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Anatomy and histochemistry of spread-wing posture in birds. 4. Eagles soar with fast, not slow muscle fibres

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Abstract

Slow fibers are typically characterized as functioning in avian postural behaviors such as soaring flight, and are described for a number of elite soarers such as vultures, pelicans and albatrosses. Golden Eagles and Bald Eagles also display soaring behavior and we examined their flight muscles for the presence of slow fibers. Surprisingly, eagles lack a deep layer to the pectoralis found in other soaring species. Additionally, the pectoralis as well as other shoulder muscles had few to no slow muscle fibers. The lack of functionally meaningful numbers of slow muscle fibers in eagle flight muscles indicates that they must rely on fast fibers for posture; these can function in that role due to their high aerobic capacity and also perhaps a “tuning” of muscle contraction frequency to function more efficiently at isometric contractions.

Introduction

Gliding and soaring flight are considered modes of energy-saving flight in comparison to flapping flight (Tucker 1972; Baudinette and Schmidt-Nielsen 1974; Goldspink 1977), and have been shown to require reduced muscle activity in Herring Gulls (Goldspink *et al.* 1978) and American Kestrels (Meyers 1993). These observations are derived from the idea that fewer muscle fibers are active during soaring and gliding, and also because during isometric contractions, the actin-myosin crossbridges are not dis-engaging and so ATP requirements are reduced (Goldspink 1977, 1981).

Slow muscle fibers are believed to be more efficient at isometric contractions utilized during posture (Goldspink 1977, 1981) and also during isometric contractions to maintain muscle length allowing tendons to store elastic energy (see Patak and Baldwin 1993). Thus, they are typically associated with muscles utilized in postural roles. Slow contracting muscle fibers have been well studied with regard to posture in birds, and a correlation between muscle function and fiber types has been well-documented (Rosser and George 1986a; Rosser *et al.* 1994; see also Meyers and Stakebake 2005 for review).

It is well known that soaring birds such as vultures, pelicans, and albatrosses (see Rosser and George 1986a; Rosser *et al.* 1994; Meyers and Stakebake 2005, and references therein) possess a deep layer to the pectoralis, uniformly comprised of slow muscle fibers, that has been associated with a function in soaring flight. Other birds, including cormorants, storks,

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and cranes also possess the deep layer (see Table 2 in Meyers and Mathias 1997), although soaring gulls (e.g., *Larus californicus* and *L. marinus*) do not have this specialized morphology (Meyers and Mathias 1997). Although the pectoralis is the most-often studied of the avian flight muscles, other forelimb muscles have also been examined and interpreted as playing a role in gliding and soaring flight. During these flight behaviors, the wing is held in a protracted and extended position, and is maintained stable with respect to the body (Meyers 1993; Meyers and Mathias 1996; Meyers and Stakebake 2005). Meyers (1993) recorded electromyographic activity from a number of muscles performing these actions in gliding kestrels, and Meyers and Stakebake (2005) suggested that a “suite” of slow-contracting muscle fibers in these muscles is used during soaring flight in albatrosses. As eagles are well-known for their soaring ability (Buehler 2000; Kochert *et al.* 2002), we sought to survey their flight muscles to determine if they possessed a significant (functional) population of slow fibers that they might use in soaring flight.

Materials and methods

Tissue samples were taken from one adult Bald Eagle (*Haliaeetus leucocephalus*) and four adult Golden Eagles (*Aquila chrysaetos*) that had been killed by vehicles and subsequently stored frozen by the Utah Division of Wildlife. A single Swainson's Hawk (*Buteo swainsoni*) obtained from the same source was also used for comparison. Frozen birds were made available to us for tissue removal, and the Eagles were immediately returned to the Utah Division of Wildlife. Previously-frozen birds are routinely used for immunohistochemistry, with normal results (e.g., Meyers and Stakebake 2005; Schroeder *et al.* 2014).

Based on our previous work, we selected muscles that should be active during soaring flight; muscles that keep the wing stable with respect to the body, protracted and extended (Meyers 1993; Meyers and Mathias 1996; Meyers and Stakebake 2005). These muscles included a deep area of M. pectoralis fascicles originating from the furcula and adjacent sterno-coracoclavicular membrane, and a deep region adjacent to the insertion of M. biceps brachii; these regions are analogous in location to the deep pectoralis layer of vultures and are positioned for body support/wing stabilization. In addition, Mm. supracoracoideus and deltoideus major are also likely to act in wing stabilization (Meyers 1993). M. coracobrachialis cranialis and cranial fascicles of M. pectoralis were examined for their role in wing protraction, and M. triceps scapularis for wing extension. As an internal control, a superficial region of the pectoralis (not considered active during soaring) was also examined. Cube-shaped muscle samples between 1 and 2 cm per side were removed from larger muscles; from smaller muscles, mid-belly sections of the entire muscle were taken. Muscles samples were mounted perpendicularly to fascicle orientation on a cork block using 5% gum tragacanth, then flash frozen in isopentane cooled in liquid nitrogen to approximately -150°C. Samples were stored at -70°C until sections (10-12 µm thick) were cut on a cryostat at -20°C and transferred to glass microscope slides.

