

Anatomy and Histochemistry of Spread-Wing Posture in Birds. 2. Gliding Flight in the California Gull, *Larus californicus*: A Paradox of Fast Fibers and Posture

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ABSTRACT Gliding flight is a postural activity which requires the wings to be held in a horizontal position to support the weight of the body. Postural behaviors typically utilize isometric contractions in which no change in length takes place. Due to longer actin-myosin interactions, slow contracting muscle fibers represent an economical means for this type of contraction. In specialized soaring birds, such as vultures and pelicans, a deep layer of the pectoralis muscle, composed entirely of slow fibers, is believed to perform this function. Muscles involved in gliding posture were examined in California gulls (*Larus californicus*) and tested for the presence of slow fibers using myosin ATPase histochemistry and antibodies. Surprisingly small numbers of slow fibers were found in the M. extensor metacarpi radialis, M. coracobrachialis cranialis, and M. coracobrachialis caudalis, which function in wrist extension, wing protraction, and body support, respectively. The low number of slow fibers in these muscles and the absence of slow fibers in muscles associated with wing extension and primary body support suggest that gulls do not require slow fibers for their postural behaviors. Gulls also lack the deep belly to the pectoralis found in other gliding birds. Since bird muscle is highly oxidative, we hypothesize that fast muscle fibers may function to maintain wing position during gliding flight in California gulls. *J. Morphol.* 233:237-247, 1997. © 1997 Wiley-Liss, Inc.

The ability to glide provides a unique way for birds to maintain flight while reducing the high energy requirements associated with this specialized type of locomotion (Rosser et al., '94). When compared to other types of flight, such as flapping or hovering, gliding requires the least amount of energy (Goldspink, '81). According to Goldspink ('81), gliding is more efficient in terms of energy expenditure for two reasons. First, gliding requires fewer active motor units. Electromyographic studies of the pectoralis muscle in herring gulls (*Larus argentatus*) (Goldspink et al., '78) and American kestrels (*Falco sparverius*) (Meyers, '93) showed smaller amplitudes during gliding flight than flapping flight, suggesting decreased muscle activity. Second, gliding utilizes isometric contractions, which use less ATP than shortening contractions. In addition, oxygen consumption decreases. Oxygen levels measured during gliding are only two times that during

resting (Baudinette and Schmidt-Nielsen, '74), whereas those during flapping flight are seven times that of resting (Tucker, '72).

Since gliding requires the wings to be maintained in an extended horizontal position, it has been suggested that slow fibers should be present to perform this function (Pennycuik, '72; Meyers, '93; Rosser et al., '94). Slow-contracting fibers are more "economical" at maintaining isometric contractions associated with postural behaviors (such as gliding). This is believed to be due to the longer actin-myosin overlap and the reduced number of ATP molecules needed to reprime the cross bridges per second (Goldspink, '80). Slow fibers in the pectoralis muscle of gliding and soaring birds such as the turkey vulture (*Cathartes aura*) (Rosser and George, '86a) and the American white pelican (*Pelecanus erythrorhynchos*) (Rosser

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et al., '94) are located in a small, deep, accessory belly of the pectoralis. Gulls are also well known for their gliding and soaring abilities (Bent, '47) and have been used as a model for muscle activity (Goldspink et al., '78) and oxygen consumption (Baudinette and Schmidt-Nielsen, '74) during gliding flight. Most species of gulls apparently lack the deep belly of the pectoralis, although Hudson et al. ('69) reported that some did possess it but did not indicate which ones.

There are conflicting reports on the presence of slow fibers in the pectoralis of herring gulls. Talesara and Goldspink ('78) found the pectoralis of the herring gull to contain approximately 6% slow-twitch fibers, though the region of the pectoralis was unspecified. Other studies have also analyzed the pectoralis muscle of herring gulls and found an absence of any slow fibers (Rosser and George, '86b; Caldow and Furness, '93).

The purpose of this study is to examine the muscles associated with maintaining wing position during gliding flight in the California gull (*Larus californicus*). Given the literature on gliding flight in gulls, our goal is to determine if slow fibers are present that may aid in supporting the wings during this type of flight.

MATERIALS AND METHODS

Four California gulls were collected at local landfills using a shotgun (permits were obtained from state and federal governments). One gull was dissected to access anatomical position of the wing in regard to gliding posture. This permitted the determination of the muscles that were sampled for histochemistry. Nomenclature follows Meyers ('93) for muscles and *Nomina Anatomica Avium* (Baumel and Witmer, '93) for bones and their processes. Immediately after death, tissue samples from Mm. coracobrachialis cranialis and caudalis, extensor metacarpi radialis, and triceps brachii were removed mid-belly from three birds and were attached to a piece of cork with 5% gum tragacanth. Multiple samples from the pectoralis were likewise removed and processed. These were taken from the region of the pectoralis analogous to the area where the deep pectoralis layer is located. This area takes origin from the deep, lateral surface of the furcula and adjacent membranes. Samples were also taken from other regions, including the cranial border of the muscle and from those fibers attaching onto the biceps tendon. All tissue was then quick-frozen in isopentane

