MAXIMUM LIFT PRODUCTION DURING TAKEOFF IN FLYING ANIMALS

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SUMMARY

Maximum lift production during takeoff in still air was determined for a wide variety of insects and a small sample of birds and bats, and was compared with variation in morphology, taxonomy and wingbeat type. Maximum lift per unit flight muscle mass was remarkably similar between taxonomic groups (54–$63 \, \mathrm{N \, kg^{-1}}$), except for animals using clap-and-fling wingbeats, where muscle mass-specific lift increased by about 25% (72–$86 \, \mathrm{N \, kg^{-1}}$). Muscle mass-specific lift was independent of body mass, wing loading, disk loading and aspect ratio. Birds and bats yielded results indistinguishable from insects using conventional wingbeats. Interspecific differences in short-duration powered flight and takeoff ability are shown to be caused primarily by differences in flight muscle ratio, which ranges from $0\cdot115$ to $0\cdot560$ among species studied to date. These results contradict theoretical predictions that maximum mass-specific power output and lift production should decrease with increasing body mass and wing disk loading.

INTRODUCTION

Flying animals display a tremendous diversity of body form and aerial ability. How does variation in morphology affect flight ability? To address this question, it is necessary to define some measure of flight ability. One important component of flight ability is the amount of power and lift an animal can generate by beating its wings. During takeoff in still air, an animal must rely solely on the beating of its wings to create all of the air movement necessary to generate a lift force sufficient to overcome its body weight. Thus, maximum still-air lift production can be quantified by determining the maximum load with which an animal can take off. Maximum load-lifting capacity has not previously been measured and used to make comparisons of lift production ability among a variety of animals.

Numerous theories make predictions about the relationship between morphology, lift production, power output and takeoff ability. One group of theories considers variation in wing size and shape. Savile (1957) used an argument based on general aerodynamic principles to assert that low wing loading, slotting (distal separation of primary feathers) and high aspect ratio should enhance lift production and takeoff ability. Various authors (Pennycuick, 1968, 1969; Epting & Casey, 1973; Rayner,

1979; Ellington, 1984) have proposed that the mass-specific power requirement for hovering is proportional to the square root of wing disk loading, such that animals with relatively longer wings require less induced power to counteract their weight. From this theory it follows that maximum lift production capacity should be inversely proportional to the square root of wing disk loading, since the model predicts that animals with longer wings should produce more lift per unit power output.

Pennycuick (1969, 1972) proposed that maximum power output scales proportionally as body mass to the two-thirds power. This model is based on the scaling of wingbeat frequency to body mass, and predicts declining maximum mass-specific power output and lift production with increasing body mass. Pennycuick supported this model with observations of takeoff difficulties of certain large birds.

Hartman (1961) observed that takeoff ability of a wide variety of birds appeared to be correlated with the percentage of body mass composed of flight muscle. Hartman claimed that birds with the highest flight muscle ratios (flight muscle mass/total body mass) had powerful, steeply angled takeoffs, whereas birds with the lowest flight muscle ratios had difficulty becoming airborne.

Weis-Fogh (1973) and Ellington (1984) have proposed that certain animals derive enhanced lift from unsteady aerodynamic effects caused by 'clapping' their opposite wings together and then 'flinging' or 'peeling' them apart. Whether this motion, termed the clap-and-fling wingbeat, causes enhancement in maximum lift production independent of muscle mass variation has not yet been established.

Experiments presented here utilize a wide variety of insects, and a small sample of birds and bats, to test these hypotheses and to show how maximum still-air lift production and power output of flying animals are related to morphology, taxonomy and wingbeat type.

MATERIALS AND METHODS

Lead weights were progressively added to abdomens of insects, thighs of birds and lower backs of bats, in increments that averaged 20 % of body mass. Weights were attached to abdomens of insects and bats with a small amount of a molten beeswax–resin mixture, or to birds by bending and taping strips of lead around the thighs (an equal amount on each leg). Animals were then placed on the floor and stimulated to attempt takeoff. If they could take off and fly, more weight was added until they could no longer do so. Each animal was allowed at least three takeoff attempts whenever it failed to lift a weight, and frequently more than three if it appeared to be exerting less than maximal effort on its initial attempts. Rest periods were taken between flights whenever animals showed signs of fatigue (poor posture, heavy breathing) until recovery appeared complete. Experiments were conducted indoors in still air, at ambient temperatures from 25 to 30°C, at 20–40 m above sea level. A sample of dragonflies was tested separately at 500 m elevation.

