Gliding Flight in the American Kestrel (Falco sparverius): An Electromyographic Study

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ABSTRACT Electromyographic (EMG) activity was studied in American Kestrels (Falco sparverius) gliding in a windtunnel tilted to 8 degrees below the horizontal. Muscle activity was observed in Mm. biceps brachii, triceps humeralis, supra- and infratrochantericus, and pectoralis, and was absent in M. deltoideus major and M. thoracobrachialis (region of M. pectoralis). These active muscles are believed to function in holding the wing protracted and extended during gliding flight. Quantification of the EMG signals showed a lower level of activity during gliding than during flapping flight, supporting the idea that gliding is a metabolically less expensive form of locomotion than flapping flight. Comparison with the pectoralis muscle of specialized gliding and soaring birds suggests that the deep layer of the pectoralis is indeed used during gliding flight and that the slow tonic fibers found in soaring birds such as vultures represent a specialization for endurance gliding. It is hypothesized that these slow fibers should be present in the wing muscles that these birds use for wing protraction and extension, in addition to the deep layer of the pectoralis.

Interest in the gliding flight of birds has focused on aerodynamics. A large number of studies have addressed aspects of the aerodynamics of gliding flight, ranging from performance, drag, and lift characteristics in free flight and in windtunnels (e.g., Pennycuick, '60,'68,'72; Parrot, '70; Tucker, '87,'88; Tucker and Heine, '90; Tucker and Parrot, '90; Videler and Groenewold, '91) to analyses of vortex wakes (Spedding, '87). Baudinette and Schmidt-Nielsen ('74) studied the oxygen consumption during gliding and flapping flight in gulls and showed that gliding consumed less than one-third of the oxygen when compared to flapping. Goldspink et al. ('78) found low electrical activity from the pectoralis (region unspecified) of herring gulls (Larus argentatus) gliding in a windtunnel. Investigations into avian gliding with regard to the evolution of flight have also been quite extensive (see Rayner, '81). A gliding ancestor of birds (and niche for Archaeopteryx) is more acceptable to some (e.g., Rayner, '81) on the basis of mechanics, although others favor a cursorial ancestor (e.g., Balda et al., '85).

Whereas recent studies of muscle function during bird flight have concentrated on flapping flight (e.g., Dial, '92; Dial et al., '88,'91), there are relatively little data on muscle activity during gliding flight. How do birds effect and maintain the wing position used during gliding? Although little experimental work has addressed this question, there is a relevant literature on the muscular anatomy of gliding birds. Mostly this emphasizes a smaller, deep layer of M. pectoralis. This deep layer of M. pectoralis was described in the New World vultures by Fisher ('46), who suggested that it played a role during gliding flight. Both Kuroda ('61) and Pennycuick ('82) noted that a wide variety of avian taxa possess a deep layer of M. pectoralis. The biomechanical leverage of this layer has been examined (Pennycuick, '72) and it is believed to support the outstretched wings and prevent the body from "falling through the wings." Rosser and George ('86) examined the histochemical profile of this deep pectoral layer in vultures, and found it to be composed of slow-tonic muscle fibers. Rosser and George indicated that this deep tonic layer is a specialization for gliding and soaring flight, whereas the fast-twitch superficial layer of pectoralis...
is specialized for flapping flight. Goldspink ('81) suggested that the low electromyographical levels recorded during gliding in gulls and vultures by Goldspink et al. ('78) may correspond to the contraction of these tonic fibers. However, although the deep layer of the pectoralis can stabilize body and wing, it cannot orient and maintain the wing into an outstretched or extended position used during gliding flight. In addition, no information is available on how birds that lack the deep layer support their bodies during glides.

American Kestrels (Falco sparverius) were selected for this study for a variety of reasons. Kestrels, although not specialized for gliding flight, do make use of it in their behavioral repertoire (Dunne et al., '88; Videler et al., '83; Videler and Groenewold, '91). Therefore, they may be used as a model for gliding in an unspecialized, or non-endurant glider. Furthermore, since kestrels are systematically related to more specialized gliders (soaring hawks, Old World vultures), they can serve as a base for future comparisons with these related and other unrelated (e.g., New World vultures, gulls) taxa.