cooled to about -150°C with liquid nitrogen and stored in an ultracold freezer at -70°C . A cryostat maintained at -20°C was used to cut the tissue into sections 10–12 μm thick. After the tissue was cut, serial sections from each muscle were placed in either acid (pH 4.2) or alkaline (pH 10.4) solutions. The histochemistry protocol of Hikida ('87) was used and produced a visible differentiation between the different fiber types found within the muscle. Alkaline preincubation causes avian fast-twitch fibers to stain darkly and the slow-twitch fibers to stain lightly, whereas acid preincubation causes a light staining of fast-twitch fibers and a darker staining of slow-twitch fibers (Hikida, '87; Meyers, '92; Rosser et al., '94) (see Fig. 1).

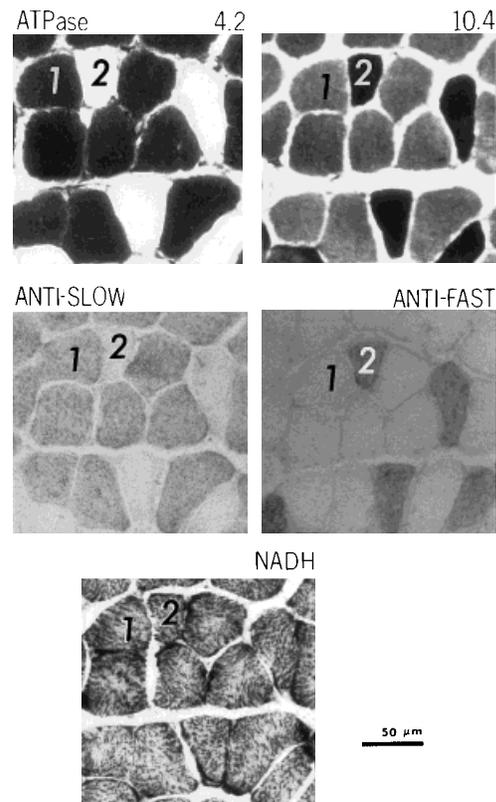


Fig. 1. *Larus californicus*. Serial sections of M. extensor metacarpi radialis using ATPase histochemistry at acidic (pH 4.2) and alkaline (pH 10.4) preincubation, anti-slow and anti-fast antibodies, and NADH. 1, slow-twitch fiber; 2, fast-twitch fiber. The positive (dark) reaction in acidic preincubation corresponds with positive anti-slow antibody reaction, and the positive reaction in alkaline preincubation corresponds with anti-fast antibody reaction product.

Tonic fibers stain an intermediate color in both acid and alkaline preincubations (Meyers, '92). Rock dove (pigeons, *Columba livia*) muscle was also prepared to use as a control for the histochemistry procedure. The fiber types in pigeon Mm. pectoralis, biventer cervicis, and latissimus dorsi pars cranialis are well documented and consist of fast-twitch, mixed fast-twitch/slow-twitch, and slow-tonic muscle fibers, respectively (Hikida, '87; Meyers, '92). Each sample was also tested for nicotinamide adenine dinucleotide diaphorase (NADH-D) activity, which determines the oxidative capacity of the individual fibers within the sampled muscles (Novikoff et al., '61).

Antibodies to fast and slow myosin were used to confirm histochemical data. The procedure followed that of Hermanson and Cobb ('92). The antifast antibody, MY32 (Sigma Chemical Co., St. Louis, MO), labels fast-twitch fibers in both mammals and birds, whereas the antislowl antibody, ALD58 (University of Iowa Hybridoma Bank) labels slow-twitch fibers in mammals and both slow-twitch and tonic fibers in birds. Samples were incubated against the antibodies in a humidified chamber at 4°C for 16 h. After being rinsed in phosphate-buffered saline, the samples were then incubated in a goat anti-mouse antibody to recognize the primary antibody and then stained with a streptavidin peroxidase system (Zymed Labs, San Francisco, CA).

Black-and-white photographs of muscle samples were taken using an Olympus BH-2 photomicroscope ($\times 40$ magnification). Overlapping photographs of the various areas within the muscle were taken and the prints taped together, forming an enlarged picture of the muscle. The number of fast and slow

fibers within a mid-belly cross-section from Mm. coracobrachialis cranialis and extensor metacarpi radialis was counted. The number of slow fibers only from a mid-belly cross-section from Mm. coracobrachialis caudalis and triceps brachii was counted. The mean number and standard error of the mean of slow fibers were calculated. Fiber percentages were also calculated for three muscles from three specimens and the mean determined (Table 1).