Some heavily loaded animals, that could not otherwise take off, became airborne for short distances (<2 body lengths) by jumping, in which case they quickly returned to the ground and it was obvious that they could not take off with that amount of weight. Most of the animals tested could not jump at all (dragonflies, damselflies, beetles, bats), or only weakly (remaining insect groups, see Table 5). Some birds ordinarily employ a powerful jump during takeoff (see for example Heppner & Anderson, 1985), but in these experiments the tightly wrapped lead weights and tape around their thighs restricted leg movement to such an extent that they could not even walk properly, much less jump. Flights were considered acceptable only when the animal moved forwards and upwards at a constant or increasing angle for a distance sufficient to demonstrate that they were generating the necessary power by wingbeats alone. How long a flight could be sustained was not of interest because sustaining flight is a function of supply and regulation (of oxygen, ATP, body temperature, etc.) rather than maximum power output. However, most animals could fly around indefinitely even when carrying loads that they could barely lift from a standing start.

Most of the animals attempted to escape by flying towards a window. For these animals, maximum takeoff angle for each weight was roughly measured by moving them closer and closer to the window until they could no longer take off steeply enough to reach the window's lower edge. At low takeoff angles (<25°) they could not reach the window at all, although they still clearly attempted to. The height at which they struck or swerved to avoid the wall beneath the window was used to determine their takeoff angle. Measurements were rejected when the angle of a flight changed after takeoff or if the animal spiralled upwards.

Animals were grouped according to wingbeat type based on whether their opposite wings came into broad, clearly visible contact with each other. Butterflies, saturniid and noctuid moths (Lepidoptera), and damselflies (Odonata: Zygoptera) used complete clap-and-fling wingbeats, in which their opposite pairs of wings clapped together, from base to tip, at the dorsal apex of each wingbeat cycle. Other animals tested, hereafter collectively referred to as conventional wingbeat fliers, showed no visible or audible contact between opposite wings, although limited contact (at the wingtips only) may have occurred.

After addition of a weight that could not be lifted, the animal was killed and a number of measurements were made. Insects were weighed with a Metler H54AR or Roller–Smith analytical balance, and birds and bats were weighed on an Ohaus triple-beam balance. Maximum lift was estimated as the force equivalent (in newtons) of the mass halfway between the maximum mass lifted (body mass plus added lead mass) and the minimum mass that the animal could not lift. Wing areas were measured from fully-spread wings or wing tracings (not including body area between the wings since that area cannot supply lift in still air) by using an electronic Zeiss planimeter (model Zidas). Wing span was measured from wingtip to wingtip of spread wings of intact animals. Disc area was computed as the area of a circle with a diameter equal to the wing span. Aspect ratio was calculated as the wing span squared, divided by wing area.

The entire pectoral musculature, ventral, dorsal and along the wing bones, was dissected from birds (as in Hartman, 1961) and bats. For weighing insect flight muscle, the following procedure was used. After cutting off the head, abdomen, legs and wings, thoraces were sectioned sagitally into two halves. Any visible oesophageal contents or non-muscular tissues were removed, and both halves were weighed. After 24 h soaking in $0.35 \, mol \, l^{-1}$ NaOH, all muscle was rinsed away with a jet of water. The exoskeleton was dried at room temperature for about 1 h, then weighed. Subtraction of exoskeleton mass from original thorax mass yielded my estimate of flight muscle mass. This method was preferable to dissection because it completely removed all of the flight muscle, and it was quicker and more replicable.

Measured flight muscle masses of birds and bats were slight underestimates, owing to small amounts of muscle left on bone surfaces, and drying and blotting during dissection. Measurements of insect flight muscle mass were slight overestimates, owing to unavoidable chemical removal of a small amount of leg muscle and non-muscular tissue from the thorax. To remedy this situation and to make muscle mass estimates of all animals directly comparable, small correction factors were applied. Bird and bat flight muscle masses were multiplied by 1.01, and insect muscle masses were multiplied by 0.97. These values were fixed prior to flight experiments and represent my best approximation for removal of systematic error.

Attachment of weights to flying animals creates a potential methodological problem because weights that do not act at the centre of mass impart a torque that may adversely affect flight performance. For two reasons, dragonflies were selected to test for this problem. First, the elongate abdomen of dragonflies presented the greatest opportunity to vary weight attachment position. Second, the usual horizontal flight posture of dragonflies should make them particularly sensitive to adverse effects of abdominal weights. Half of the dragonflies flown at 500 m elevation had weights attached to their anterior abdomen (segments 1–2), just posterior to their centre of mass (assumed to be between the meso- and metathoracic wing bases). The other half had weights attached to their extreme posterior abdomen (segments 9–10), five to six times farther from their centre of mass. Maximum lift production was compared between these two treatments.