To allow fiber type differentiation, serial sections were reacted with ALD58 (University of Iowa Hybridoma Bank), an antibody binding to slow myosin heavy chains. Reactions were also carried out with MY32 (Sigma Chemical Co., St. Louis, MO) to identify fast twitch fibers. Samples were incubated against the antibodies in a humidified chamber at room

temperature for 2 hours, or at 4° C for 18 hours. After rinsing in phosphate-buffered saline, samples were incubated in a goat anti-mouse antibody to recognize the primary antibody, and stained with a streptavidin peroxidase system (Zymed Labs, San Francisco, CA). Figure 1 shows the typical reactions observed with both fast and slow antibodies.

Slides were viewed under a Zeiss Axioskop 40/40 FL microscope and images of each muscle with a corresponding scale bar were obtained using a Nikon Coolpix 995 digital camera. Although both reactions were used to determine fiber identities, slow fibers were photographed and quantified using the ALD58 reaction, since this offered the best contrast. Cross sectional areas of select muscles were determined using CanvasX (ACD Systems, Miami, FL).

Results

Despite the large size of these birds, the flight musculature in general and the specific muscles studied can be described as “typical” for raptors (see Orosz *et al.* 1992; Corvidae *et al.* 2006). Brief descriptions of each muscle follow, along with the corresponding fiber type data. Anatomical nomenclature is from Baumel *et al.* (1993).

M. pectoralis is the principal flight muscle in volant birds. It arises from the sternal body, sternal carina, furcula, and sterno-coraco-clavicular membrane and inserts onto the pectoral crest of the humerus. The superficial region of the pectoralis arising from the furcula was entirely fast in all individuals examined (Figures 1 and 2A).

Deep fascicles arising from the sterno-coraco-clavicular membrane have a secondary attachment to the tendon of origin of M. biceps brachii, a not-uncommon occurrence in birds (Beddard 1898; Meyers 1993 and references therein). Neither Eagle species possessed the deep layer as seen in vultures and albatrosses, although the Golden Eagle pectoralis could be described as “partly-divided” (*sensu* Meyers 1993) and the Bald Eagle as undivided. Although not a distinct muscle, we examined tissue from the origin of the corresponding region, and found that it possessed fewer than 100 slow fibers in only one Golden Eagle (Figure 2B); none of the other four Eagles had any slow fibers in this region. The deep region inserts onto the biceps brachii tendon (see Meyers and Stakebake 2005) and had no slow fibers in any of the five eagles and the hawk (Figure 2C). Both M. supracoracoideus and M. deltoideus major are wing elevators, and likely function in wing stabilization during gliding (Meyers 1993; Meyers and Stakebake 2005). M. supracoracoideus lies deep to the pectoralis. It arises from the sternum, coracoid, and sterno-coraco-clavicular membrane and its tendon passes through the triosseal foramen to insert onto the *tuberculum dorsalis* of the dorsal humerus. A single Golden Eagle had a small population (~150) of slow fibers (Figure 2D). M. deltoideus major arises from the cranial aspect of the scapula and inserts broadly over the dorsal pectoral crest of the humerus. It was without any slow fibers in all the individuals examined.

The cranial-most fascicles of the pectoralis (overlying M. coracobrachialis cranialis), shown to be active in gliding kestrels (Meyers 1993) had 10 slow fibers in two Golden Eagles (Figure 2E), fewer than 50 in the Swainson's Hawk, and no slow fibers in the other two

Golden Eagles and the Bald Eagle. *M. coracobrachialis cranialis* crosses the anterior surface of the shoulder girdle, extending from the coracoid to the *impressio coracobrachialis* of the humerus. It has been described as a wing protractor in Turkey Vultures (Fisher 1946) and to maintain the protracted wing (see Meyers and Stakebake 2005). It had no slow fibers in two Golden Eagles and the Bald Eagle (Figure 2F, G), and 10 and 24 slow fibers in the other two Golden Eagles and 50 slow fibers in the Swainson's Hawk. *M. triceps scapularis*, a wing extensor, extends from the scapula to the olecranon process of the ulna. It had no slow fibers in any of the five birds examined (3 Golden Eagles, Bald Eagle, Swainson's Hawk) (Figure 2H).