RESULTS

Gliding requires the wings to be extended and held in a horizontal position. This requires protraction of the wings at the shoulder, support of the body to keep it from falling through the wings, and extension of the wing at the elbow and wrist. Dissection revealed that five major muscles should play a role in wing posture during gliding: Mm. coracobrachialis cranialis in wing protraction, coracobrachialis caudalis and pectoralis in body support, extensor metacarpi radialis in wrist extension, and triceps brachii in elbow extension. Electromyographic data from kestrels (Meyers, '93) show low amplitude signals from the triceps and deep and cranial pectoralis regions. A description of the gross morphology and histochemical data for each muscle follows.

All muscles sampled possess fast-twitch and slow-twitch fibers only. No slow-tonic fibers were identified. This determination gains confidence by comparison to control data from pigeons. In the present study, the three fiber types described by Hikida ('87) were clearly distinguished in control tissue; muscles from the gull, however, lacked fibers with intermediate staining following

TABLE 1. Total fiber numbers, mean number of slow fibers, and relative slow fiber percentages, for four muscles in the California gull, *Larus californicus*

Muscle	Gull	Number of fibers		Mean number of slow fibers \pm SE	% slow fibers	Mean % of slow fibers \pm SE
		Slow	Fast			
M. coracobrachialis cranialis	1	1,059	11,030	960 \pm 265	8.7	8.1 \pm 1.6
	2	660	13,680		4.6	
	3	1,163	9,484		10.9	
M. coracobrachialis caudalis	1	1,294	—	1,239 \pm 115		
	2	1,107	—			
	3	1,318	—			
M. extensor metacarpi radialis, pars dorsalis	1	929	2,595	1,181 \pm 365	26.4	28.7 \pm 3.0
	2	1,433	3,180		24.8	
	3	933	1,761		34.6	
M. extensor metacarpi radialis, pars ventralis	1	668	10,346	773 \pm 95	6.1	5.8 \pm 0.38
	2	800	15,088		5.0	
	3	852	12,916		6.2	

both alkaline and acid preincubation (slow-tonic). Additional muscles of the shoulder, *Mm. biceps brachii* and *supracoracoideus*, were uniformly fast-twitch in fiber composition.

All samples stained moderately to intensely for oxidative capacity. Slow fibers stained moderately for oxidative capacity, whereas fast fibers stained moderately to intensely. This oxidative staining was found in all muscles sampled. In all muscle samples examined, anti-slow and anti-fast antibodies corresponded with the histochemical identification for slow and fast fibers, respectively.

M. coracobrachialis cranialis

The *M. coracobrachialis cranialis* (CBCr) originates on the processus acrocoracoideus of the coracoid, lateral to the coraco-furcular articulation (synd. acrocoraco-clavicularis). The muscle crosses over the dorso-cranial aspect of the shoulder joint, crossing in front of the coraco-humeral joint, and inserts on the impressio coracobrachialis of the cranial surface of the humerus, proximal to the insertion of *M. pectoralis* (Fig. 2).

The CBCr functions to protract the humerus, which is necessary to keep the wing in proper gliding position. All gulls sampled contain a mixture of fibers with an average of 960 slow-twitch fibers (8.1%) (Table 1). The majority of the slow-twitch fibers are concentrated in the caudo-ventral region of the muscle (Fig. 3).

M. coracobrachialis caudalis

The *M. coracobrachialis caudalis* (CBCa) originates from the lateral surface of the linea intermuscularis ventralis of the coracoid and adjacent membranes, lateral to the origin of *M. supracoracoideus*. The muscle crosses dorsally and inserts via a tendon onto the tuberculum ventrale of the ventral surface of the proximal humerus (Fig. 2).

The CBCa functions to depress (and possibly supinate) the humerus. All gulls sampled show a mixed population of slow-twitch/fast-twitch fibers, with an average of 1,239 slow-twitch fibers (Table 1) within the belly lateral to the internal tendon. The portion of the muscle medial to the tendon possesses uniformly fast-twitch fibers (Fig. 3).

M. pectoralis thoracicus

The *M. pectoralis thoracicus* (PT) is the largest muscle found in birds. This muscle originates from the sternal body, the ventro-lateral edge of the sternal keel, and the lateral surface of the furcula. The majority of its fascicles insert onto the crista deltopectoralis of the humerus. Some deep fascicles insert onto the tendon of origin of the humeral head of the biceps, forming the "partly-divided" pectoralis morphology of Meyers ('93).