Statistical analyses were performed by using BMDP software on the DEC-2060 computer at the University of Vermont. All analyses utilized data from individual animals rather than species means because there was considerable morphological variation within species (see Appendix).

RESULTS

Animals tested

Maximum lift force during takeoff was determined near sea level (20–40 m) for 147 insects (49 species), 10 birds (9 species) and 7 bats (3 species). An additional 26 dragonflies (5 species) were tested at 500 m elevation; their results will be treated separately. A species list with associated data is shown in the Appendix.

Table 1. *Correlation coefficients and coefficients of determination for log-transformed morphological variables* versus *maximum lift force*

Variable	r	r^2
Body mass	0·986	0·972
Flight muscle mass	0·995	0·990
Wing area	0·780	0·609
Wing span	0·882	0·779
Aspect ratio	−0·044	0·002

Table 2. *Correlation coefficients and coefficients of determination for log-transformed mass-specific morphological variables (and aspect ratio)* versus *maximum body mass-specific lift force*

Variable	Pooled data		Conventional wingbeat		Clap-and-fling wingbeat	
	r	r^2	r	r^2	r	r^2
Flight muscle ratio	0·782	0·612	0·919	0·845	0·728	0·530
Wing loading	−0·693	0·480	−0·717	0·514	0·098	0·010
Disk loading	−0·728	0·530	−0·697	0·486	−0·303	0·092
Aspect ratio	−0·370	0·137	−0·479	0·229	0·479	0·229

Effects of morphological variation

Four of the five morphological variables (all log-transformed) each explained >60 % of the observed variation in maximum lift force (Table 1). However, intercorrelation of these independent variables prevents determination of the cause and effect relationships underlying the results. That is, the question remains whether variation in wing span, for instance, caused 78 % of the variation in maximum lift, or if that correlation only occurred because wing span was highly correlated with other morphological variables.

This problem was resolved by comparing maximum mass-specific lift force with mass-specific morphological variables, since factoring out body mass largely removed intercorrelation of the independent variables. Flight muscle ratio (flight muscle mass/unladen body mass) was the best single determinant of body mass-specific lift (Table 2), explaining 61 % of the observed variation, or 85 % and 53 % of variation when the data were grouped according to wingbeat type (Table 2; Fig. 1).

What remained to be determined was whether the other variables explained significant portions of the variation in lift production after the effect of flight muscle ratio had been accounted for. This was accomplished by examining partial correlation coefficients of these variables *versus* body mass-specific lift (Table 3), and by observing how these variables affected muscle mass-specific lift (Figs 2–4). These results showed that none of the wing characteristic variables was highly successful in explaining variation that remained after the effect of flight muscle had been accounted for. Aspect ratio did explain 23 % of remaining variation among clap-and-fling wingbeat fliers (Table 3), but this success was probably an artefact, for it
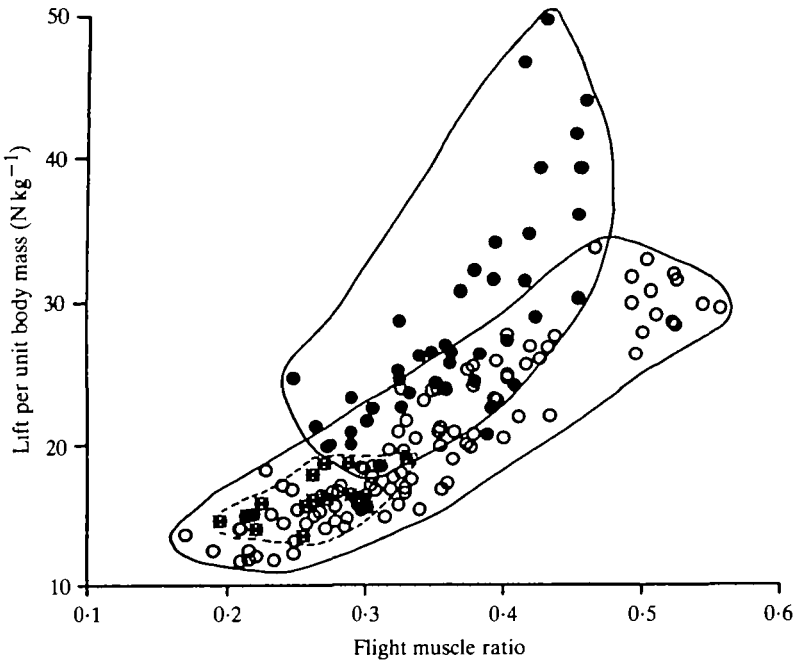
Fig. 1. Plot of flight muscle ratio *versus* maximum body mass-specific lift force for each animal tested. Solid circles represent clap-and-fling wingbeat fliers, and open circles represent conventional wingbeat fliers. Open circles containing asterisks represent birds and bats; this set of points is enclosed by a dashed line.