MATERIALS AND METHODS

Windtunnel

A 5-meter-long, variable-speed windtunnel was used (see Biewener et al., '92, for detailed specifications). The working section (flight chamber) of the windtunnel, constructed of plexiglas, has dimensions of 0.914 m (length) \times 0.584 m (height) \times 0.584 m (width). A 17-cm diameter hole located 0.711 m from the front of the flight chamber was used for entry of the birds. Air flow was generated by a d.c. powered fan, located at the exhaust section of the windtunnel. Laminar flow was created by placing a 10-cm-thick portion of aluminum honeycomb (cell diameter 3.2 mm) placed 46 cm upward of the front of the flight chamber, and also by two aluminum screens (1 mm diameter) placed 45.7 cm upward and at the front of the flight chamber. Turbulence levels (see Biewener et al., '92, for details) were determined via a hotwire anemometer to be below 1%. Airspeeds were measured by a hand-held Taylor 3100 air speed meter.

The windtunnel was modified to permit kestrels to glide by positioning hinges at the bottom portion of the flight chamber to permit a downward tilt of the flight chamber of up to 10 degrees below the horizontal. For this study, an angle of 8 degrees and an air speed of approximately 9 meters/second were used. These values were selected because Videler and Groenewold ('91) showed that wild European Kestrels (Falco tinnunculus) engage in "hanging" flight at this angle and speed.

Animals

Live American Kestrels (Falco sparverius) were obtained from the Macdonald Raptor Research Centre in Québec, Canada. Four male birds ranging in weight from 105 to 120 g were used for this study. The training protocol involved getting the kestrels to enter into a period of gliding directly off the trainer's fist, to glide for periods of about 10 seconds, and then to fly back to the fist. In the best glides, birds would remain motionless for up to 30 seconds.

Anatomical material for dissection was obtained from the American Museum of Natural History and from the Macdonald Raptor Centre. A detailed description of the shoulder musculature of the kestrel can be found in Meyers ('92a).

Electromyography

Birds were anaesthetized with ketamine (45 mg/kg) and xylazine (4.5 mg/kg) and surgically implanted with bipolar electrodes (insulated silver, 100 µm diameter, 0.5 mm tip exposure, 0.6 mm intertip distance) with a 25-gauge hypodermic needle. Electrodes were sutured to adjacent fascia and threaded subcutaneously to a connector plug (Amphenol) fixed on the bird's back. Electrode positions were verified by post-mortem dissection (in one individual) and pre- and post-experimental surgical back-stimulations. A Grass S88 stimulator unit was used to stimulate the muscles via the recording electrodes. Voltages were increased until a muscle twitch was noticed—this indicated the region of the muscle implanted. Recordings were made on the day following surgery.

Birds were filmed either with a Photometrics camera at 50 frames/second or a Panasonic video camera at 30 images/second. An electrical spike emitted from the camera synchronized each frame of the film with the electromyography record. Electromyograms (EMGs) from a gliding sequence (containing the bird at rest on the fist, gliding, and flapping back to the fist) were amplified and recorded onto computer disk via a Nicolet digital oscilloscope. Actual voltage values can be found via the calibration bars in Figures 2 and 3.

RESULTS

Wing posture

Kestrels maintain a relatively dihedral during gliding flight (wet), in contrast to the positiv utilized by kites and pigeons or dihedral used by frigatebirds (F).

Whereas the position of the flapping flight changes relatively throughout the wingstroke (791), the position of the wing's is relatively stable (although tion of the wings changes with glider angle; see Pennycuick, '68). In order to position the wings f kestrel opens the wing by ext elbow joint. This elbow extensor is a simultaneous extensor joint due to the relationship of the ulna as "drawing parallels" to the relationship of the elbow and wrist to muscle action, produced a lin tments between elbow and wrist the open wing must be rotate to the shoulder. This protractor muscle positions and maintain full extension, and assist in p leading edge of the wing perp the direction of flight.

Myology

Muscles and muscle region electrode implantation were t
approximately 9 meters/second were selected because Vid
newold ('91) showed that wild strels (F. tinnunculus) engage
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Animals

A Kestrel (Falco sparverius) 1 from the Macdonald Raptor
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Electromyography

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Electrodes

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ures 2 and 3.

Two kestrels were each used for two separ-
ate experiments as they proved to be excel-
ent gliders. Following the first experiment
and subsequent electrode removal, the birds
were given approximately 14 weeks to heal
before the second implantation.

Quantification of the EMG's was done via
a LabView computer program (National In-
mstruments, Austin, TX) which calculated the
root mean square (RMS) of amplitude values.
The RMS is an average of the amplitude of
the electrical signal over a time period of
muscle activity (burst length). Burst lengths
were determined by taking the average dura-
tion of a muscle burst (during its activity
during flapping flight) and quantifying that
duration repeatedly across a gliding bout.
Thus, each muscle during gliding was com-
pared in its RMS relative to an equivalent-
length burst of flapping flight. Comparisons
are thus restricted to gliding vs. flapping for
each muscle, and gliding/flapping ratios be-
etween muscles.