During flapping flight the pectoralis produces the downstroke motion of the wing, but in gliding this muscle is in a position to

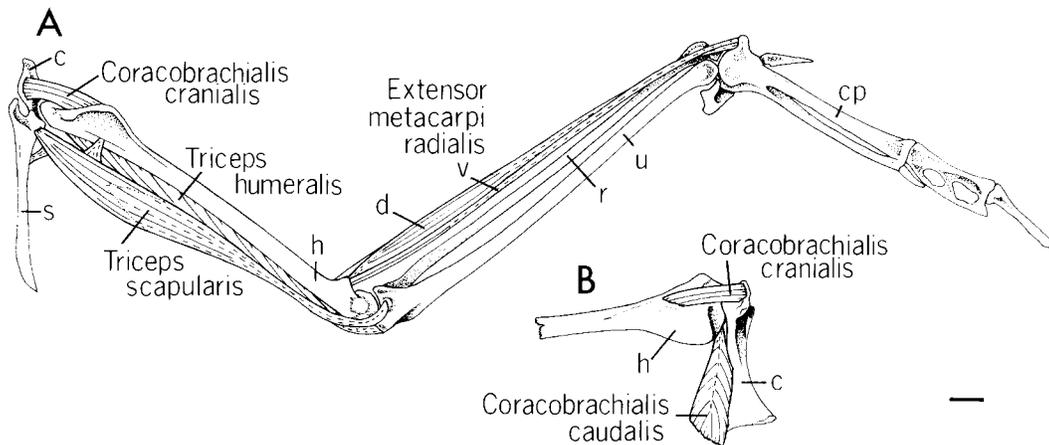


Fig. 2. *Larus californicus*. Illustration of the right wing skeleton of the California gull identifying gliding muscles discussed in this paper. **A:** Dorsal view of entire wing. **B:** Cranial view of coracoid and humerus. c, coracoid; cp, carpometacarpus; d, extensor metacarpi radialis dorsalis; h, humerus; r, radius; s, scapula; u, ulna; v, extensor metacarpi radialis ventralis. Scale bar = 1 cm.

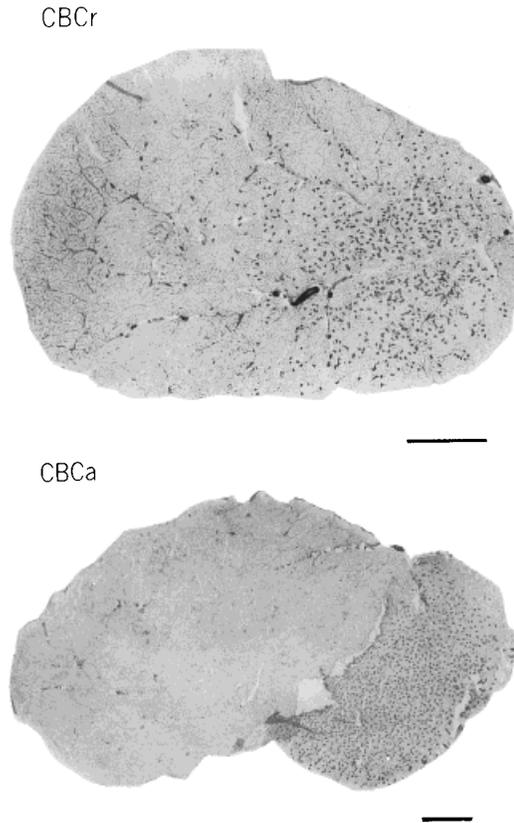


Fig. 3. *Larus californicus*. Whole muscle sections of pH 4.2 preincubation ATPase histochemistry showing distribution of fast- and slow-twitch fibers of *M. coracobrachialis cranialis* (CBCr) and *M. coracobrachialis caudalis* (CBCa). Slow-twitch fibers stain darkly. Cranial is to the top and dorsal to the left (CBCr), and dorsal is to the top and medial to the left (CBCa). Scale bars = 1 mm.

act as a strut to support the body between the wings. Dissection reveals that *Larus californicus* lacks the deep layer to the pectoralis found in specialized gliding birds (see Table 2). A maximum of about 20 slow-twitch fibers was found only in the area analogous to the deep layer in only one gull sampled (Fig. 4, top).

M. triceps brachii

The *M. triceps brachii* (TB) consists of two parts in birds: triceps scapularis and triceps humeralis. Both lie along the caudal border of the humerus. Triceps scapularis arises by a short tendon from the scapula adjacent (caudal) to the glenoid fossa. It inserts onto the processus cotylaris dorsalis of the ulna, lateral to the olecranon and insertion of *M.*

triceps humeralis. The triceps humeralis originates from the proximal two-thirds of the caudal border of the humerus. It inserts via a mixed fleshy and tendinous insertion onto the olecranon of the ulna, cranial to the insertion of *M. triceps scapularis* (Fig. 2).

Both triceps humeralis and triceps scapularis function to extend the wing at the elbow. Histochemistry shows that these muscles are almost entirely fast-twitch yet possess a small number of slow-twitch fibers (fewer than 40) in only two of the three gulls sampled (Fig. 4, bottom). The slow fibers are restricted to the caudo-ventral edge of the midbelly of these muscles.