failed to occur within either of the two types of animals with clap-and-fling wingbeats (partial $r^2 = 0.11$ and 0.01 for Lepidoptera and Odonata, respectively), and thus arose only because of differences in lift production between these two taxa, which happened to differ greatly in wing shape.

Multiple regression of flight muscle ratio, body mass, wing loading and aspect ratio *versus* body mass-specific lift (Table 4) resulted in little improvement in explained variation over that achieved by flight muscle ratio alone. Without flight muscle ratio, the best multiple regression explained only about 40 % of the observed variation (Table 4).

Table 3. *Partial correlation coefficients and coefficients of determination for log-transformed mass-specific morphological variables (and aspect ratio) versus maximum body mass-specific lift force, after effect of flight muscle ratio has been removed*

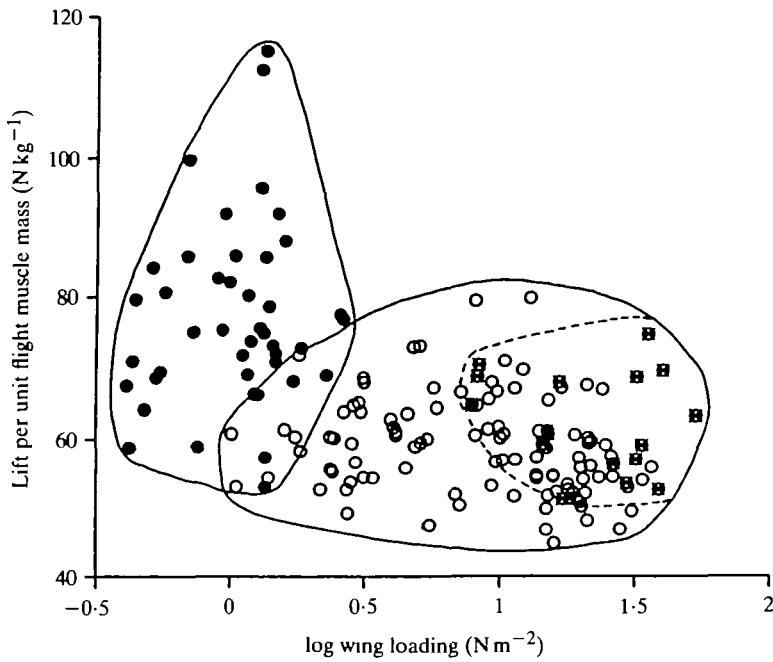| Variable	Conventional wingbeat r	r^2	Clap-and-fling wingbeat r	r^2
Wing loading	−0·358	0·128	0·125	0·016
Disk loading	−0·251	0·063	−0·271	0·073
Aspect ratio	−0·370	0·137	0·481	0·231

Fig. 2. Maximum muscle mass-specific lift *versus* wing loading for each animals tested. Symbols are as in Fig. 1.
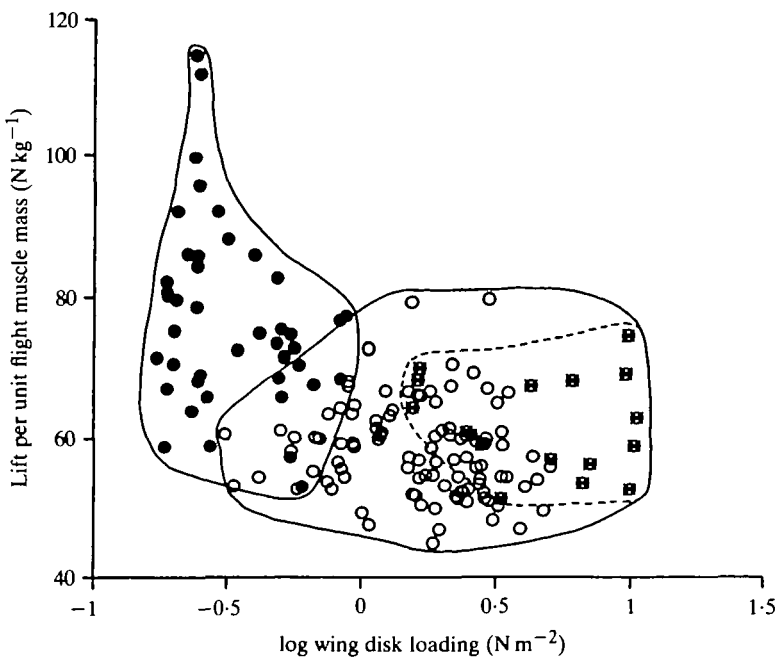