RESULTS

Wing posture

Kestrels maintain a relatively neutral wing
dihedral during gliding flight (wings horizon-
tal), in contrast to the positive dihedral as
utilized by kites and pigeons or the negative
dihedral used by frigatebirds (Rüppell, '77).

Whereas the position of the wings during
flapping flight changes relative to the body
throughout the wingstroke (see Dial et al.,
'91), the position of the wings during gliding
is relatively stable (although the configura-
tion of the wings changes with airspeed and
glide angle; see Pennycuick, '68; Tucker, '87).

In order to position the wings for gliding, the
kestrel opens the wing by extension of the
ebony joint. This elbow extension is accompa-
nied by a simultaneous extension of the wrist
joint due to the relationship of the radius and
ulna as "drawing parallels" (Fisher, '57).

Fisher demonstrated experimentally that the
nature of the elbow and wrist joints, and not
muscle action, produced a linkage of move-
ments between elbow and wrist. In addition,
the open wing must be rotated cranially at
the shoulder. This protraction of the hu-
merus positions and maintains the wing in
full extension, and assists in positioning the
leading edge of the wing perpendicularly to
the direction of flight.

Myology

Muscles and muscle regions selected for
electrode implantation were chosen follow-
ing dissection of the forelimb musculature
and are based on predicted actions to orient
the wing into a gliding position. A complete
description of the musculature of the kestrel
forelimb can be found in Meyers ('92a). Brief
descriptions of the relevant muscles and their
proposed functions are included below.

M. pectoralis thoracicus (PT)

M. pectoralis thoracicus is a large, complex
muscle of the ventral aspect of the shoulder.
lt takes origin from the keel and caudo-
lateral half of the sternum, the lateral sur-
face of the furcula, and the Lig. sternocorac-
clavicularis and Lig. cristaclavicularis. PT
can be divided into pars sternobrachialis (SB)
and pars thoracobrachialis (TB) on the basis
of origin (Fig. 1). Functional studies (Dial,
'92; Dial et al., '88, '91) have shown that SB
contributes to depression and protraction of
the wing, and TB contributes to depression
and retraction of the wing. PT inserts onto
the pectoral crest of the humerus.

Within the SB portion of the pectoralis,
cranial superficial fascicles extend from the
furcula to the humerus. These fibers cross
the shoulder cranially to the articulation and
thus should be able to protract the wing (Fig.
1).

At a deeper aspect of the SB, a distinct
group of fascicles arise from the deep surface
of the furcula and insert onto the tendon of
M. biceps brachii over the latter muscle's hu-
meral origin (Fig. 1; see Meyers, '92a).

These deep fascicules of the pectoralis were
selected as potentially analogous to the deep
layer of M. pectoralis found in vultures and
hypothesized to act during gliding (Fisher,
'46; Pennycuick, '72; Rosser and George, '86).

The TB portion of the pectoralis has a
depressive and retractive action (Dial, '92;
Dial et al., '88) and was therefore used as a
control: a priori it should not be active during
gliding since the wing is protracted during
gliding and the TB functions as a retractar.

M. supracoracoides (SC)

M. supracoracoides is the principal eleva-
tor of the avian wing and lies deep to M.
pectoralis. It is a bipinnate muscle and arises
from the body of the sternum lateral to the
keel, from the medial and lateral surfaces of
the coracoid, and from the Lig. sternocorac-
clavicularis. SC tapers and passes through a
bony canal formed by the coracoid cranially,
the furcula medially, and the scapula caudal-
ly (triosis foramen). SC inserts onto a
small process on the cranial border of the humerus. During flapping flight, SC is believed to function in wing elevation (Dial et al., '91), although its role has been questioned (Sokoloff et al., '91). Salt ('63) hypothesized SC to function during gliding based on its muscle fiber composition. Goslow and his colleagues (personal communication) observed SC muscle activity during intermittent gliding bouts during electromyographic studies in starlings.

M. deltoideus major (DT)

M. deltoideus major is a large muscle of the dorsal aspect of the shoulder region and extends from the scapula to the humerus. DT arises from the Os humeroscapulare, the cranial aspect of the scapula, and adjacent shoulder ligaments. It extends laterally and inserts along the dorsal aspect of the pectoral crest and adjacent proximal humeral shaft. DT shares a role in wing elevation with M. supracoracoideus, and may function during gliding flight as well.