M. extensor metacarpi radialis

The *M. extensor metacarpi radialis* (EMR) is comprised of two bellies in *Larus californicus*: pars ventralis and pars dorsalis. This muscle lies on the cranial surface of the antebrachium and arises from the processus supracondylaris dorsalis and adjacent surface of the humerus. The dorsal belly lies more distal than the ventral belly and originates from a short, thin tendon of origin from the processus only and becomes fleshy at a point distal to the attachment of the aponeurosis of the propatagial sling to the EMR. The ventral belly originates via mixed tendinous and fleshy fibers from the underside of the processus and a small adjacent area on the humeral shaft. The bellies of EMR extend for approximately one-third the length of the ulna. Tendons from each belly run along the radius, pass over the cranial aspect of the wrist, and insert together onto the processus extensorius of the carpometacarpus. The tendon from the ventral belly begins caudal to that of the dorsal belly. Midway along the shaft of the radius, the two tendons switch orientation, and the ventral tendon lays on top of the dorsal tendon as they pass over the cranial aspect of the wrist (Fig. 2).

The EMR functions to extend the wrist and hand as part of the automatic extension-flexion mechanism of the avian wing (Fisher, '57; Vazquez, '94). This muscle is in a position to maintain wrist extension during gliding flight. Histochemistry shows that both bellies contain slow-twitch fiber populations. The dorsal belly contains an average of 1,181 slow-twitch fibers (28.6%) that are evenly distributed throughout the muscle (Fig. 5, top; Table 1). The ventral belly contains an average of 773 slow-twitch fibers (5.8%) which are concentrated in the dorso-

TABLE 2. Taxonomic distribution of the divided pectoralis in birds (Taxonomy from Sibley and Monroe, '90)

Taxon, Common name	Scientific name	Reference(s)
Order Ciconiiformes		
Family Procellariidae		
Laysan albatross	<i>Diomedea immutabilis</i>	Kuroda, '60a
Black-footed albatross	<i>D. nigripes</i>	Kuroda, '60a
Albatross	<i>Diomedea</i> sp.	Pennyquick, '82
White-chinned petrel	<i>Procellaria aequinoctialis</i>	Pennyquick, '82
Dove prion	<i>Pachyptila desolata</i>	Pennyquick, '82
Giant petrel	<i>Macronectes</i> sp.	Pennyquick, '82
Gadfly petrel	<i>Pterodroma hypoleuca</i>	Kuroda, '60b
Gadfly petrels	<i>Pterodroma solandri, P. inexpectata</i>	Kuroda, '60a
Shearwaters	<i>Puffinus bulleri, P. tenuirostris, P. nativitatis</i>	Kuroda, '60a
Northern fulmar	<i>Fulmaris glacialis</i>	Kuroda, '60a
"Tubinares"	—	Gadow and Selenka, 1891 (species unspecified)
Harcourt's storm petrel	<i>Oceanodroma castro</i>	Kuroda, '60a
Phaethontidae		
Tropicbird	<i>Phaeton</i> sp.	Gadow and Selenka, 1891
Sulidae		
Blue-footed booby	<i>Sula neboxii</i>	Kuroda, '61b
Booby	<i>Sula</i> sp.	Gadow and Selenka, 1891
Fregatidae		
Magnificent frigatebird	<i>Fregata magnificens</i>	Kuroda, '61b (three-layered)
Pelecanidae		
American white pelican	<i>Pelecanus erythrorhynchos</i>	Kuroda, '61b
Pelican	<i>Pelecanus</i> sp.	Gadow and Selenka, 1891
Phoenicopteridae		
Flamingo	<i>Phoenicopterus</i> sp.	Beddard, 1898
Anhingidae		
Anhinga	<i>Anhinga anhinga</i>	Owre, '67
Phalacrocoracidae		
Flightless cormorant	<i>Compsohalieu harrisi</i>	Kuroda, '61b ("not divided," Livezey, '92)
Cormorant	<i>Phalacrocorax</i> sp.	Gadow and Selenka, 1891 ("indistinct")
Ciconiidae		
Marabou Stork	<i>Leptoptilos crumeniferus</i>	Vanden Berge, '70
"Storks"	—	Beddard, 1898 ("partial")
New World vultures	<i>Cathartes aura, Coragyps atratus, Gymnogyps californicus, Vultur gryphus, Sarcoramphus papa</i>	Gadow and Selenka, 1891 (species unspecified) Fisher, '46
Accipitridae		
Grey-faced buzzard	<i>Butastur indicus</i>	Kuroda, '60a
Old World vultures	—	Pennyquick, '82
Laridae		
Various gulls	—	Hudson et al., '69 (species unspecified)
Order Gruiformes		
Family Gruidae		
Crowned crane	<i>Balearica pavonina</i>	Beddard, 1898
Wattled crane	<i>Grus (Bugeranus) carunculatus</i>	Beddard, 1898
Whooping crane	<i>Grus americana</i>	Fisher and Goodman, '55 (division absent in <i>G. canadensis</i> , sandhill crane [Berger, '56])

cranial region of the muscle (Fig. 5, bottom; Table 1).