Fig. 3. Maximum muscle mass-specific lift *versus* wing disk loading for each animal tested. Symbols are as in Fig. 1.
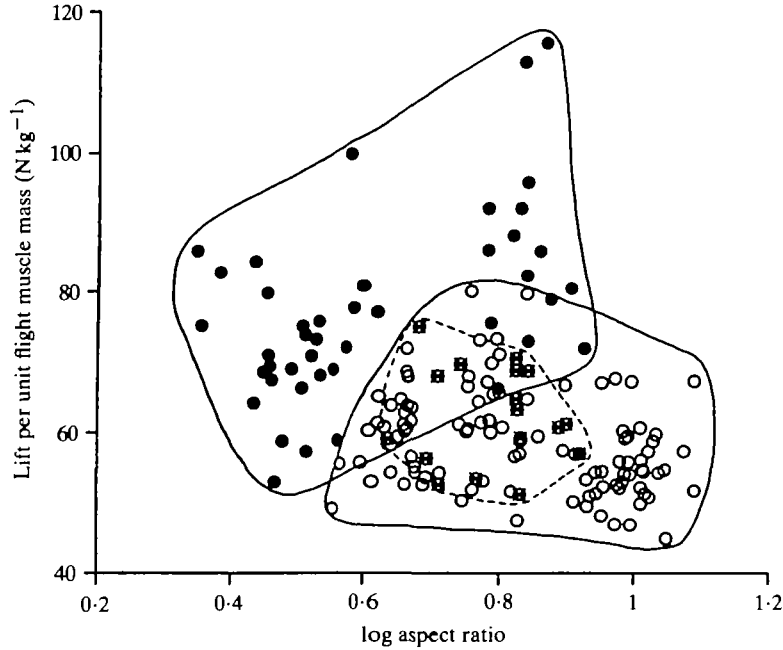
Fig. 4. Maximum muscle mass-specific lift *versus* wing aspect ratio for each animal tested. Symbols are as in Fig. 1.

Table 4. *Coefficients of determination for the multiple regression of all morphological variables, with and without flight muscle ratio,* versus *body mass-specific lift*

Model	Pooled data r^2	Conventional wingbeat r^2	Clap-and-fling wingbeat r^2
All morphological variables	0·689	0·876	0·678
All morphological variables except flight muscle ratio	0·419	0·398	0·478
Flight muscle ratio alone	0·612	0·845	0·530

Also shown are the results using flight muscle ratio alone. Disk loading was omitted here because it is highly correlated with wing loading. Substitution of disk loading for wing loading in the multiple regressions results in a slight decrease in r^2 values.

