



# Muscle function in avian flight: achieving power and control

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Citation	Biewener, A. A. 2011. "Muscle Function in Avian Flight: Achieving Power and Control." <i>Philosophical Transactions of the Royal Society B: Biological Sciences</i> 366 (1570) (April 18): 1496–1506. doi:10.1098/rstb.2010.0353. h
Published Version	doi:10.1098/rstb.2010.0353
Citable link	<a href="http://nrs.harvard.edu/urn-3:HUL.InstRepos:33085956">http://nrs.harvard.edu/urn-3:HUL.InstRepos:33085956</a>
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**Muscle function in avian flight: achieving power and control**

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Andrew A. Biewener  
Concord Field Station, Harvard University  
100 Old Causeway Road  
Bedford, MA 01730

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16 email: [abiewener@oeb.harvard.edu](mailto:abiewener@oeb.harvard.edu)

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**7305 words (including figure captions and references), 28 pp. text, 6 figures (0**

22

**tables)**

**key words:** bird flight, neuromuscular function, muscle power, fascicle strain

24 **Abstract:**

26 Flapping flight places strenuous requirements on the physiological performance  
26 of an animal. Bird flight muscles, particularly at smaller body sizes, generally contract at  
high frequencies and do substantial work in order to produce the aerodynamic power  
28 needed to support the animal's weight in the air and to overcome drag. This is in contrast  
to terrestrial locomotion, which offers mechanisms for minimizing energy losses  
30 associated with body movement combined with elastic energy savings to reduce the  
skeletal muscles' work requirements. Muscles also produce substantial power during  
32 swimming, but this is mainly to overcome body drag rather than to support the animal's  
weight. Here, I review the function and architecture of key flight muscles related to how  
34 these muscles contribute to producing the power required for flapping flight, how the  
muscles are recruited to control wing motion, and how they are used in maneuvering. An  
36 emergent property of the primary flight muscles, consistent with their need to produce  
considerable work by moving the wings through large excursions during each wing  
38 stroke, is that the pectoralis and supracoracoideus muscles shorten over a large fraction of  
their resting fiber length (33-42%). Both muscles are activated while being lengthened or  
40 undergoing nearly isometric force development, enhancing the work they perform during  
subsequent shortening. Two smaller muscles, the triceps and biceps, operate over a  
42 smaller range of contractile strains (12-23%), reflecting their role in controlling wing  
shape through elbow flexion and extension. Remarkably, pigeons adjust their wing stroke  
44 plane mainly via changes in whole-body pitch during take-off and landing, relative to  
level flight, allowing their wing muscles to operate with little change in activation timing,  
46 strain magnitude, and pattern.

48

Birds power flight primarily by large pectoralis muscles that depress the wings at the  
50 shoulder. The dominant role and large size of the pectoralis muscle, therefore, enables a  
critical assessment of how muscle function is tailored to meet the mechanical power  
52 requirements of flapping flight over a range of flight conditions. The smaller  
supracoracoideus muscle of birds, about one-fifth the size of the pectoralis, is the primary  
54 wing elevator active during upstroke, particularly at slow to moderate speeds and during  
hovering (at faster flight speeds, wing elevation is likely produced passively by aerodynamic  
56 forces acting on the wings, which remain extended during upstroke to maintain lift through  
bound circulation [1, 2]). Smaller extrinsic and intrinsic wing muscles assist in modulating  
58 wing orientation and controlling wing shape. These muscles likely contribute to adjustments  
of the wing's performance as an airfoil [3-7] and, thus, may indirectly affect flight power  
60 requirements. However, because of their small size the intrinsic muscles of the wing likely  
contribute little additional mechanical power for flight.

62 Prior analyses of muscle-tendon architecture have shown that muscles differ widely  
in their design for changing length while producing force, but due to their conservative  
64 properties for force production and relative fiber strain (ratio of activated length change  
relative to resting fiber length), skeletal muscles generally perform about the same amount of  
66 work in proportion to their mass [8-11]. Longer fibered muscles, such as the avian pectoralis,  
however are well suited to producing the larger movements required for moving the wings to  
68 produce effective aerodynamic power for weight support and to overcome drag. In addition  
to having longer fibers, greater operating strains also enhance the range of movement that a  
70 muscle generates. Thus, the operating strains of certain flight muscles are expected to be

greater than those of muscles that support an animal's weight during terrestrial locomotion  
72 [12] that contract over more limited strain ranges, allowing more economical force  
production. Muscles, having short fibers that attach to a longer tendon such as those found in  
74 the legs of terrestrial animals, produce large forces and can recover substantial elastic energy  
from their tendon and aponeurosis [12-15]. These muscles are best used for movements that  
76 require little net shortening or lengthening of the muscle. Consequently, pinnate muscles  
having these architectural features are commonly found in distal limb regions. The intrinsic  
78 wing muscles of birds are commonly short fibered and pinnate, and have long tendons. This  
enables these muscles to control distal movements of the wing while, at the same time, being  
80 small and light weight. Their function has not been much studied to date, beyond a few  
comparative functional anatomical descriptions [7, 16, 17] and assessment of their  
82 neuromuscular activity patterns [3, 16, 17]. Even so, these studies are important because they  
provide a framework for future studies that seek to assess how the smaller intrinsic wing  
84 muscles are used to achieve flight across different conditions, and in birds with differing  
wing designs and flight styles.

86 In the context of this earlier work, the functions of the two primary flight muscles of  
birds, the pectoralis and supracoracoideus, are reviewed here in relation to the mechanical  
88 power needed to meet the aerodynamic requirements for flapping flight. The vast majority of  
morphological and physiological work has largely focused on the pectoralis because of its  
90 dominant role in powering avian flight. Consequently, much of the review of avian muscle  
function will focus on the pectoralis, with particular comparison to its antagonist, the  
92 supracoracoideus. Preliminary in vivo analyses of the triceps and biceps muscles, which  
control wing shape via elbow extension and flexion, are also considered in relation to

94 changes in flight performance required for take-off, landing, and maneuvering flight. Future  
directions for research to improve our understanding of the neuromuscular control and  
96 functional design of avian flight are also identified.

98 *Functional anatomy of primary avian flight muscles.*

The pectoralis is a large muscle (~8-11% body mass; [15,16]) that attaches to the  
100 humerus of the wing at the deltopectoral crest (DPC; Fig. 1). Its main portion  
(sternobrachialis, SB) originates from an enlarged sternal keel, with more anterior fibers  
102 [Figure 1 here]  
arising from the furcula, or 'wishbone'. A much smaller portion (thoracobrachialis, TB)  
104 originates dorsally from ribs. The fibers of the thoracobrachialis and posterior region of the  
sternobrachialis insert on an internal aponeurosis that merges with the more anterior SB  
106 fibers before attaching to the DPC. In addition to producing mechanical work during  
downstroke, the pectoralis also pronates the wing. The smaller supracoracoideus lies deep to  
108 the pectoralis, also originating from the keel of the sternum and is about one-fifth of the  
pectoralis in mass (~2% body mass). By means of its tendon, which inserts and acts dorsally  
110 at the shoulder as a pulley, the supracoracoideus elevates and supinates the wing during  
upstroke [18-21]. Whereas the pectoralis is comprised of generally long fibers with modest  
112 pinnation (pigeon: 31 to 67 mm, mean 41 mm), the supracoracoideus is a classic bipinnate  
muscle with short fibers (pigeon: 15-21, mean 18 mm). It produces elevation and supination  
114 of the wing by means of a long tendon that passes dorsally over the shoulder, via the triosseal  
foramen of the avian pectoral girdle, before attaching to the dorsal surface of the proximal  
116 humerus adjacent to the DPC. The pectoralis is comprised mainly of fast-oxidative (Type

118 Ila) fibers (~85% in pigeons) with a smaller component of fast-glycolytic (Type IIb) fibers  
[20, 21]. Fiber type composition of the supracoracoideus, to my knowledge, has not been  
examined in pigeons, but in the European starling is comprised of a greater fraction (68%) of  
120 fast-glycolytic versus fast-oxidative fibers [22]; whereas, in zebra finches, Anna's  
hummingbirds [23], and Atlantic puffins [24], the supracoracoideus is exclusively comprised  
122 of fast-oxidative fibers.