DISCUSSION

Although it has been hypothesized that muscles involved in postural activities (such as gliding) should contain slow-contracting fibers (Pennyquick, '72; Meyers, '93), we were surprised by the low number of slow-twitch fibers found in gull muscles sampled in this study. The lack of slow fibers in the pectora-

lis and triceps was unexpected. These muscles appear to play an important role in wing position during gliding (Meyers, '93) but contained only scattered individual slow fibers. It seems unlikely that these scattered fibers alone can produce the isometric contraction necessary to maintain gliding posture.

Muscles involved in gliding posture

The CBCr is in a position to protract the wing and should be involved in moving the

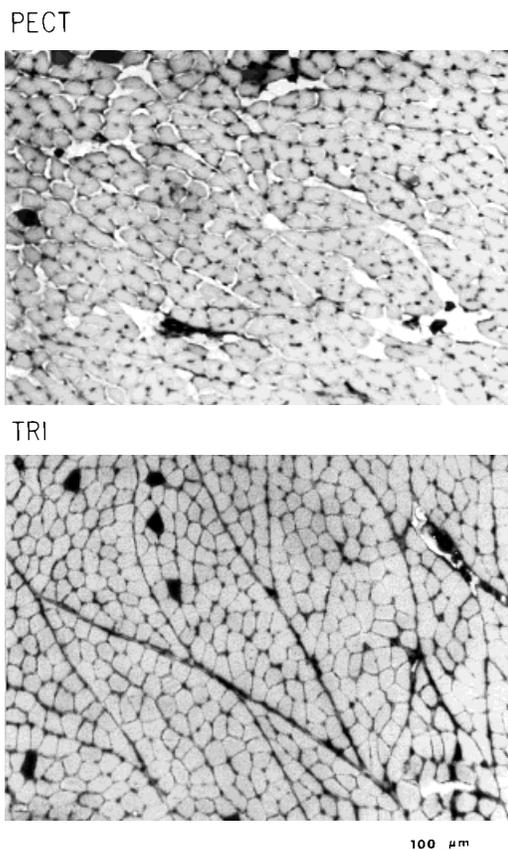


Fig. 4. *Larus californicus*. Sections of pH 4.2 preincubation ATPase histochemistry showing the small number of slow-twitch fibers in M. pectoralis (PECT) and M. triceps brachii (TRI). Slow-twitch fibers stain darkly.

wing into gliding position. Histochemical studies of the CBCr in the pigeon (Simpson, '79) found the presence of tonic fibers, but the kestrel CBCr lacked any tonic or slow-twitch fibers (Meyers, '92). The CBCr in condors is large and is believed to be an adaptation for soaring (Fisher, '46), although its histochemical profile is unknown. In *Larus californicus* this muscle contained an average of 960 slow fibers (8.1%).

The spread wing is the result of extension at the wrist and elbow. The EMR extends the wing at the wrist, whereas the triceps extends the wing at the elbow. Contraction of the triceps extends the wing via the automatic flexion-extension mechanism (Fisher, '57; Vazquez, '94). Both the triceps humeralis and triceps scapularis are comprised almost exclusively of fast-twitch fibers. The

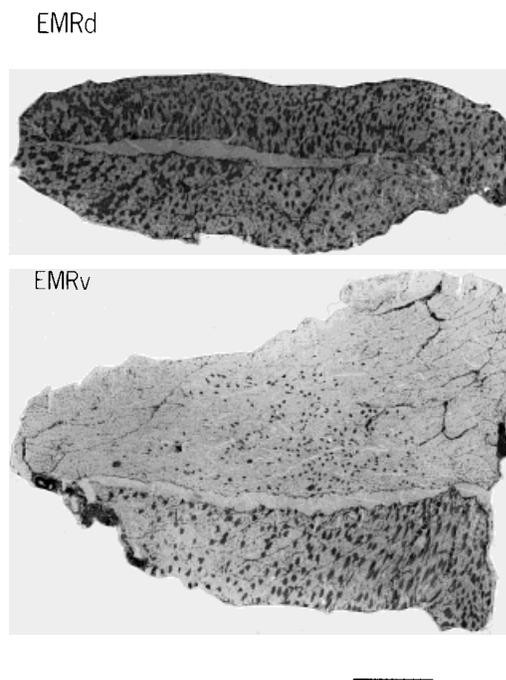


Fig. 5. *Larus californicus*. Whole muscle sections of pH 4.2 preincubation ATPase histochemistry showing distribution of fast- and slow-twitch fibers of M. extensor metacarpi radialis pars dorsalis (EMRd) and M. extensor metacarpi radialis pars ventralis (EMRv). Slow-twitch fibers stain darkly. Cranial is to the right and dorsal to the bottom. Muscles fibers in the dorsal part of EMRv appear larger due to oblique sectioning. Scale bar = 1 mm.

few slow-twitch fibers found in two individuals may not be sufficient to maintain wing extension during gliding flight.