M. triceps humeralis (TH)

M. triceps humeralis lies along the caudal border of the humerus, and extends from the humeral shaft to the ulna. TH arises from the proximal two-thirds of the caudal border of the humerus. It extends distally, and inserts by mixed fleshy and tendinous fibers.
Fig. 2. Sample electromyograms from three subregions of M. pectoralis in the kestrel: cranial fascicles (CP), deep fascicles (DP), and thoracohumeralis (TB). The traces under "a" indicate the baseline of the EMG signal as the birds were at rest on the handler's fist in the wind tunnel, and not yet flying. The traces under "b" show the activity during a period of gliding. The traces under "c" show the contrasting activity of the same muscle region during two wingbeats. EMG amplitude scale = 75 mV.
Fig. 3. Sample electromyograms from M. supracoracoideus (SC), M. deltoideus major (DT), M. biceps brachii (BB), and M. triceps humeralis (TH). Conditions are the same as described for Figure 3.
onto the olecranon process of the ulna. TH can extend the antebrachium and, by virtue of the linkage between the elbow and wrist (Fisher, '57), the manus as well. Thus TH may be responsible for maintaining the extended position of the wing during gliding flight.

M. biceps brachii (BB)

M. biceps brachii, a two-joint muscle, lies along on the cranial border of the brachium. It arises by tendons from the coracoid and from the bicipital crest of the humerus. The single belly extends distally and inserts tendinously onto the proximal radius and ulna. By virtue of this two-joint arrangement, BB may be able to protract the humerus (via the coracoid-humeral articulation) in addition to flexing at the elbow. This elbow flexion can help stabilize the elbow joint, and with simultaneous activity of the elbow extension, may help maintain the proper angle of the elbow (and thus the amount of wing extension).

Electromyography

The following muscles show electromyographic (EMG) activity during gliding flight: deep and cranial fascicles of Mm. pectoralis, supracoracoideus, triceps humeralis, and biceps brachii. The following muscles show no EMG activity during gliding flight: M. deltoideus and the TB region of M. pectoralis (Figs. 2, 3).

Quantification of the electromyographic signals (Fig. 4) reveal that for all muscles, the RMS amplitudes of the gliding bursts are less than equivalent-length bursts during flapping flight. Mm. biceps brachii and triceps humeralis show less than half the intensity level during gliding than they exhibit during flapping flight. Both portions of the M. pectoralis ("deep" and "cranial"), in addition to M. supracoracoideus, show more than half the level of activity during gliding than they exhibit when compared to flapping flight.

DISCUSSION

Muscle activity during gliding

Muscle activity was found in those muscles producing support of the body, wing extension, and wing protraction. The muscle used as a control, the TB region of the pectoralis, showed no activity, as predicted.

![RMS amplitude values (in mV) from gliding and flapping data from the five muscles that showed activity during gliding: M. biceps brachii (BB), M. triceps humeralis (TH), M. supracoracoideus (SC), and M. pectoralis (deep and cranial fascicles) (DP, CP). Bar extensions indicate 95% confidence intervals.](image)
Body support

Support of the body during gliding is accomplished by the actions of pectoralis (deep part) and supracoracoideus. The deep part of the pectoralis probably does "keep the body from falling through the wings" as explained by Pennycuick ("72). The supracoracoideus, although an elevator of the wing, may function as an antagonist to the deep part of the pectoralis, and may help stabilize the shoulder joint, or protect the integrity of that joint from a sudden downburst of air. Both of these muscles showed periodic burst patterns of about 50 Hz during glide periods in at least one bird (Figs. 2, 3). (During flapping flight at 9 m/s, wingbeat frequency is about 8 Hz; Meyers, '90). These "mini-bursts" of 50 Hz may function to produce an "unfused" tetanic contraction. This can occur when the muscle contracts and relaxes at the frequency rate observed. The contractions produce force, and are spaced apart such that upon contracting again, another rise in muscle force is produced before the previous one has subsided. This contraction pattern may allow the muscle to produce the effect of relatively constant force with intermittent muscle activity.

A functional role of the supracoracoideus in gliding warrants a reevaluation of the function of this muscle. Studies of muscle weight and relative function (e.g., Hartman, '61) indicate that gliding and soaring birds possess relatively small supracoracoideus muscles. How this muscle contributes to gliding flight remains to be examined in these species.

Wing extension and protraction

The humerotriceps (with the scapulotriceps) is the principal extensor of the elbow. Thus activation of the triceps can maintain wing extension during gliding flight. The linkage between elbow and wrist as described by Fisher ('57) may produce full wing extension by contraction of the triceps muscles alone. The biceps may also assist in elbow stabilization and fixation since it acts antagonistically to the triceps. In addition, biceps and triceps probably act to adjust the amount of flexion that exists at the elbow.