124 *In vivo assessment of avian muscle function during flight.*

Because of its focal insertion on the ventral surface of the DPC in pigeons (Fig. 1B),  
126 doves, cockatiels, budgerigars, magpies, and certain other species of birds, forces produced  
by the pectoralis can be estimated directly by means of strains recorded using a strain gauge  
bonded to the dorsal surface of the DPC (in several avian species the pectoralis also inserts  
128 along the ventral proximal shaft of the humerus, preventing this approach). Details for  
exposing and attaching metal foil strain gauges to obtain strain-calibrated *in vivo* recordings  
130 of pectoralis force are described elsewhere [25, 26]. Although some uncertainty exists in the  
calibration of DPC-strain to pectoralis muscle force [27], such recordings provide a reliable  
132 and temporally detailed recording of time-varying muscle force. Other methods for obtaining  
muscle force and estimates of mechanical power output for bird flight also have their  
134 limitations [28, 29]. A similar skeletal-strain based approach to extract the time-varying  
force transmitted by the supracoracoideus muscle via the muscle's tendinous insertion on to  
136 the proximal dorsal shaft of the humerus has also been used [30].

138 In combination with DPC strain-force recordings of the pectoralis and the  
supracoracoideus, *in vivo* measurements of muscle fascicle strain are obtained in localized

140 muscle sites by means of sonomicrometry, a technique based on measurements of the  
propagation of sound pulses within the muscle to determine length changes [31]. Because  
142 the sonomicrometry transducers lie adjacent to muscle fascicle bundles, they provide a  
measure of fascicle strain rather than muscle fiber strain *per se*. Nevertheless, the two  
144 measures are likely to be quite similar. In the large pectoralis, sonometric measurements  
obtained from multiple sites (anterior and posterior SB and TB) in pigeons showed similar  
146 fascicle strain levels in the larger SB portion of the muscle, but smaller strains in the most  
posterior SB and TB portions of the muscle [32]. By averaging the sonomicrometry data for  
148 fascicle strain across recording sites (weighted by the estimated fraction of muscle mass that  
each site represents) or by relying on a single recording site within the muscle and assuming  
150 the site is representative for the muscle as a whole, the total work of the muscle can be  
assessed based on the muscle's length change. Muscle work is therefore determined by  
152 averaging fascicle strain multiplied time fascicle length, in relation to the time-varying force  
the muscle produces. The product of muscle fascicle length change and force is visualized  
154 as a work loop over the course of a wingbeat, or muscle contraction, cycle (see Fig. 3). The  
timing of muscle activation is recorded simultaneously using fine-wire electromyography  
156 (EMG) electrodes inserted into and anchored adjacent to those fascicles for which a  
sonometric evaluation of strain is recorded [31]. The EMG provides a measure of the timing  
158 of muscle activation and relative motor recruitment in relation to muscle force and length  
change. In total, the force, strain and neuromuscular activation recorded from the muscle  
160 serve to describe the temporal dynamics of the muscle's contractile performance across a  
range of flight conditions.

162



*Functional analysis of pectoralis and supracoracoideus muscles during flight.*

164           The pectoralis muscle is activated to contract late in upstroke, prior to wing  
reversal (Figs. 2A). Force development follows soon after the start of activation (~ 2-8  
166 ms in pigeons and cockatiels) and peaks early in the downstroke, continuing until the end

[Figure 2 here]

168 of downstroke. The pectoralis undergoes a slight stretch or remains nearly isometric  
(depending on the species and flight condition studied), as force develops late in upstroke  
170 and through wing reversal to begin the downstroke (Figs. 2 & 3). By developing force  
while nearly isometric or being briefly stretched, the rate of force rise and the magnitude  
172 of peak force are appreciably enhanced due to force-velocity effects [33, 34]. As a result,  
the work that the pectoralis performs is substantially increased while the muscle shortens  
174 during the remainder of downstroke. Deactivation of the pectoralis occurs early in the  
downstroke, almost coincident with the timing of peak force generation. This allows the  
176 muscle to relax to near zero force prior to being stretched passively in the upstroke.

Importantly, this reduces the antagonistic ('negative') work required of the  
178 supracoracoideus to elevate the wing. The timing of pectoralis deactivation relative to its  
continuing force production points to the problematic nature of inferring muscle force  
180 production based on EMG recordings alone.

[Figure 3 here]

182           For those species studied [27, 35, 36], the in vivo force-length work behavior of  
the pectoralis is generally similar across a range of flight speeds and conditions (Fig. 3).  
184 As noted above, activation of the pectoralis in these species occurs late in upstroke, as the  
muscle is being lengthened (this is most extreme in the mallard, Fig. 3B) or is nearly

186 isometric, allowing the muscle to develop force rapidly for a given level of activation. In  
contrast to classical expectations for the operating fascicle strain of a muscle (~10-15%  
188 of resting length) based on isometric force-length properties [33, 34]), the pectoralis of  
these species undergoes strains of 32-40% during different flight conditions (take-off,  
190 ascending and descending flight, and changes in speed during level flight), stretching 20-  
30% beyond the muscle's resting length (measured when the wings are folded against the  
192 bird's body on the perch), and shortening 8-12% less than resting length. This large strain  
excursion underlies the ability of the pectoralis to perform substantial work during the  
194 downstroke of each contraction cycle. Forces produced by the pigeon pectoralis were  
found to vary about 40% across flight conditions, ranging from take-off and ascending  
196 flight to landing and descending flight [26]. Forces produced by the cockatiel pectoralis  
during level flight across speeds ranging from 1 to 14 m/s in a wind tunnel were found to  
198 vary 65% [35]. These forces are estimated to be less than 40-60% of the peak isometric  
force that the muscle can generate [26], reflecting in part the rapid shortening that the  
200 muscle undergoes to produce work. In cockatiels, doves and pigeons, the pectoralis  
achieves 58-73% of the maximum theoretical work output possible for the observed force  
202 and active strain range [30, 35] (Fig. 3A).

[Figure 4 here]

204 Not surprisingly, the supracoracoideus of pigeons exhibits mirror-like force,  
length and activation timing patterns relative to the pectoralis [30] (Fig. 4). As the main  
206 upstroke muscle, the supracoracoideus is activated late in downstroke just prior to wing  
reversal. The muscle develops force rapidly while being nearly isometric, reaching peak  
208 force very early in the upstroke. The early onset of force development by the

supracoracoideus likely reflects the its role in decelerating and re-accelerating the wing  
210 during the downstroke-upstroke transition, as well as its role in wing supination [19].  
Estimates of the elastic energy storage within the supracoracoideus tendon ( $51\pm 62$  mJ  
212 during level and  $88\pm 85$  mJ during ascending flight) are consistent with this role, given  
that the magnitude of inertial kinetic energy exceeds the amount of elastic energy stored  
214 and returned by the supracoracoideus tendon [30]. The additional inertial power of the  
wing's motion is likely transformed into useful aerodynamic power mainly in the  
216 downstroke, as has been traditionally assumed [37] . The rapid supination of the wing  
produced by the supracoracoideus is important for achieving a short duration upstroke,  
218 with the potential for positive lift generation in birds with wing-tip reversal flight  
kinematics [38] or for minimizing unwanted negative lift. It also maximizes the duration  
220 of downstroke lift production and was likely an important feature in the evolution of an  
active flapping flight stroke [19]. Rapid supination of the wing to initiate upstroke in  
222 rufous hummingbirds [39] is key to this species' ability to generate positive upstroke lift,  
which has been estimated to be 25-33% of their total lift production [40]. In pigeons, the  
224 amount of force produced antagonistically between the two muscles was estimated to be  
small [30]. During slow level flight, the negative work of the pigeon pectoralis just prior  
226 to the end of the upstroke is about 18% of the positive work the muscle performs during  
the downstroke. This may well reflect a role in absorbing inertial energy of the wing as it  
228 is decelerated late in upstroke [30]. By comparison, negative work of the pigeon  
supracoracoideus is 14% of the positive work that the muscle performs and occurs late in  
230 downstroke to decelerate the wing at this time.