Discussion

Our most notable result was the unexpected absence of slow fibers in the eagle flight muscles. Given the soaring abilities of these birds, we had expected to find functionally-relevant populations of slow fibers in muscles used for soaring, as seen in albatrosses and vultures (Meyers and Stakebake 2005; Rosser and 1986a). Albatrosses possess the greatest number of slow muscle fibers seen in any bird studied, with *Mm. coracobrachialis cranialis* [and extensor metacarpi radialis dorsalis, a wrist extensor] completely slow, and the cranial region of the pectoralis possessing 38% slow fibers. Other albatross muscles, *Mm. supracoracoideus* and *deltoideus* (wing elevation), showed 14 and 13% slow fibers, respectively. Although slow percentages were not calculated for the triceps muscle, slow fibers numbered around 4500 and 5900 in the triceps scapularis of two albatrosses. In contrast, none of the triceps muscles of any of the eagles examined had *any* slow fibers. Whereas the *coracobrachialis cranialis* was *completely* slow in albatrosses (over 13,000 fibers - Meyers and Stakebake 2005), this muscle averaged about 8% slow fibers in gulls; that 8% corresponded to about 960 slow fibers (Meyers and Mathias 1997). This is in stark contrast to the fewer than 30 slow fibers seen in two-out-of-five eagle individuals. Clearly, the number of slow fibers must be put into the context of the size of the muscle. Although most of the muscle blocks were pieces taken from much larger muscles, *M. coracobrachialis cranialis* was sectioned in its entirety through the midbelly. It had 10 and 24 fibers in two Golden Eagles, and had cross sectional areas of 0.51cm² and 0.79cm², respectively. Based on the cross sectional areas of leg muscles of avocets and the total number of muscle fibers in them (e.g., 3 samples of *M. iliotrochantericus caudalis* averaged 0.36 cm² and 16,458 total muscle fibers - McFarland and Meyers 2008), we can conservatively suggest that these two *coracobrachialis cranialis* muscles (that are between 1.4 and 2 times the area of the avocet *iliotrochantericus caudalis*) would possess between 23,000 and 32,000 muscle fibers. The 10 and 24 slow fibers would give a percentage of 0.04% and 0.075% slow muscle fibers in these two muscles, respectively. It is difficult to imagine the functional effectiveness of such a low percentage of slow fibers.

Much has been written about the deep pectoralis muscle of vultures, pelicans, albatrosses and its slow fibers as an adaptation for soaring flight (see Kuroda 1961; Pennycuik 1972; Rosser and George 1986a; Rosser *et al.* 1994; Meyers and Stakebake 2005, and references therein). Although there are species with a deep pectoralis that have not been examined histochemically (e.g., Old-World Vultures (Pennycuik 1972) and Whooping Cranes (Fisher and Goodman 1955), it is assumed that the deep layer is slow in all species that possess one

(Pennycuick 1972). Jollie (1957) reported that Golden and Wedge-tailed Eagles do not possess the separate deep layer, though data on other species is rare. An undivided or partially-divided pectoralis is seen in raptors (Corvidae *et al.* 2006; pers. obs), although the difference between the two eagle species in this study was surprising. Perhaps a developmental explanation is more likely than a functional one (see Jollie 1957; Meyers and Stakebake 2005). The partly-divided type of pectoralis morphology is also seen in American Kestrels (Meyers 1993), Herring Gulls (Meyers and Mathias 1997) and Black Kites (*Milvus migrans*; George and Naik 1959). Although Rosser and George (1986b) reported about seven and eight percent slow fibers in the deepest fasciculi of Red-tailed Hawks and Double-crested Cormorants, respectively, no slow fibers were found in that region of those species by Corvidae *et al.* (2006) or Meyers (1997). This discrepancy may have resulted from the various investigators not looking at equivalent regions of the same muscles.

Why no slow fibers?