In the gull, the EMR is divided into two bellies. The dorsal belly contains the highest slow-twitch fiber population, with its fibers distributed throughout the entire muscle. The ventral belly contains a smaller population of slow-twitch fibers concentrated in the dorso-cranial region of the muscle. The number of slow-twitch fibers found in the EMR may be sufficient to maintain wrist extension during gliding flight. Similar percentages were found in this muscle in the double-crested cormorant where they were hypothesized to function in spread-wing posture in that species (Meyers, '97). Studies conducted by Maier ('83) and Rosser and George ('85) examined forearm muscles in rock doves using a histochemical analysis, but both of these studies focused on muscle spindles rather than fiber type analysis. Ma-

ier ('83) found relatively low percentages of slow fibers in the forelimb, with the flexor carpi ulnaris and supinator muscles possessing 5% and 10% slow-twitch fibers, respectively, and EMR showing no slow fibers. Torrella et al. ('96) found EMR and triceps to possess no slow fibers in the mallard (*Anas platyrhynchos*).

The automatic flexion-extension mechanism of the avian wing can also help maintain wrist extension (Fisher, '57; Vazquez, '94). Nair ('54) suggested that the division of EMR is characteristic of gliding species and prevents the muscle from fatiguing by alternative belly recruitment. Thus, one belly can maintain contraction while the other belly is in a relaxed state, allowing the relaxed belly to recover (Nair, '54). To date, there is no experimental evidence that this occurs.

The pectoralis is ideally located to support the body between the wings during gliding. Electromyographic studies of the herring gull (Goldspink et al., '78), American kestrel (Meyers, '93) and budgerigars (*Melopsittacus undulatus*) (Tobalske and Dial, '94) found this muscle to be active while the birds were gliding. We examined several regions of the pectoralis and found few slow-twitch fibers only in a deep area of this muscle. The total number of fibers in this region was very small (either absent or <40 fibers), and it is unlikely that these fibers alone could function to support the body during gliding flight. However, since the pectoralis in birds is very large, it is difficult to sample the entire muscle. Additional slow fibers may have been missed during sampling. Studies conducted on herring gulls have produced conflicting results with regard to slow-twitch fibers in the pectoralis. Talesara and Goldspink ('78) found the pectoralis to contain approximately 6% slow-twitch fibers. They sampled one gull and did not specify the area where the fibers were found. Rosser and George ('86b) examined three different areas of the pectoralis in two herring gulls. Samples were taken from the most superficial fibers of the proximal one-half of the muscle, from the deepest fibers of the proximal one-half of the muscle (deep to the previous sample), and from the deepest fibers of the distal one-third of the muscle. They found these areas to be uniformly fast with no slow fibers. Similar results were described by Caldow and Furness ('93), who also sampled three regions of the pectoralis but in only one herring gull. Their samples were taken near

the cranial edge of the muscle; one sample was superficial, and the other two were from successively deeper regions. They did not find any slow fibers in the areas sampled; this may be the result of individual variation, a difference in histochemical technique, or a sampling error associated with regional sampling of this large muscle.

The *M. coracobrachialis caudalis* is also in a position to assist the pectoralis in wing depression (see also Raikow, '85). Since this muscle contains a population of slow-twitch fibers, it is possible that it may assist the pectoralis in support of the body. In comparison, pigeons possess a similar histochemical profile (personal observations), which may function in their V-shaped gliding wing position. The role of this muscle during a variety of flight modes needs to be assessed by future *in vivo* studies.

An obvious question arises concerning the number of slow fibers and the relative percentage of them within a muscle. Perhaps absolute fiber number and resulting cross-sectional area are more important than the relative percentage. According to Tötösy de Zepetnek et al. ('92), the number of muscle fibers per motoneuron is an important determination of motor unit force. In the gull extensor metacarpi radialis (EMR), the percentage of slow fibers in pars dorsalis is five times that of pars ventralis yet only has about 1.5 times the number of fibers. Similar data exist for the EMR in the cormorant as well (Meyers, '97). Studies examining the enduring properties of avian slow fibers as well as the force production of these small numbers of slow fibers are warranted.