The short fibers of the bipinnate supracoracoideus muscle require them to operate  
232 over large strains, similar to those of the pectoralis. Supracoracoideus fascicle strains  
range from 33 to 40% of the muscle's resting length during descending, ascending and  
234 level flight [30]. The supracoracoideus fascicles also undergo a smaller degree of stretch  
relative to their rest length (6 to 12% across flight conditions) compared with their net  
236 shortening strain (-27% for all flight conditions). This pattern of fascicle length change  
relative to resting length is opposite to the pattern of strain observed within pectoralis  
238 fascicles, which lengthen by 20 to 30% of their resting length before shortening to ~10%  
less than rest at the end of downstroke (Fig. 4). Interestingly, the modulation of muscle  
240 strain in the supracoracoideus reflects mainly differences in the degree of wing  
depression (stretching the supracoracoideus and its tendon) that occur at the end of  
242 downstroke across the three flight conditions that were studied. Because of its relatively  
small size, the pigeon supracoracoideus generates 1.6 times the mass-specific muscle  
244 power output of the pectoralis. This reflects the much greater operating stresses (force  
normalized to physiological cross-sectional area) of the supracoracoideus, which ranged  
246 from 85 to 125 kPa for descending versus ascending flight, compared with stresses of 50  
to 58 kPa in the pectoralis across the same flight condition [30], and 57 to 76 kPa in an  
248 earlier study of the pigeon pectoralis when corrected for the muscle's estimated  
myofibrillar area [26].

250

*Comparative data for avian pectoralis power output versus speed.*

252 [Figure 5 here]

254 Because the pectoralis is the dominant avian flight muscle (in pigeons, the  
pectoralis represents 60% of total wing muscle mass, unpublished data), the muscle's  
power output can be used to assess how whole body power output and, indirectly,  
256 aerodynamic power output vary as a function of flight condition and speed in a bird.  
Measurements of pectoralis mechanical power output and wingbeat frequency have been  
258 published for black-billed magpies (*P. pica*), cockatiels (*N. hollandicus*), and ringed-neck  
doves (*S. risoria*) across a range of flight speeds while flying level and steady in a wind  
260 tunnel [27, 41] (Fig. 5). Except for magpies, the other two species showed a U-shaped  
power versus flight speed curve, generally consistent with aerodynamic theory. This  
262 reflects high induced power costs at slow flight speeds and hovering that decrease as  
speed increases, and high profile and parasite power costs (due to increasing wing and  
264 body drag) at higher flight speeds. The absence of an observed increase in pectoralis  
muscle power at higher flight speeds in magpies may reflect either an inability of this  
266 species, with its lower aspect ratio and less pointed wings, to achieve sufficient thrust in  
order to overcome the profile and parasite drag costs it incurs at higher flight speeds  
268 limiting the top speed that it can achieve [27], or that the birds were unwilling to fly at  
faster speeds in the wind tunnel. Although the wind tunnel used to study the magpies  
270 was smaller (50% less in cross-dimensions of the working section) than that used to study  
the cockatiels and doves, artifacts such as a possible ground or wall effect [42] were not  
272 judged by the authors to be the basis for the magpies' lower power cost at faster flight  
speeds. In the two other species (cockatiels and doves), pectoralis muscle power output

274 at the fastest flight speeds exceeded that produced when the birds were nearly hovering  
(Fig. 5). Thus, although pectoralis power output was high as expected during 1 m/s flight  
276 in the magpies, it remains unclear why the muscle's power output did not reach or exceed  
this level at faster flight speeds.

278         Given that other muscles are involved in flapping flight and do mechanical work,  
it is certainly the case that the total muscle mechanical power requirement for flight is  
280 greater than estimates based on the pectoralis alone. In the study of pigeons, for which  
pectoralis and supracoracoideus muscle power output were both determined [30],  
282 inclusion of supracoracoideus power output increases the total power output of flight by  
nearly 25%. Pectoralis power output across flight modes was 3.2 times greater than that  
284 of the supracoracoideus but less than the nearly 5-fold difference in muscle mass.  
Together, these two muscles represent 71% (unpublished data) of the total flight muscle  
286 mass of a pigeon. If the remaining smaller extrinsic and intrinsic wing muscles perform  
the same relative mass-specific work, this would suggest a total power requirement that  
288 may be nearly 40% greater than that determined for the pectoralis alone.

Aerodynamic models for estimating the power requirements of the flight of birds  
290 at different speeds [43-45] are commonly used to infer ecological strategies for  
maximizing a bird's flight range or minimizing the metabolic power requirement for  
292 flight as a function of time [46]. Although measurements of pectoralis muscle  
mechanical power output are consistent with the general change in power versus flight  
294 speed (being highest at slow and fast speeds, with a minimum at an intermediate flight  
speed), the absolute magnitude of the power cost for flapping flight across species and  
296 speeds remains uncertain. Arguments for one approach and/or method being superior to

another remain unconvincing. This is due to assumptions and simplifications that quasi-  
298 steady aerodynamic theory makes to estimate flight power requirements, and  
uncertainties in the calibration of pectoralis force and assessment of regional fascicle  
300 strain profiles from localized fascicle recordings on the experimental side. More recent  
attempts to estimate muscle power output based on isolated work loop muscle  
302 measurements in relation to EMG recordings made during flight [28, 29] also have their  
limitations. These include estimating muscle recruitment from relative EMG magnitude  
304 across flight speeds to adjust the maximally stimulated muscle power measurements  
derived from *in vitro* work experiments. Such an approach necessarily determines the  
306 change in flight power requirements based on changes in recorded EMG intensity. It also  
results in lower estimates of flight muscle power requirements of cockatiels (minimum  
308 power cost = ~40 W/kg at 7 m/s) compared with those (74-79 W/kg at 5-7 m/s) obtained  
using DPC-based force measurements [27, 35]. Additional studies that refine the use of  
310 these approaches, or use other methods [47], will improve our ability to quantify the  
absolute power costs of flapping flight for particular species operating across various  
312 flight conditions. Consistent with the *in vitro* muscle work and EMG intensity results  
that ascribe change in muscle power output across flight speed due to changes in EMG  
314 intensity [28, 29], results based on *in vivo* fascicle strain, EMG, and DPC-strain  
calibrated force recordings [27, 35] also showed EMG intensity to be highly correlated  
316 with muscle force ( $R^2=0.92$ ). In the latter studies, changes in EMG intensity accounted  
for 65% of the modulation of muscle power, with changes in fascicle strain amplitude  
318 accounting for 25% and changes in wingbeat frequency only 10% of the modulation in  
muscle power [27, 35].

320 Using measurements of DPC strain-calibrated pectoralis force and fascicle strain  
to determine *in vivo* pectoralis power output, the comparative power curves for the  
322 different species studied to date suggest that wing loading, as well as wing and tail shape,  
are likely important determinants of a species' relative muscle power cost. Doves have  
324 the highest wing loading ( $36 \text{ N/m}^2$ ) of the species studied to date [2] and correspondingly  
have the highest relative flight power cost over a broad range of speeds (Fig. 5).  
326 Magpies, have the lowest aspect ratio wings (5.0 versus budgerigars: 7.3, cockatiels: 7.0,  
and doves: 5.7) and rounded wingtips, which likely helps to lower their muscle mass-  
328 specific power requirements but may also limit the fastest speeds they can achieve.