The biceps, due to its origin from the coracoid, is in a position to protract the humerus (Ostrom, '76; Meyers, '92a). In addition, the cranial fascicles of the pectoralis, which cross cranially to the shoulder joint from the furcula to the humerus, can also produce a protractive action. These two muscles probably participate in the positioning and maintenance of wing protraction during gliding.

One muscle which can function in wing protraction, but that was not examined in this study (due to its small size), is M. coracobrachialis cranialis. It extends from the coracoid to the cranial aspect of the humerus, and therefore has good mechanical advantage to protract the wing. It has been suggested to function during gliding flight (Fisher, '46; Stegmann, '64). This muscle probably plays a role in wing positioning in larger birds such as vultures.

Unactivated muscles

Both M. deltoideus major and the TB part of M. pectoralis showed no EMG activity during gliding. Their lack of activity can be explained biomechanically. Although the deltoid muscle acts as an elevator of the avian wing (Dial et al., '91), and might be presumed to function for the same reason as M. supracoracoideus, it was silent during gliding flight in the kestrel. This may be due to the fact that although the deltoid can elevate the wing when the wing is in the downstroke position, it may be beyond its effective shortening length when the wing is at the horizontal. In addition, the caudal deltoid can also protract the humerus, an action not consistent with the humeral protraction of the wing during gliding. However, birds that possess a different wing orientation during gliding (such as the positive dihedral of the wing in pigeons) may show a morphology of the deltoid to assist in the further elevation of the wing needed to produce the positive dihedral.

The TB part of the pectoralis was also silent during periods of gliding. These fibers are oriented such that they retract the humerus. Activity of this region would oppose the protraction needed during gliding.

Evolution of gliding morphology

As suggested by numerous authors (Kuoda, '61; Pennycuick, '82; Rosser and George, '86), the deep layer of the pectoralis is often thought of as the essential element in the gliding flight of "specialized" gliders, such as albatrosses or vultures. In addition, this layer is proposed to comprise slow-tonic fibers in all gliding and soaring birds (Pennycuick, '72, '82) although it has only been examined histochemically in Turkey Vultures (Rosser and George, '86). The deep part of the pectoralis in the kestrel is hypothesized to be functionally analogous to the deep parts, even though it contains twitch fibers (Rosser and Georg unpublished data). A possible scenario that may evolve the deep tonic layer in "specialized" gliding is described below. Both the superficial "intermediate" morphologies across unrelated avian taxa.

Undivided pectoralis

All of the muscle fibers in pectoralis attach onto the peak of the humerus. Examples of situation can be found in galliform and Lanzillotti, '68, pigeon, '03, and most passerine bird, '02; and Berger, '66).

Divided pectoralis

This type of pectoralis consists of superficial and deep pectoralis muscle. Both Kuroda, '72, '82 suggest a deep layer in soaring flight, anatomy can be thought of as being gliding or soaring flight. Pennycuick et al., '90, cranies and stegodons (Goodman, '55; Berger, '66; Den Van Berge, '72;), gannets (Garrod, '87; Selenka, '91), Anhingas (Owre, '67), the Flightless Coptohaleus [Nannopithecus] Ki World vultures (Fisher, '74; Berger, '67; frigatebirds (Kur and Berger, '66), albatrosses a rod, '87; George and Berg, '82), and pelicans (Geo, '66). Interestingly, one species is the two avian orders: Gruiformes (Sibley et al., '88), Sibley contain the vast majority of deep layer. A detailed examination of this morphology examined in phylogeny within this group, whether this deep part is part of the group or if it has de
These two muscles probably perform the postioning and maintenance during gliding, which can function in wing it that was not examined in to its small size), is M. coracoides. It extends from the coracoid process of the humerus, and has good mechanical advantage. It has been suggested to gliding flight (Fisher, '46; Leyden and Morgan, '47). This muscle probably plays a role in larger birds such as the bald eagle.

oidus major and the TB part is showed no EMG activity. Their lack of activity can be explained by the deltoid's function when the bird is in the downstroke. The coracoid process is at the horizon-
to, the caudal deltoid can also be viewed, an action not consistent with the protraction of the wing. However, birds that possess a greater inclination during gliding are able to do this.

of gliding morphology

by numerous authors (Kuroda, '82; Rosser and George, '86). The pectoralis is often the essential element in the "specialized" gliders, such as vultures. In addition, this layer comprises slow-tonic fibers in soaring birds (Pennycuick, '81). The deep part of the pectoralis is hypothesized to functionally analogous to the deep layer in vultures, even though it contains only fast twitch fibers (Rosser and George, '86; Meyers, unpublished data).

