant wing spreading show similar percentages of slow fibers in the gull forelimb (Meyers and Mathias, in press.). This also fits the functional hypothesis of a postural role for slow muscle fibers, as the spread cormorant wing and spread gliding wing are in a similar position.

Slow muscle fibers and posture

Slow muscle fibers are better suited to a postural isometric role than fast fibers (Goldspink, '77). Awan and Goldspink ('72) found slow muscles to be three times more efficient than fast for isometric contractions in the hamster. This efficiency appears to be related to the longer actin-myosin interactions during slow muscle contraction and the relatively fewer ATP molecules needed to reprime the cross-bridges per second (Goldspink, '80). It is also possible, however, that the highly aerobic fast fibers may be able to assist in isometric postural contractions.

A discrepancy exists between slow-twitch and slow-tonic fibers within the avian histochemistry literature. For example, slow-twitch fibers react darkly in acidic and faintly in alkaline preincubations (Fig. 1) whereas slow-tonic fibers have a moderate ATPase activity in both acidic and alkaline preincubations (Fig. 2). In Rosser and George's ('86b) histochemical survey of the avian pectoralis, many of their slow fibers stain darkly in acid, yet are labelled as slow-tonic. Studies

on the deep layer of the pectoralis in vultures (Rosser and George, '86a) and pelicans (Rosser et al., '94) describe this muscle as "slow," distinguishing neither twitch nor tonic. In these papers, the slow fibers react darkly in acidic preincubation and thus appear to stain like "slow-twitch" fibers.

Physiologically, the functional properties of avian slow-tonic (Page, '69; Kiessling, '76) and fast-twitch (Welsford et al., '91) fibers are well known. In addition, the ultrastructural differences between the two have also been documented (Torrella et al., '93). Avian slow-twitch fibers are so-named due to a histochemical staining profile similar to that of mammalian slow-twitch fibers. However, unlike slow-twitch fibers in mammals, those in birds are multi-innervated and not highly oxidative (Torrella et al., '93). Electrophysiological studies of avian slow-twitch fibers are needed to determine whether these fibers are functionally more like tonic or twitch fibers. The distribution of slow-twitch and tonic fibers within the wing may represent a distinct functional difference between these fiber types. Tonic fibers may be so specialized for posture that they appear in muscles positioned for long-term postural events such as elbow and shoulder flexion (Meyers, '92) and gliding (Rosser et al., '94). Khan ('79) has suggested "type I white or slow-twitch glycolytic," as alternate names for the slow-twitch fibers in birds, to differentiate them from true slow-twitch oxidative fibers found in mammals.

Differential recruitment of fast and slow muscle fibers

It is well known that a motor unit is uniform with respect to the type of muscle fibers innervated by a motor neuron (Burke and Edgerton, '75). Thus, birds with populations of fast and slow fibers should be able to activate them separately to function in posture or locomotion, as suggested for some mammalian muscles (Hermanson and Hurley, '90; Suzuki, '91; Armstrong et al., '92; Petrie et al., '93). Therefore, muscles may be functionally divided between posture and locomotion.

The pectoralis muscle of birds is usually believed to be uniformly fast, since birds "can't afford the luxury" of several populations of fiber types (Talesara and Goldspink, '78). However, in pigeons (Kaplan and Goslow, '89; Welsford et al., '91) and great skuas (Caldow and Furness, '93), two types of fast fibers within the pectoralis appear to pro-

vide different functional possibilities. In pigeons, the larger fast glycolytic fibers are believed to function during takeoff, whereas the smaller fast oxidative fibers are used during cruising flight (Welsford et al., '91). In the skua, the pectoralis is more oxidative and glycolytic (compared to gulls), suggesting a specialization for the kleptoparasitic behavior of this species (Caldow and Furness, '93). It appears from the present study that avian wing muscles have multiple fiber types for different functional capabilities. Further study of avian wing muscles beyond the pectoralis is needed to assess the variety of fiber types in birds.

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