At present, it would be imprudent to place heavy reliance on the accuracy of  
330 experimental or theoretical modeling results to specify precisely whether a species has a  
minimum power cost at a particular flight speed, given the uncertainty and limitations to  
332 the resolution and accuracy of currently available approaches used to estimate flight  
power costs. For example, whereas oxygen consumption data for cockatiels [48, 49]  
334 indicate a minimum metabolic power cost at 10 m/s, measurements of pectoralis muscle  
power data suggest a minimum in the range of 5 to 7 m/s [27, 29]. Combining the  
336 metabolic power results for cockatiels with their mechanical muscle power results [49]  
indicates that muscle efficiency increases with flight speed, ranging from 6.9 to 11.2%  
338 based on the muscle power data of Morris and Askew [29], or from 12.2 to 28.3% based  
on the DPC-pectoralis force and fascicle strain recordings of Tobalske et al. [27].

340 Differences in muscle efficiency are likely given that the shortening velocity of  
the pectoralis muscle fascicles varies with flight speed. For cockatiels [27, 35], fascicle  
342 shortening velocities ranged from 5.19 to 6.73 muscle lengths/s across flight speeds from



1 to 13 m/s. The range of efficiencies derived from in vitro muscle measurements  
344 adjusted for EMG intensity [29] are low compared with those expected for vertebrate  
skeletal muscle, which range from 20-28% at optimal shortening velocities [50]. It seems  
346 surprising that the evolution of flight muscle function in cockatiels and other birds would  
be constrained to substantially lower efficiencies. Although wingbeat frequency varies  
348 only slightly across flight speeds (10% in cockatiels), the magnitude of pectoralis fascicle  
strain changes in a shallow U-shaped pattern, paralleling changes in pectoralis force [29],  
350 which results in the overall muscle power versus speed relationship that is observed for  
cockatiels (Fig. 5). Although fascicle strain rate varies with flight speed, the generally  
352 uniform contractile properties of the pectoralis across a range of flight speeds [27, 29]  
(Fig. 3) reflect the strikingly uniform fiber type characteristics of the avian pectoralis [21-  
354 23]. This is in contrast to the much larger change in fascicle shortening velocity with  
running speed that occurs in the leg muscles of terrestrial animals [51-54].

356

358 *Muscle function in relation to the control of take-off, landing and maneuvering flight.*

Whereas the pectoralis and supracoracoideus are mainly responsible for  
360 producing the mechanical power required for sustained flapping flight in birds, it is  
unclear whether the activity of these large flight muscles is modulated to achieve  
362 maneuvering flight behaviors, or whether the smaller wing extrinsic and intrinsic muscles  
are recruited to adjust wing orientation and wing shape. Past work based on 3D  
364 kinematics, muscle force, and EMG recordings suggest two possibilities. In pigeons [6,  
55] left and right pectoralis muscles appear to exhibit differential timing of force

366 development and magnitude, with downstroke of the outside wing phase advanced  
relative to the inside wing of a turn. In rose-breasted galahs [5], little difference in the  
368 kinematic timing of downstroke or pectoralis EMG activity was noted during 90° turns.  
Instead, there was evidence of differential activation of the left and right biceps muscles,  
370 with the inside biceps showing stronger activity, indicative of increased elbow flexion  
and reduction of inside wing span. In both sets of studies, however, more detailed  
372 kinematics of wing shape and motion during these maneuvers was not available given the  
limited resolution of the motion-analysis systems used at the time. Future work will  
374 benefit from improved kinematic resolution during turning flight, combined with further  
study of left wing versus right wing muscle contractile asymmetry.

376 [insert Figure 6 here]

In studies of pigeons taking-off from an elevated perch platform, flying level and  
378 landing on a similar perch, measurements of wing, body and tail kinematics reveal little  
change in wing or tail movements relative to the bird's body [56]. Instead, most of the  
380 change in global orientations of the tail, wing and wing stroke plane, which determine the  
aerodynamic properties of the bird's flight stroke, are achieved by changes in body pitch  
382 (Fig. 6A). During take-off, pigeons pitch forward (head down) inclining their stroke  
plane to a more vertical orientation to provide increased thrust for acceleration after the  
384 take-off jump from the perch. During landing, the pigeon pitches back (head up),  
changing its stroke plane to a more horizontal orientation to help decelerate as it lands.  
386 Changes in global stroke plane angle during take-off and landing are significantly greater  
and less, respectively, than observed during level flight.

388           The uniform motion of the pigeon's wings relative to its body during take-off,  
level and landing flight, suggests that the control of wing and body movement across  
390 these key phases of flight relies on subtle shifts in aerodynamic and inertial forces  
produced by the tail and wings relative to the body to control body pitch. The pitch  
392 moment of inertia of a bird, though greater than its roll moment of inertia, is still quite  
small. As a result, slight shifts in the orientation of net aerodynamic force produce the  
394 observed pitch acceleration. In pigeons, the shift in direction of net aerodynamic force  
need only be ~8 mm relative to its center of mass to produce the observed pitch moment  
396 [56]. Consistent with this, no significant differences were observed in the neuromuscular  
activation (EMG) or contractile strain behavior of the wing muscles examined (Fig. 6B)  
398 [57]. This result suggests that the control of body orientation and wing motion relative to  
the body does not require substantial changes in flight muscle activation and contractile  
400 function. Instead, the highly maneuverable bodies of many birds (low pitch, roll and yaw  
moments of inertia) enables them to achieve changes in body and wing orientation that  
402 allow rapid sharp turning, or to shift from take-off to landing flight, with subtle changes  
in neuromuscular function that are likely to prove challenging to identify.

404

*Discussion and Summary.*

406           Muscle function in bird flight depends on the production of substantial  
mechanical work performed at a high rate. Although skeletal muscles generally have a  
408 similar capacity for generating mass-specific work, the avian pectoralis is well suited to  
performing work with large length excursions. This is a prerequisite for powering flight  
410 because the wings must move through a large excursion during downstroke to produce

effective aerodynamic lift. The pectoralis achieves this by having relatively long  
412 fascicles that shorten over a large fraction (up to 42%) of their length. The timing of  
muscle activation late in upstroke also allows the pectoralis to rapidly develop force  
414 under nearly isometric or stretching conditions. This elevates the work that the muscle  
performs as it shortens (Fig. 3).

416       Because of its large size and principal role in producing aerodynamic lift, the  
contractile function of the avian pectoralis provides a valuable index for the power  
418 requirements of flight based on measurements of its force production, contractile strain  
and neuromuscular activation. This is in contrast to the multiple muscle groups in the  
420 limbs of running animals that contribute to muscle power for movement. Nevertheless, a  
functional examination of the broader suite of wing muscles is needed in order to  
422 understand how flight movements, particularly those during maneuvering, are controlled.  
Although much smaller wing muscles may not contribute significantly to the mechanical  
424 power underlying flight, by adjusting the orientation and shape of the wing they can alter  
the wing's aerodynamic properties and, thus, influence how aerodynamic forces and  
426 power are shifted between the wings for maneuvering.

An unexpected result is that shifts in body, tail and wing movement during take-  
428 off, level and landing flight of pigeons are achieved mainly by changes in whole body  
pitch, rather than by changes in wing or tail motion relative to the body itself. The degree  
430 to which turning flight is achieved by left versus right asymmetries of smaller wing  
muscles, acting to 'steer' the bird around a turn, as opposed to modulation of the larger  
432 power producing pectoralis and/or supracoracoideus muscles remains unclear. Evidence  
exists that both sets of muscles may contribute to the necessary aerodynamic asymmetries

434 that result in a turning maneuver. The low moments of inertia and highly maneuverable  
bodies of birds means that left versus right asymmetries in turning flight, or fore-aft  
436 asymmetries in aerodynamic force production during take-off and landing flight are  
likely to be small and challenging to identify.