A possible scenario that may suggest the evolution of the deep tonic layer of the pectoralis in "specialized" gliding birds is described below. Both the specialized and "intermediate" morphologies can be found across unrelated avian taxa.

Undivided pectoralis

All of the muscle fibers in the undivided pectoralis attach onto the pectoral crest of the humerus. Examples of such a construction can be found in galliform birds (Huxley and Lanzillotti, '64), pigeons (Führinger, '82), and most passerine birds (Führinger, '02; George and Berger, '06).

Divided pectoralis

This type of pectoralis construction consists of superficial and deep layers of the pectoralis muscle. Both Kuroda ('61) and Pennycuick ('72, '82) suggest a direct role of this deep layer in soaring flight, and this morphology can be thought of as being specialized for gliding or soaring flight. Pennycuick has proposed that the deep layer in these birds is made up of slow tonic muscle fibers as a specialization for wing posture during sustained glides (although he indicates that albatrosses possess a shoulder "lock" and suggests the deep layer has an alternate function in this group). This separation has been specifically mentioned or described in Old World vultures (Pennycuick, '82), some gulls (Hudson et al., '69), cranes and storks (Fisher and Goodman, '55; Berger, '56, '60; George and Berger, '66; Vander Berg, '70; Pennycuick, '82), gannets (Garrod, 1876; Gadow and Selenka, 1891), Anhingas (Garrod, 1876; Owre, '87), the Flightless Cormorant Compso- phalus (Nannopterus) (Kuroda, '61), New World vultures (Fisher, '46; George and Berger, '66), frigatebirds (Kuroda, '61; George and Berger, '66), albatrosses and petrels (Garrod, 1876; George and Berger, '66; Pennycuick, '82), and pelicans (George and Berger, '66). Interestingly, not all of these bird lie within two avian orders: Gruiformes and Ciconiiformes (Sibley et al., '88). Sibley's Ciconiiformes contain the vast majority of species with this deep layer. A detailed examination of pectoralis morphology examined in the light of a phylogeny within this group may elucidate whether this deep part is a primitive character of the group or if it has developed repeatedly in all soaring birds within the group. The presence of a divided pectoralis in hummingbirds (Zusi and Bentz, '84) suggests a different function in this group.

An attachment of this deep layer to the tenon of the biceps has been reported in Sandhill Cranes (Berger, '56), New World vultures (Fisher, '57), and gulls (Hudson et al., '69). Führinger ('02) mentioned a number of taxa which possess the biceps insertion, including Acipiter, Steganopodes, Gruidae, Charadriidae, and large owls, but these are not illustrated or described in detail. The presence or absence of this distinct insertion site in other species with a deep layer has not been reported.

Partly divided pectoralis

This type of pectoralis morphology has been described for American Kestrels (Meyers, '92a), Sandhill Cranes (Berger, '56), some Ciconiiformes (Vanden Berg, '70), ravens (Shufeldt, 1890), and dippers (Goodge, '57; Meyers, pers. obs.). It consists of a principal muscle belly that attaches to the pectoral crest, and also distinct, deep fascicles that insert onto the tenon of M. biceps brachii over the bicipital crest of the humerus (see Fig. 1). It is unclear whether this attachment onto the biceps tendon over the bicipital crest confers a mechanical advantage to this muscle or is merely an available attachment site on the proximal ventral humerus. This location is believed to reduce the force of depressing the cranial edge of the humerus (Fisher, '46). George and Berger ('66) mention a partly divided pectoralis in the loon Gavia, the goose Chen, and crowned pigeon Goura, but do not describe the specific morphology with regard to the insertion of the muscle. Gadow and Selenka (1891) also mention an indistinct separation of the pectoralis in the cormorant Phalacrocorax.