Effects of body mass

Maximum lift force scaled as the 1·0 power of muscle mass (Fig. 5A,B). Slopes of log–log regressions of maximum lift force *versus* muscle mass did not differ significantly from 1·0 ($P > 0·05$) in any taxonomic group (Table 5; Fig. 5B), and all were significantly greater than 0·67 ($P < 0·01$), the slope predicted if maximum lift force scaled as mass to the two-thirds power. Thus, muscle mass-specific lift did not decrease with increasing body mass.
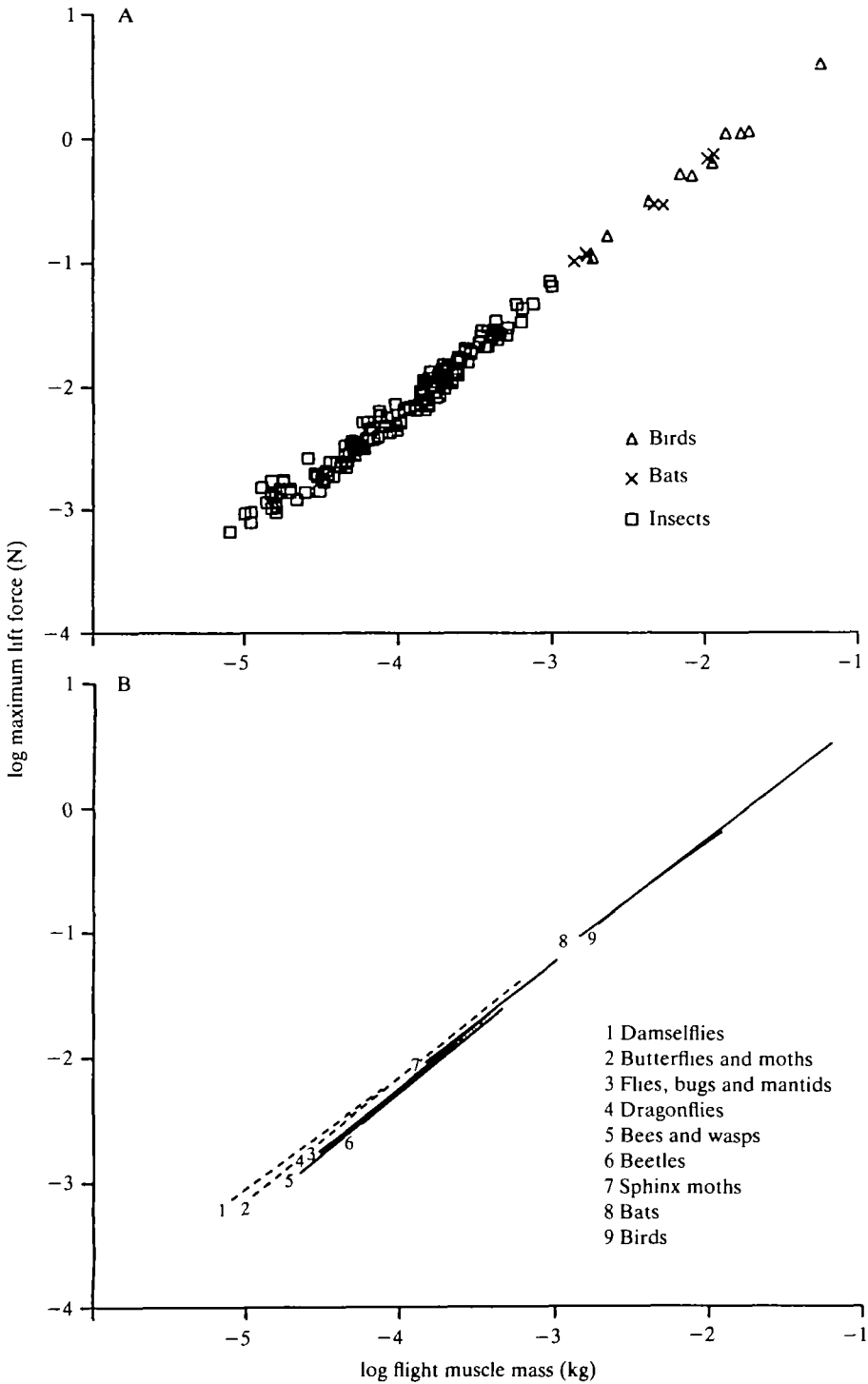
Fig. 5. (A) Scatter plot of maximum lift force *versus* flight muscle mass for each animal tested. (B) Least-squares regression lines for maximum lift force *versus* flight muscle mass in each taxonomic group. Equations for these lines are given in Table 5.

Table 5. *Log–log regressions of flight muscle mass* versus *maximum lift force among each taxonomic group*

Group	Slope	Intercept	r^2	N	Mean lift force ($N kg^{-1}$)
Clap-and-fling wingbeat					
Damselflies	0·91 (0·06)	1·48	0·94	15	86·2 (3·58)
Butterflies and moths	1·00 (0·02)	1·84	0·99	28	72·2 (1·83)
Conventional wingbeat					
Flies, bugs and mantids	0·95 (0·09)	1·58	0·88	16	59·3 (1·72)
Dragonflies	1·03 (0·02)	1·89	0·99	29	59·9 (0·94)
Bees and wasps	1·01 (0·02)	1·76	0·99	33	54·9 (0·92)
Beetles	1·02 (0·03)	1·80	0·99	5	53·9 (1·20)
Sphinx moths	0·97 (0·05)	1·69	0·95	21	63·2 (1·93)
Bats	0·93 (0·04)	1·61	0·99	7	62·3 (2·42)
Birds	0·98 (0·07)	1·76	0·99	10	62·3 (2·40)

Flies, bugs and mantids are grouped together because each had a small sample size and narrow range of flight muscle mass.

Standard errors are shown in parentheses. N is the number of individual animals in each group.