438 Future studies will benefit from improved imaging that will allow detailed  
changes in wing shape, orientation and movement to be quantified and related to the  
440 timing and magnitude of muscle activation, and where possible, changes in muscle  
length, force and work. These measurements become increasingly difficult for smaller  
442 muscles, located more distally in the wing. Force measurements, in particular, are  
difficult to obtain for most muscles, hampering the ability to assess muscle force and  
444 work output in relation to maneuvering flight. In the case where muscles are too small, or  
forces cannot be recorded directly, in vitro or in situ measurements of muscle force [29]  
446 can play an important role for assessing the muscle's contractile properties and role(s) in  
flight. The remarkable ability of birds to fly over a range of speeds while often  
448 maneuvering through complex environments, makes understanding the neuromuscular  
and aerodynamic features of these flight behaviors of considerable interest to  
450 physiologists, biomechanists and aeronautical engineers.

Similarly, the aerodynamic and metabolic power requirements for flight are of  
452 considerable interest to avian and evolutionary ecologists interested in the strategies that  
birds use to forage and migrate to ensure a successful life history. For this reason,  
454 additional free flight data on bird metabolism, characteristic flight speeds and behavior  
need to be linked to additional experimental assessments of flight energy metabolism and  
456 musculoskeletal function. While quasi-static aerodynamic models can provide a rough

estimate of flight costs, the importance of non-steady aerodynamic effects on flight  
458 power costs are now well recognized and cannot be ignored. Thus, additional modeling  
and experimental studies that seek to yield improved measurements of muscle function  
460 and aerodynamic power output are needed.

462 **Acknowledgements.** The author thanks his many past students, postdocs and  
collaborators for the fun and exciting work shared to understand bird muscle function in  
464 relation to flight performance. He also thanks Mr. Pedro Ramirez for his expert and  
devoted help in caring for the birds. Much of the author's work has been funded by the  
466 National Science Foundation, most recently by IOS-0744056.

468

470 **Figure Captions.**

472 Figure 1. A) Anatomical organization of avian wing musculature (adapted from [3]),  
showing key muscles that have been studied, and B) showing the general sites used to  
474 record pectoralis force via deltopectoral crest (DPC) bone strain, pectoralis fascicle  
strain, and neuromuscular activation (EMG).

476 Figure 2. Representative *in vivo* recordings of pectoralis fascicle strain, neuromuscular  
478 activation (EMG), and force for three wingbeats in a cockatiel flying at 7 m/s in a wind  
tunnel. Adapted from [35].

480 Figure 3. Representative *in vivo* work loop patterns produced by the A) pectoralis of  
482 cockatiels (*N. hollandicus*) at three different flight speeds (adapted from [35]), and B) the  
pectoralis of three other species: ring-neck doves (*S. risoria*), pigeons (*C. livia*) and  
484 mallard ducks (*A. platyrhynchos*) (adapted from [27, 31, 36]). The force produced by the  
muscle is plotted against its fascicle strain ( $L/L_0$ , where  $L_0$  is the muscle's resting length:  
486 strain = 1.0). In the first panel of (A) the dashed rectangle denotes the maximum work  
that the muscle could produce for its maximum force and strain; the realized work of the  
488 muscle is 68% of its theoretical maximum. The strain range for all muscles is the same  
(0.9 to 1.3, or 40% range of muscle length change), but force ranges differ in (B) due to  
490 the different sized muscles. The bold gray portion of each work-loop represents the  
period of neuromuscular activation measured by EMG. Arrows denote the direction of  
492 force and fascicle length changes.

494 Figure 4. Representative recordings of the pigeon supracoracoideus (wing elevation)  
fascicle strain, EMG and force, and pectoralis (wing depression) fascicle strain, EMG and

496 force recorded during takeoff from an elevated perch platform and level free flight at ~  
4.5 m/s (7 wingbeats are shown). Gray panels represent the downstroke for the initial  
498 four wingbeat cycles, with the upstroke in white background (adapted from [30]).

500 Figure. 5. Comparative flight power curves for three avian species, showing changes in  
pectoralis mass-specific muscle power (determined from calibrated DPC-strain force and  
502 fascicle strain recordings) versus flight speed in a wind tunnel (adapted from [27]).

504 Figure 6. A) Changes in wing stroke plane ( $SPA_{loc}$ ) and body pitch angle (in global  
space) of a pigeon during successive wingbeats of take-off, mid-level flight, and landing  
506 (adapted from [56]). The strong correlation of wing stroke plane angle versus body angle  
is shown to the right. B) Representative in vivo recordings of muscle strain and activation  
508 (EMG) of extrinsic and intrinsic wing muscles of a pigeon during take-off, level (~ 4.5  
m/s) and landing flight corresponding to a similar sequence shown in A) above (adapted  
510 from [57]).

512

**running head:** *Muscle function during avian flight*

514



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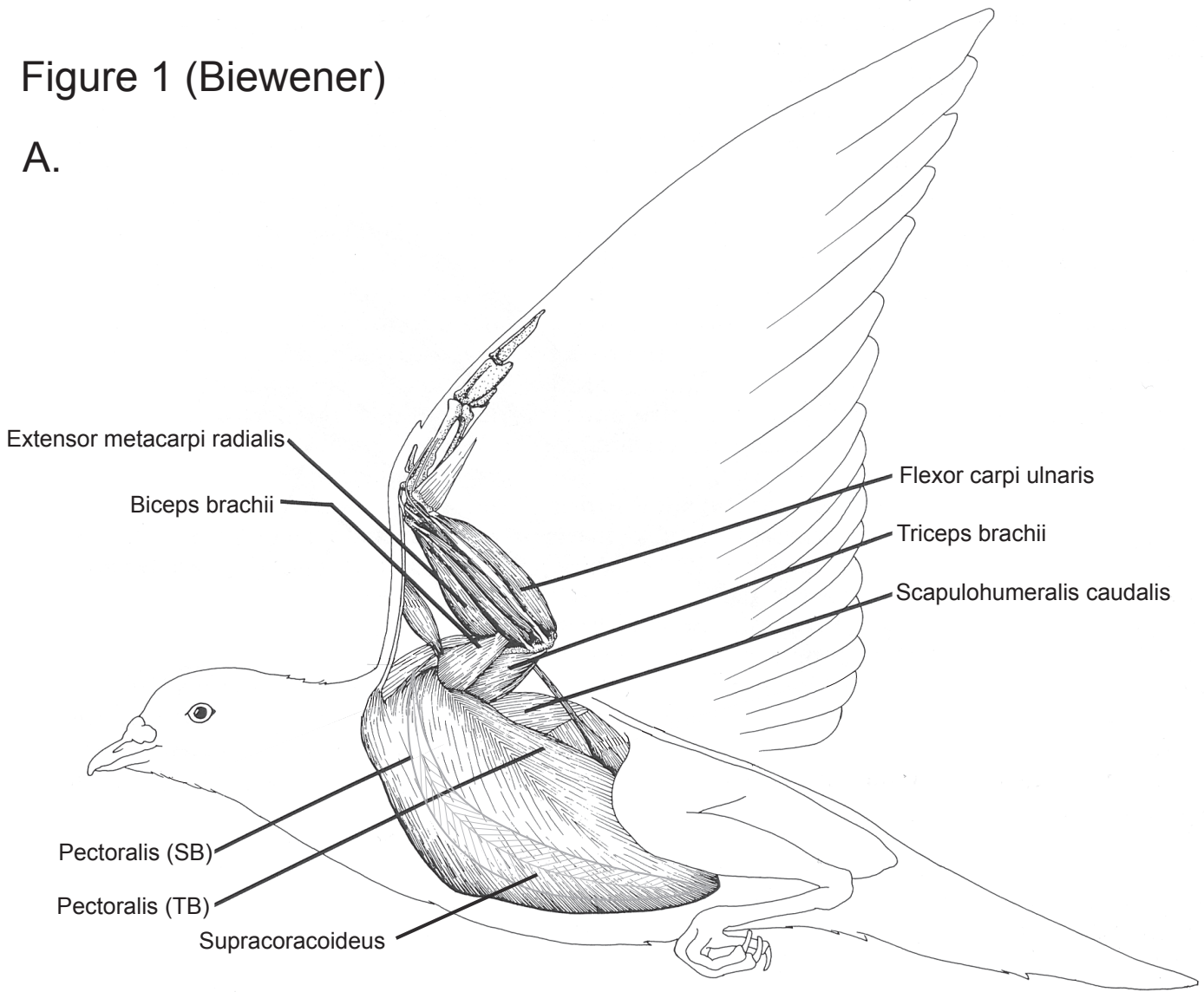
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650

Figure 1 (Biewener)

A.