Whereas those species with the divided pectoralis are specialized for gliding and soaring flight, and those with the undivided pectoralis use gliding flight seldom or for very short durations, the partly divided pectoralis can be found across a wide diversity of avian taxa, many of which use gliding flight to some extent but do not appear as specialized as gulls or vultures. Within a taxon, or across multiple taxa, this morphology may represent an intermediate in the evolution of a gliding morphology. Perhaps the change from the partly divided to completely divided pectoralis requires a complete splitting off of the deep layer and a transition to the slow-tonic
fiber type. Two possible transitions can therefore be suggested: One possibility is a pectoralis that has split off to form the deep layer, but has not yet developed the slow muscle fibers. The other is a pectoralis that has not yet split off the deep layer, but has deep fascicles that are slow-tonic. One way to approach this question is to examine the pectoralis construction and histochemical profile within a group of closely related birds. For example, the Sandhill Crane (Grus canadensis) possesses the partly divided pectoralis morphology (Berger, ’56), whereas a congen-ener, the Whooping Crane (Grus americana), shows the divided pectoralis morphology (Fisher and Goodman, ’55; Berger, ’56). Furthermore, within the Falconidae, the kestrel shows the partly divided pectoralis, and deep fascicles that are uniformly fast-twitch in their histochemical profile (Rosser and George, ’86; Meyers, unpublished data); perhaps the larger falcons that use gliding and soaring flight more extensively (for example, peregrines and gyrfalcons) possess the divided pectoralis and tonic fibers. Examination of other avian taxa that can be thought of as “unspecialized” or “non-endurant” gliders (e.g., swifts, terns) might add to our understanding of the convergence of this morphological construction across unrelated taxa.

Differential recruitment

This study has described a situation where a single muscle, M. pectoralis, is recruited differently between differing modes of flight. During gliding, the deep part and cranial fascicles of M. pectoralis show activity, while the TB portion remains silent. During flapping, the TB portion, however, is activated. Dial et al. ’88 have shown in pigeons that the TB and SB (sternobrachialis) heads of M. pectoralis are recruited differently during takeoff/landing and horizontal flight, with the TB portion showing greater intensity during takeoff and landing. This is shown to reflect both muscle fiber-type and fiber-size (Kaplan and Goslow, ’89) and spinal cord organization (Sokoloff et al., ’89) in this species. These studies showed a difference in fiber-type and -size throughout the pectoral and also a segregation on the spinal cord motoneuron pools of the SB and TB. Differential use of pectoral regions during gliding and flapping may also show spinal cord segregation, although this has yet to be shown. Study of the possible motoneuron segregation between tonic deep-layer fibers and twitch superficial-layer fibers in the vulture pectoralis might be a first step in addressing this question.

Since EMG activity levels during gliding were less than those observed in flapping flight (Fig. 4), it can be inferred that the motor unit recruitment during gliding is different than in flapping flight. The reduced amplitude of the electrical signal suggests that either fewer motor units are being recruited or the firing frequency of the activated units is reduced (or both) during gliding flight. This supports the study of Baudinette and Schmidt-Nielsen (’74) (see also Goldspink, ’81), whose oxygen consumption values indicate that gliding is a metabolically “less-expensive” form of locomotion than flapping.

Gliding as a postural mechanism

Muscles associated with the postural control of a limb are usually slow-twitch or tonic in their histochemical and physiological profiles (for review, see Meyers, ’92b). Gliding flight is a postural activity and the activated muscles are needed to assume an “anti-gravity” role and maintain the outstretched wing. Electromyographical studies of gulls and vultures (Goldspink et al., ’78) showed activity of the pectoralis during gliding and concluded that this activity was needed for wing support. Although no mention was made of the electrode placement or muscle fiber type in these pectoralis muscles, it is assumed that the slow tonic fibers were being recorded. In the kestrel, fast-twitch muscle fibers in the wing account for all of the postural control for gliding (personal observation; but see Meyers, ’92b). Although fast contracting oxidative muscle fibers (FOG) can be fatigue-resistant, isometric contractions (in which the muscles are active but not shortening; this is presumed to be the type of muscle activity during gliding flight) are usually thought of as being most efficient if performed by slow-twitch or tonic muscle fibers (Goldspink, ’77). Perhaps the mechanism for an isometric contraction with fast-twitch muscle may be exemplified with the type of recruitment observed in the deep region of the pectoralis (Fig. 2). The 50-Hz “mini-bursts” observed in the Kestrel may produce an unfused tetanic contraction to maintain an overall “isometric” contraction. Thus, we may need to reevaluate our assumption that only slow muscles can function in postural roles.

Kestrels and other “non-endurant” gliders may make use of less efficient fast-fibers during the relatively short period of gliding. Those species that glide stably should be under selective advantage to have a more efficient contraction in slow muscle). Furthermore, tonic fibers may be more widely expressed species than just in the pectoralis.