Effects of taxonomic position and wingbeat type

Muscle mass-specific lift showed little variation between taxa (Table 5), ranging from 53·9 to 63·2 N kg^{-1} among conventional wingbeat groups, but increased significantly ($P < 0.001$), by about 25 % (72·2–86·2 N kg^{-1}), among taxa using complete clap-and-fling wingbeats.

Vertebrates considered separately

Birds and bats showed results indistinguishable from conventional wingbeat insects. Body mass-specific lift was positively related to flight muscle ratio (Fig. 1, $r^2 = 0.45$, $P < 0.003$), whereas wing loading, disk loading and aspect ratio had no effect on muscle mass-specific lift (Figs 2–4, $r^2 = 0.03$, 0.02, 0.006, respectively, $P > 0.49$). Average muscle mass-specific lift of vertebrates (62·3 N kg^{-1}) fell within the range of values measured for conventional wingbeat insects (Table 5).

Marginal flight muscle ratios

Table 6 shows a value for each group that I have termed the 'marginal flight muscle ratio'. This quantity is the ratio of flight muscle mass to total mass (body mass plus attached weights) when takeoff ability was marginal, that is the minimal proportion of flight muscle needed for a standing takeoff. Because muscle mass-specific lift was nearly constant, groups of conventional wingbeat fliers also had similar mean marginal flight muscle ratios (0·158–0·183), despite considerable variation in their original (unladen) flight muscle ratios (0·17–0·56). Clap-and-fling wingbeat fliers had lower marginal flight muscle ratios in accordance with their higher lift force per unit flight muscle mass.

Table 6. *Mean marginal flight muscle ratios, and range of unladen flight muscle*
ratios (i.e. prior to attachment of weights) for each taxonomic group

Group	Mean marginal flight muscle ratio	Range unladen flight muscle ratio
Clap-and-fling wingbeat		
Damselflies	0·116	0·291–0·473
Butterflies and moths	0·138	0·249–0·430
Conventional wingbeat		
Flies, bugs and mantids	0·168	0·191–0·396
Dragonflies	0·165	0·351–0·560
Bees and wasps	0·179	0·209–0·401
Beetles	0·183	0·216–0·248
Sphinx moths	0·158	0·170–0·436
Bats	0·159	0·224–0·311
Birds	0·159	0·195–0·331

Effect of altitude

Dragonflies tested at 500 m above sea level achieved significantly less muscle mass-specific lift than dragonflies tested at 20–40 m above sea level ($55\cdot5$ *vs* $59\cdot9$ N kg^{-1}, s.d. = $7\cdot9$, $5\cdot0$; $N = 26$, 29, respectively; Kruskal–Wallis test, $P < 0\cdot05$). This 7 % reduction in muscle mass-specific lift closely corresponds to the 5 % reduction in air density between these two altitudes.

Effect of position of weights

Dragonflies with weights attached to their anterior abdomens did not differ in muscle mass-specific lift from those with posteriorly attached weights ($55\cdot4$ *vs* $55\cdot6$ N kg^{-1}, s.d. = $9\cdot5$, $6\cdot5$; $N = 12$, 14, respectively; $P > 0\cdot5$). Thus, there were no observable differences in lift production brought about by weight attachment position, either within these dragonflies, or among different taxa, where muscle mass-specific lift was nearly constant even though weights were attached in a variety of positions depending on the difficulties presented by the anatomy of each species.