B.

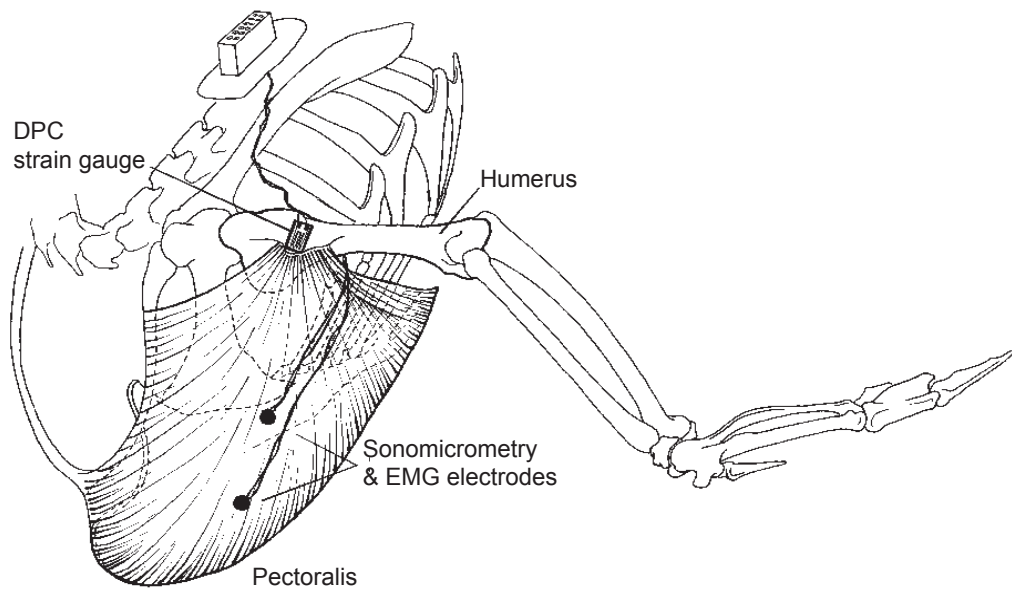
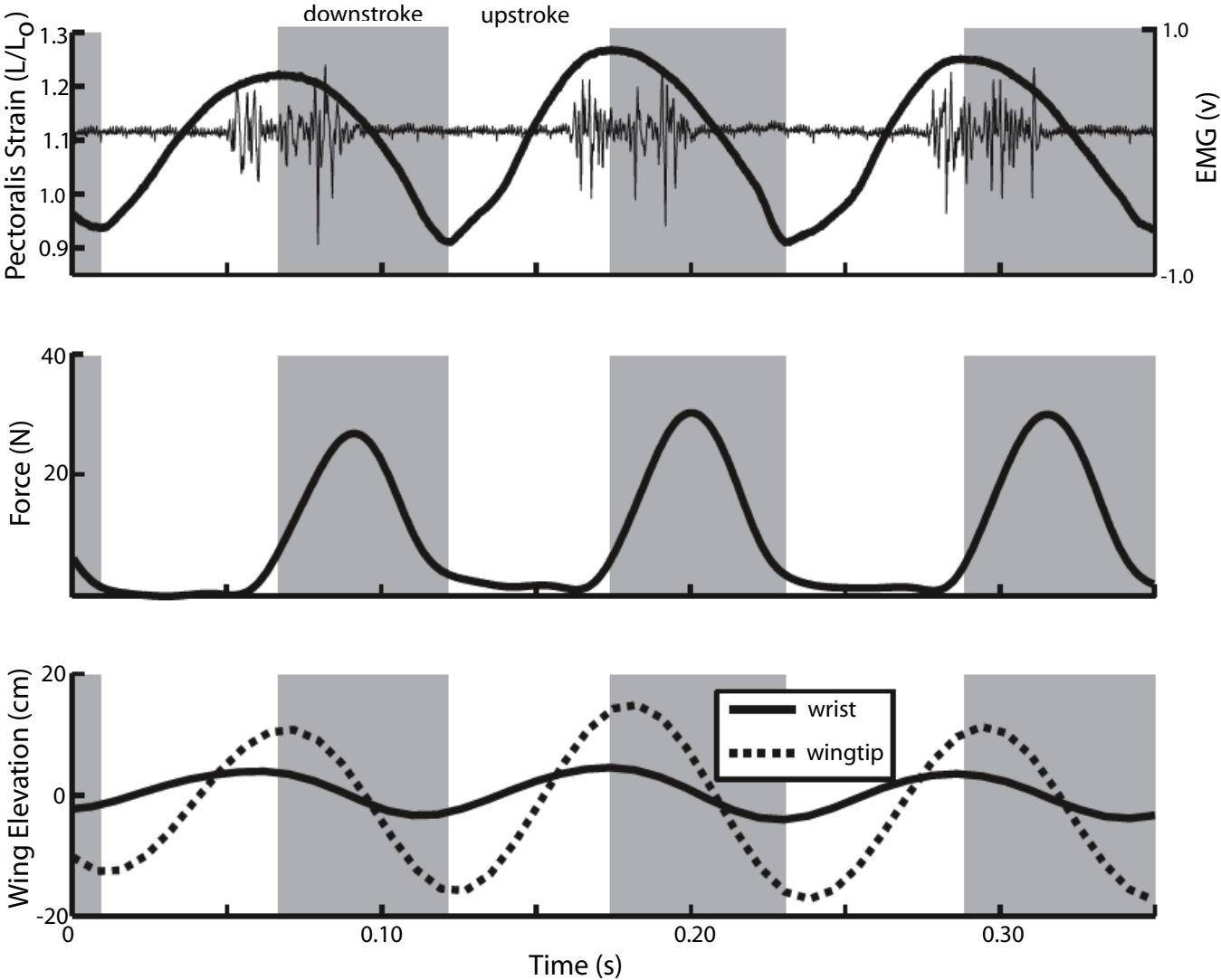


Figure 2 (Biewener)