GENERAL CONCLUSION

Previous research has suggested that the deep layer of the pectoralis is the primary muscle for gliding flight. This study shows that muscle function is more complex than the activated layer often cited. Muscles must produce and maintain the stretched wing. Perhaps the fibrous (slow-twitch) seen in assumed to be present in all are more widespread among these species. Where uses fast-twitch muscle fiber to keep the wing extended, have slow-twitch or tonic fiber to facilitate long glides. Fibers which possess different v form of positive or negative may show variations in muscle fiber type specialization across particular postural configurations is open to further research taxa within a phylogenetic framework varies in the grid across unrelated and related .

ACKNOWLEDGMENTS

Live birds were obtained from D.M. Bird at the Mac Research Centre. Anatomical section was obtained from G at the American Museum of_Technical assistance during this project was provided by D.R. Carri G.E. Goslow, Jr., J.A. Gray Parrish, A.J. Sokoloff, E. Vison, and J. Wotton. G.E. T Bertness, S. Gaines, C. Janis Ryan, and two anonymous helpful comments on this portion of the Dept. of Engineering, sly graciously offered his assistance and increasing the lar windtunnel. J.D. Harry was the LabView program system and assisted in its u
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tion, activity levels during gliding and those observed in flapping飞行, it can be inferred that the muscle activity during gliding is different from that during flapping. The reduced activity of the motor units is being reflected in the firing frequency of the action potentials. Reduced (or both) during gliding, he supports the study of Schmidt-Nielsen (1974) (see '81), whose oxygen consumption indicated that gliding is a metabolically-pensive form of locomotion.

is a postural mechanism associated with the postural control, especially during slow-twist or tonic, semisupine and physiological processes, see Meyers, '92b). Gliding involves the activation of a muscle or muscle fiber pectoralis muscles. The slow tonic fibers involved are being used, fast-twist muscle fiber action potential for all of the postor gliding (personal observation, Meyers, '92b). Although fast twitch muscle fibers (FOG) are resistant, isometric contraction of the muscles are active but not unless is assumed to be the type of muscle involved during gliding flight) are usually being most efficient if per-
thrust or tonic muscle fibers). The mechanism for contraction with fast-twist muscles exemplified with the type of serves in the deep region (Fig. 2). The 50-Hz microprocessor in the Kestrel may produce tonic contraction to maintain metrical contraction. Thus, the evaluation of our assumption that gliding function in postural muscles is not an "endurant" glider of less efficient fast-fibers during the relatively short periods in which they glide. These species that glide or soar extensively should be under selective pressures for a more efficient contraction mechanism (e.g., slow muscle). Furthermore, these slow muscle fibers may be more widely distributed in these species than just in the deep layer of the pectoralis.

GENERAL CONCLUSIONS

Previous research has suggested that the deep layer of the pectoralis in birds such as quirls is the primary muscle component for gliding flight. This study of the kestrel shows that muscle function during gliding is more complex than the activity of the deep layer often cited. Muscles must be activated to produce and maintain the spread and protruded wing. Perhaps the fiber type specializations (slow-tonic) seen in various species (and assumed to be present in all soaring birds) are more widespread among the wing muscles in these species. Whereas the kestrel uses fast-twist muscle fibers in the triceps to keep the wing extended, a vulture may have slow-twist or tonic fibers in this muscle to facilitate long glides. Furthermore, species which possess different wing profiles (in the form of positive or negative dihedrals) may show variations in muscle activity and fiber type specializations associated with this particular postural configuration. This topic is open to further research across various taxa within a phylogenetic framework to elucidate variations in the gliding-morphology across unrelated and related avian taxa.

ACKNOWLEDGMENTS

Live birds were obtained for this study from D.M. Bird at the MacDonald Raptor Research Centre. Anatomical material for dissection was obtained from G. Barrowclough at the American Museum of Natural History. Technical assistance during the experiments was provided by D.R. Carrier, S.K. Crider, G.E. Goslow, Jr., J.A. Gray, A. Parker, J. Parrish, A.J. Sokoloff, E. Valerie, D.S. Wilson, and J. Wotton. G.E. Goslow, Jr., M. Bertness, S. Gaines, C. Janis, S.K. Meyers, J. Ryan, and two anonymous reviewers made helpful comments on this paper. S. Karlsson of the Dept. of Engineering, Brown University graciously offered his assistance in measuring and increasing the laminar flow of the wind tunnel. J.D. Harry and his students wrote the LabView program for EMG quantification and assisted in its use. S.K. Meyers translated portions of the Fürbringer and Gadaw papers. This study was completed in partial fulfillment of the Ph.D. degree at Brown University and was supported by a Sigma Xi grant-in-aid of research, NSF grant BSR-8904370 to G.E. Goslow, Jr., and the DGG financial group.

LITERATURE CITED


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