Divided pectoralis

The divided pectoralis is a specialization found in gliding and soaring species in which the muscle is divided into superficial and deep parts (Kuroda, '61a; Pennycuik, '72, '82). It has been suggested that the deep layer should be composed of slow tonic fibers to aid in soaring (Pennycuik, '72). Studies of the pectoralis in the turkey vulture (Rosser and George, '86a) and the white pelican (Rosser et al., '94) found the deep layer to be comprised entirely of slow fibers, while the superficial layer consisted completely of fast-twitch fibers. The deep layer has also been described in a number of species (see Table 2), all of which are members of the avian orders Ciconiiformes or Gruiformes (Sibley and Monroe, '90). Previous work on pelicans (Rosser et al., '94) and vultures (Rosser and

George, '86a) are the only studies that examined the histochemistry of the deep layer in gliding species. The slow fibers found in our gull are located in a region analogous to the deep layer found in other gliding species. Although Meyers ('93) observed electromyographic activity from this region in gliding American kestrels, there have been no electromyographic studies performed on species with the divided pectoralis.

The majority of birds with the deep layer are larger birds like the albatross, pelican, and vulture. A larger bird might require more muscle fibers devoted to posture and hence a distinct muscle relegated to a completely postural role. *Larus californicus* is a smaller bird; this may account for the absence of the deep pectoralis layer. We therefore examined the pectoralis morphology of a large gull, the great black-backed gull (*Larus marinus*), which weighs an average of 1,829 g (three times the average weight of *L. californicus*) and is in the same weight class as turkey vultures and frigatebirds (Dunning, '93). The great black-backed gull has a similar pectoralis morphology to *L. californicus* and also lacks the deep pectoralis layer. This suggests that the evolution of a deep layer of the pectoralis does not correspond with large body size in all flying birds.

Interestingly, in addition to gulls, hawks and eagles also seem to lack the deep layer. A thorough systematic study of these two avian groups is needed to determine which (if any) gliding members of these families possess the divided pectoralis morphology.

Fast fibers and isometric contraction

Since gulls lack large populations of slow fibers in muscles usually associated with gliding (such as the pectoralis), we suggest that there is another mechanism used by *Larus californicus* to maintain wing position while gliding. We found two different types of fast fibers in the muscles sampled. One fiber type stained moderately for NADH activity, while the other stained intensely. Many bird muscles are highly oxidative (Talesara and Goldspink, '78; Rosser and George, '86b). Because of the rate at which energy is replenished during contraction of fast fibers, their high aerobic capacity (see Kaplan and Goslow, '89) may therefore permit them to function in posture. Welsford et al. ('91) describe aerobic fast fibers in pigeons which can maintain tension with high resistance to fatigue. Awan and Goldspink ('72) found that the "fast" biceps muscle of

the Syrian hamster could replenish its energy supply during contraction faster than the "slow" soleus muscle. They also found that most of the energy used during isometric contraction is used during the development of tension. Far less energy is needed for the maintenance of isometric contraction. Thus, a muscle with a small percentage of slow fibers (apparently too small to maintain wing position) may be able to function isometrically due to the high oxidative capacity of the fast fibers. Reiser et al. ('96) have shown that fibers that appear uniform histochemically can have up to a twofold difference in contraction speeds; this is related to heterogeneity of the individual fibers at the protein level. Thus, fast fibers show a range of contraction speeds, some of which may be slow enough to be of postural use. Since gulls possess a slow wingbeat, the speed of shortening of these fibers is relatively slow; it has been suggested that they may be inherently better for posture (Goldspink, personal communication).

CONCLUSIONS

The muscles sampled in this study were expected to contain a high proportion of slow fibers to reduce energetic costs associated with gliding. It is possible that small populations of slow fibers can maintain isometric contraction when gliding, but the lack of these fibers in some muscles suggests that 1) fast fibers are involved in maintaining wing position and 2) gulls have other flight requirements making populations of slow fibers inefficient. Physiological studies of these muscles are needed to determine if fast fibers are being used to maintain wing position and how enduring these fibers are at isometric contractions. This study also raises the question of how much gliding is required to cause a change in muscle morphology such as a divided pectoralis and slow fiber populations. Perhaps the highly maneuvering flight style of gulls or their requirement of continuous minor adjustments to their wings during gliding make large populations of slow fibers disadvantageous for gliding flight.

ACKNOWLEDGMENTS

We thank Brad Chadwell and Brett Clarke for the many hours spent working in lab and Shawn Murray, who assisted in collecting specimens. Thanks go also to Drs. Sue Fairbanks, John Hermanson, Carl Marti, and

two anonymous reviewers for reading a draft of the manuscript. Gulls were collected with the cooperation of the Davis County and Bountiful City landfills. The great black-backed gull specimen was provided by the American Museum of Natural History. Anti-slow antibodies were obtained from the Developmental Studies Hybridoma Bank maintained by the Department of Pharmacology and Molecular Sciences, Johns Hopkins School of Medicine, and the Department of Biology, University of Iowa, under contract NO1-HD-2-3144 from the NICHD. Thanks to Brett Clarke for his photographic and proofreading skills. Funding for this study was provided through a Weber State University research scholarship and professional growth grant to Ron Meyers and a vitality grant for undergraduate research provided through Carl Marti and the Weber State University Zoology Department.

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