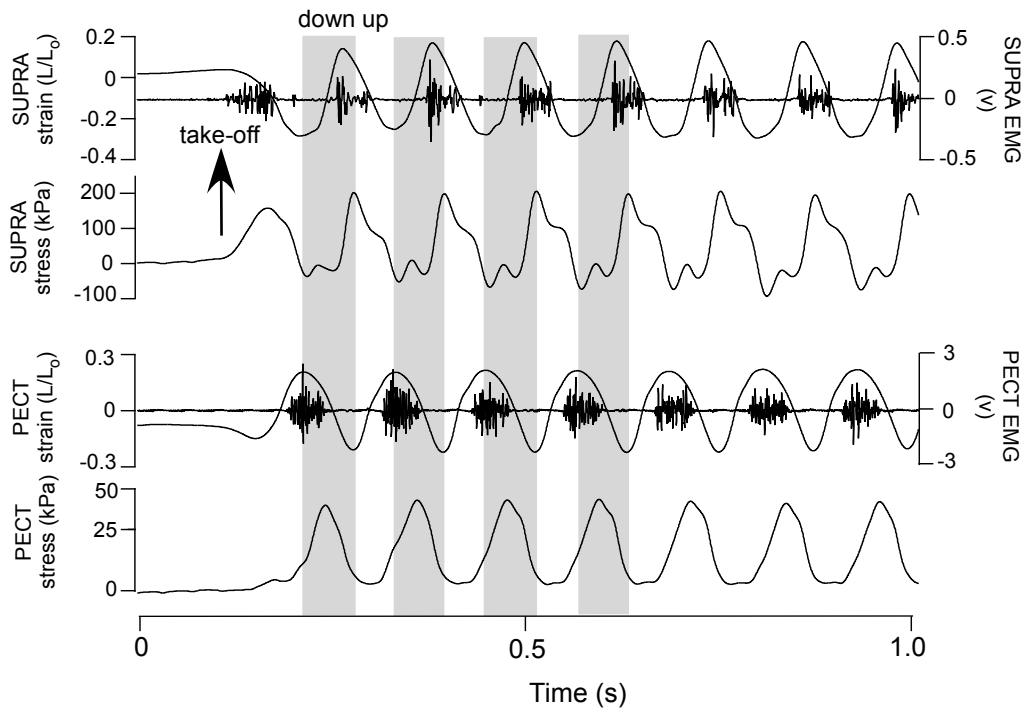
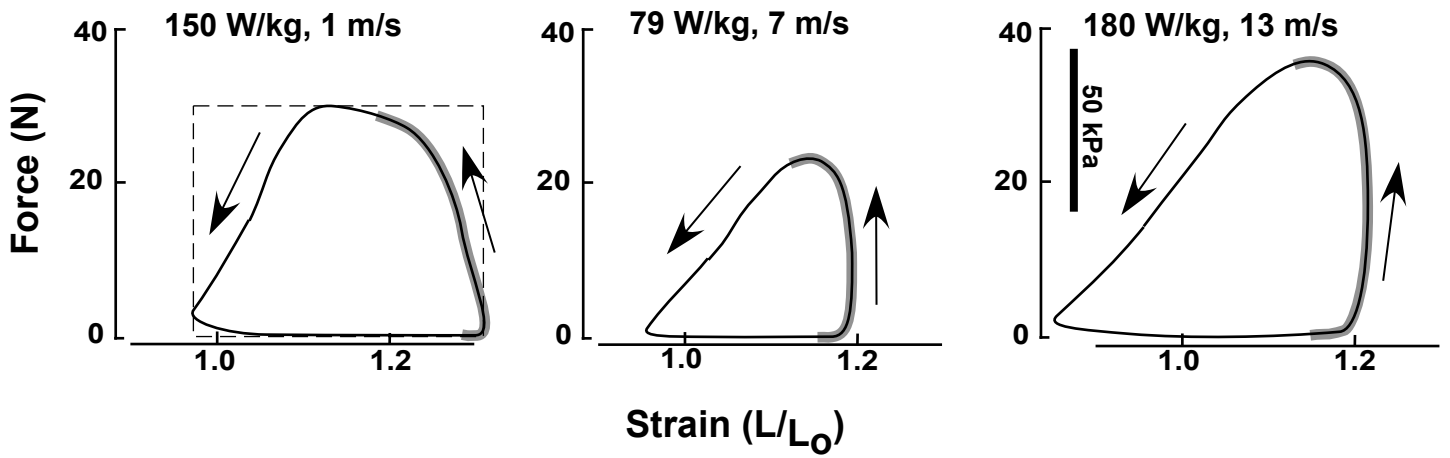


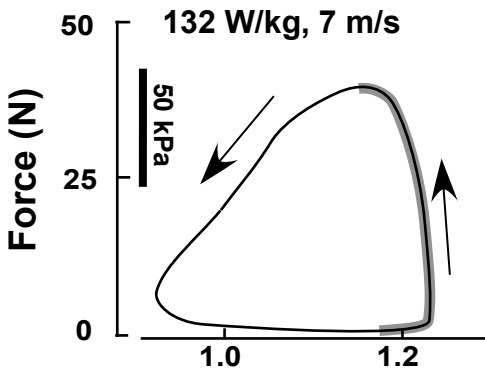
Figure 4 (Biewener)