The absence of slow fibers in the flight muscles of eagles in any appreciable quantity was very surprising, just as it was in gulls (Meyers and Mathias 1997). We previously suggested that oxidative fast fibers could accommodate the postural control of gliding and soaring (Meyers and Mathias 1997). It is possible that the slow wing beats of eagles have resulted in their fast fibers being “matched” to a lower optimal contraction frequency (see Goldspink 1981) that, while still faster than slow fibers, is more efficient at isometric contractions than the fast muscle fibers of a starling, say, with a wingbeat frequency of about 14 Hz (Williams and Swaddle 2003). Still, it is odd that some birds such as albatrosses, which have wingbeat frequencies of less than 3 Hz (Pennycuick 1996), would have evolved a slow deep layer to the pectoralis, whereas eagles and hawks did not. Different modes of soaring could be a factor in the distribution of muscle fiber types. Raptors make use of thermal (static) soaring, with periodic flapping, whereas albatrosses are well known to use dynamic soaring (Videler 2005) or gust soaring (Pennycuick 2002). The presence of the slow, deep pectoralis layer could be seen as an adaptation for the latter, whereas its absence in raptors could be related to their use of thermals. However, Turkey Vultures show a more albatross-like morphology and engage in static soaring like eagles, whereas gulls display a more raptor-like morphology and soar in a manner more similar to albatrosses. There may be a phylogenetic explanation to this; perhaps these raptors have an evolutionary or functional constraint that minimizes the number of slow fibers in their flight muscles.

Why any (few) slow fibers?

Another interesting observation is that since the slow fibers are rare and variable across individuals, why do they possess any slow fibers? For example, *M. coracobrachialis cranialis* had no slow fibers in three of the five eagles examined. In the other two, only 10 and 24 fibers were seen. The presence of this small number suggests that these slow fibers are not adaptive and are likely not functioning in these birds. Sokoloff *et al.* (1998) found that three fast oxidative motor units averaged 274 fibers and produced an average force of 0.01 N in pigeons. How can 24 fibers affect movement in a 3-5 kg bird? It is possible that the presence of small numbers of slow fibers in the few eagle flight muscles is a developmental vestige. Slow fibers are quite numerous ontogenetically in the fast pectoralis of the adult chicken, but become restricted to the anterior region two days post hatching (Matsuda *et al.* 1983).

Likewise, in the pectoralis of pigeons (Rosser *et al.* 1998) and bats (Schutt *et al.* 1994), slow fibers are plentiful developmentally and are replaced completely by fast fibers in adults. The opposite occurs in the rat soleus, where larger numbers of fast fibers give way to a slow adult phenotype (Wigston and English 1992). It is well known that neurons make multiple connections (hyper-innervation) to inappropriate muscle fibers developmentally and then the incorrect connections are terminated (e.g., Fladby and Jansen 1990). It is possible that the few (and variable) low numbers of slow fibers throughout the flight muscles of eagles represents incorrect termination events or the persistence of immature myosins. Although avian non-pectoralis muscles have rarely been studied with regard to their fiber ontogeny, it is possible that similar changes occur in them as well, and the small populations of slow fibers in the these muscles of eagles could be a developmental holdover.

Conclusions

This paper presents the first immunohistochemical analysis of flight muscles in eagle species. In contrast to our predictions, the flight muscles of these soaring birds had remarkably few slow fibers; this raises the likelihood the fast muscle fibers must perform the isometric, postural function in eagles, just as they must in gulls (Meyers and Mathias 1997). Since avian muscles are typically highly aerobic (Goldspink 1981; Turner and Butler 1988), it is likely that fast fibers can play a role in posture, even though the traditional assumption is that slow fibers are the primary players (Goldspink 1977) in postural behaviors.

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Figure 1. Serial cross sections of *M. pectoralis* (superficial furcular origin) from a Bald Eagle, *Haliaeetus leucocephalus*, reacted with anti-slow antibody ALD58 (top) and anti-fast antibody MY32 (bottom) to show characteristic staining of all of the muscles in this study. This region of the pectoralis had no slow fibers in any of the birds studied. Scale bar = 100 μ m

Figure 2.

Representative cross sections of flight muscles from Golden Eagles, *Aquila chrysaetos* (A-F; H) and a Bald Eagle, *Haliaeetus leucocephalus* (G) reacted with anti-slow antibody ALD58. Positively-reacting slow fibers appear dark red. Flight muscles show very few slow muscle fibers and are overwhelmingly fast, suggesting that Eagles can maintain their soaring spread-wing posture with fast muscle fibers. A: M. pectoralis (superficial furcular origin); B: M. pectoralis (deep furcular origin); C: M. pectoralis (deep biceps brachii insertion); D: M.

supracoracoideus; E: M. pectoralis (superficial cranial fascicles); F: M. coracobrachialis cranialis; G: M. coracobrachialis cranialis; H: M. triceps scapularis. Scale bars = 100µm

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