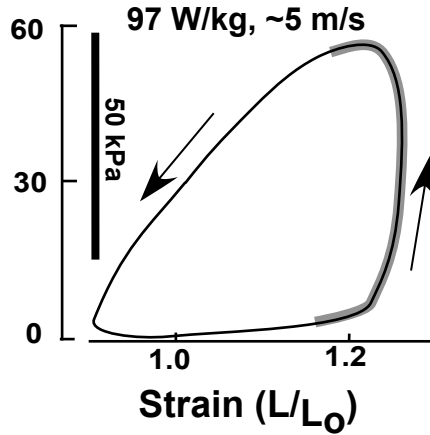
**A. Cockatiel pectoralis**



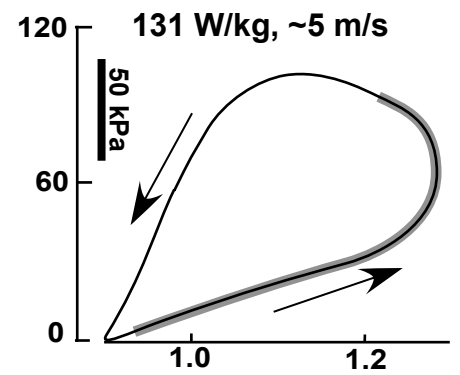
**B. Dove pectoralis**



**Pigeon pectoralis**



**Mallard pectoralis**



**Figure 3 Biewener**

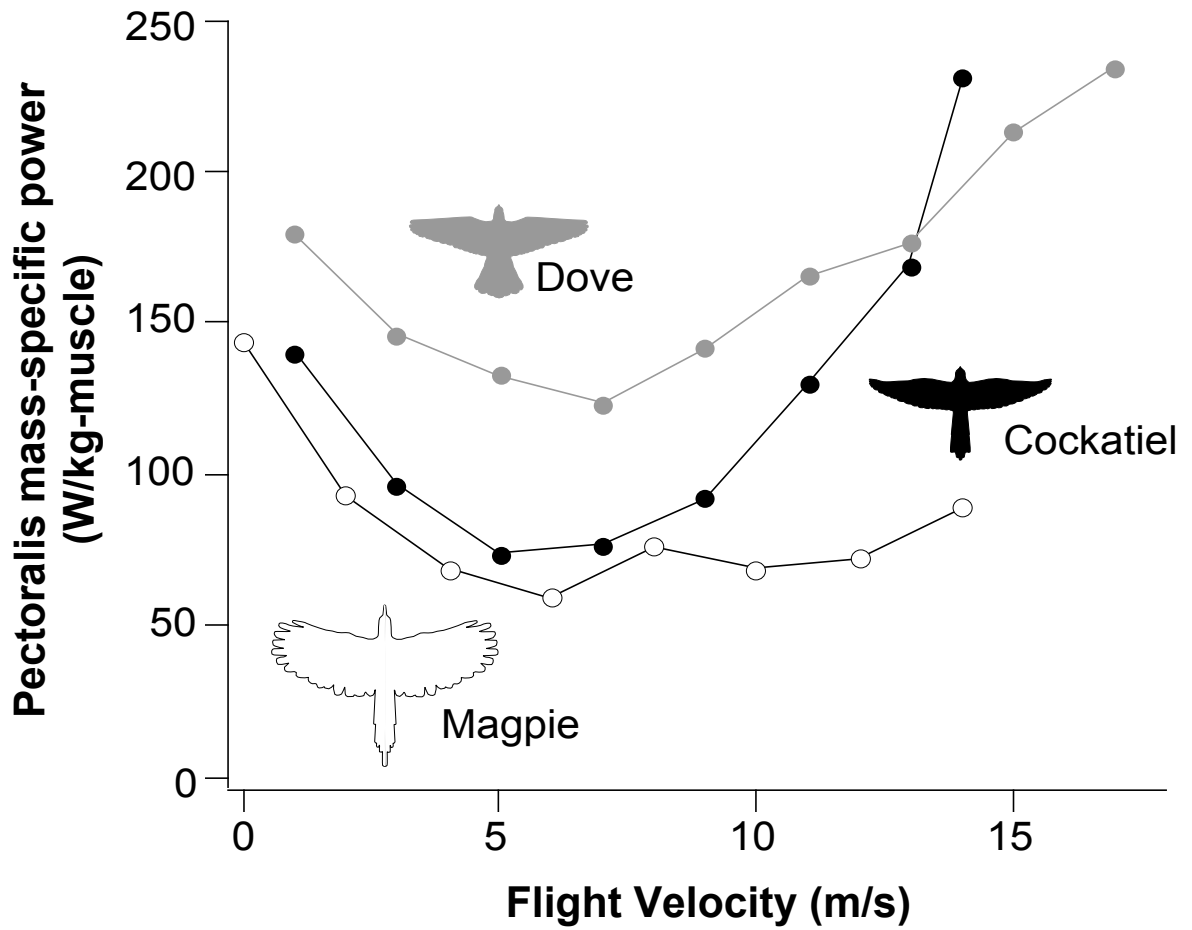
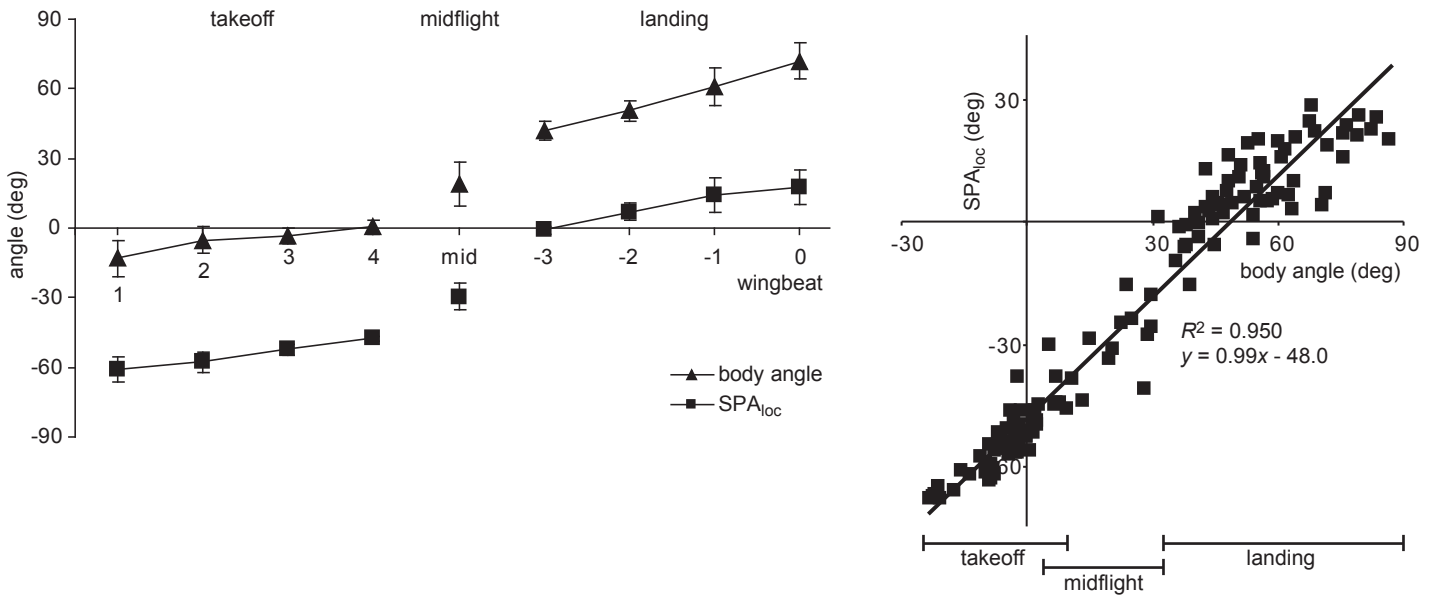


Figure 5. (Biewener)

A.



B.

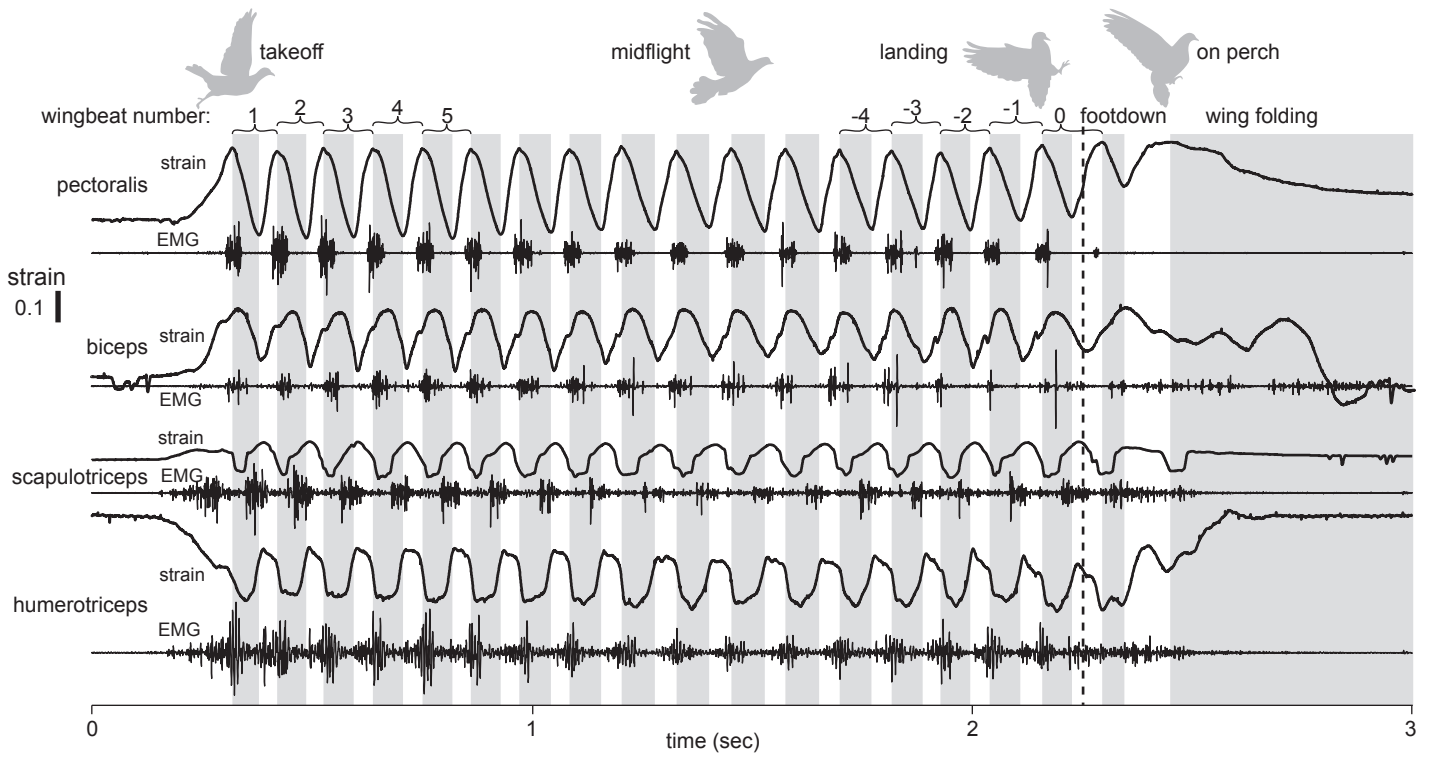


Figure 6. Biewener