Takeoff angles

Takeoff angles were measured as loads of attached weights were increased for 77 individuals (7 birds, 5 bats and 65 insects). At each weight load, using 1–6 different weight loads per individual (with rest periods between each weight load), I determined the ratio of flight muscle mass to total mass (body mass plus added weights), and compared those ratios to respective takeoff angles (Fig. 6). Within each wingbeat group there was a significant positive relationship between takeoff angle and flight muscle ratio ($P < 0\cdot001$, $r^2 = 0\cdot58$, $0\cdot52$, arcsine-transformed ratios, sine- and square-root-transformed angles). This relationship differed significantly between the two wingbeat groups ($P < 0\cdot001$). The observed decreases in take-off angles with increasing weight loads were not caused by fatigue, for weights frequently came loose and fell off during flights, in which case the animals' flight path
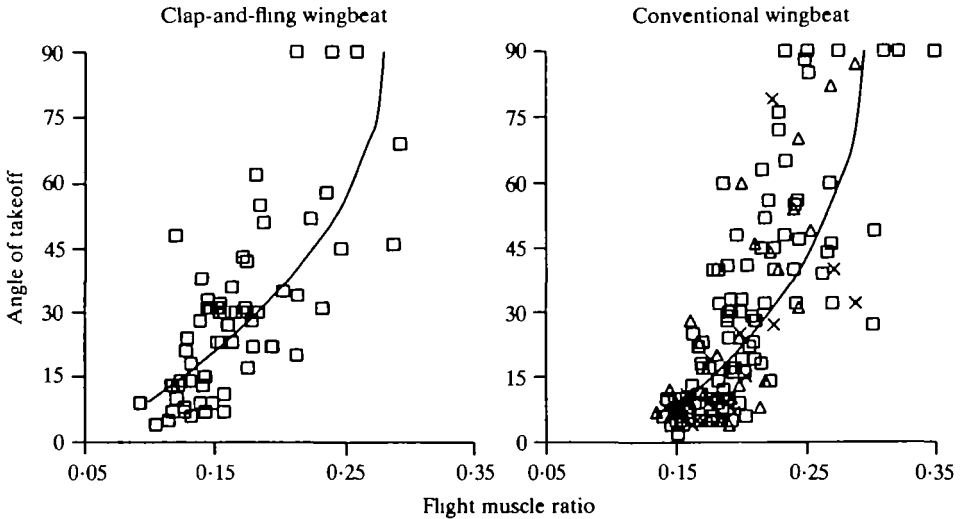
Fig. 6. Takeoff angles as a function of flight muscle ratio. Curves are based on linear regressions of transformed variables (see text). Open squares represent insects, triangles represent birds, and crosses represent bats.

instantly changed and they shot upwards at angles similar to those they achieved prior to weight loading.

Animals with clap-and-fling wingbeats achieved low-angle takeoffs with flight muscle ratios as low as 0·10, and first achieved vertical takeoffs with ratios of about 0·25. The relationship among conventional wingbeat fliers was similar in slope, but shifted to the right. Low-angle takeoffs were possible at muscle ratios as low as 0·15, and vertical takeoffs were first possible at ratios of about 0·26.

DISCUSSION

Lift, power and flight muscle

Takeoff ability was found to depend on flight muscle ratio. Conventional wingbeat fliers with up to 56 % of their unladen body mass composed of flight muscle were capable of vertical takeoffs, and were able to lift up to three times their mass (Fig. 1). Those with less than 20 % flight muscle could take off only at shallow angles (Fig. 6) and could lift very little additional weight (Fig. 1). All conventional wingbeat fliers showed marginal flight ability when weight attachment reduced their flight muscle ratios to 0·16–0·18 (Table 6). This near-constancy of marginal flight muscle ratios occurred because maximum muscle mass-specific lift was nearly constant among all animals with conventional wingbeats (Table 5) and was independent of body mass, wing characteristics and taxonomic position.

Pennycuick (1969, 1972) proposed that maximum power output of flying animals scales as $mass^{2/3}$. To compare the experimental results presented here, which address lift production, with predictions about power output, we must first consider how power output and lift are related during takeoff. To project any object into the air requires that the power applied be proportional to the object's weight, forward

velocity and sine of the angle of flight above horizontal (e.g. Johnson, 1980). Thus, to take off in still air, an animal must achieve an induced power output proportional to its weight, speed and angle of takeoff. Since any animal has a finite amount of induced power it can produce, experimental increases in an animal's weight load should cause progressive decreases in the angle and speed of takeoff, until finally the animal's maximum induced power can only counteract its weight, with no excess power to propel it through the air. As such, results obtained from weight-loading experiments not only measure the maximum lift force developed, but can also serve as an index of the maximum still-air induced power output, provided that takeoff angles and flight velocities approached zero as weight loads were increased. Fig. 6 shows that takeoff angles did indeed approach zero as weight loads were increased (i.e. at low flight muscle ratios). Forward velocity of some animals was never completely reduced to zero (they buzzed along the floor when they could no longer get airborne), which introduces a small amount of error into the results. Even so, the measured maximum lift forces should be an accurate enough index to evaluate general predictions about the scaling of maximum induced power output. Pennycuick's model was not supported, as maximum weight loads scaled as the 1·0 power of muscle mass (Table 5; Fig. 5), rather than the two-thirds power of body mass. The prediction that mass-specific maximum lift and induced power output should scale inversely as the square root of wing disk loading was also rejected (Fig. 3).

Animals of extreme mass and wing loading

These experiments utilized a wide variety of animals between 0·02 and 270 g body mass. Could it be possible that among larger flying animals, with which Pennycuick was largely concerned, the relationships between mass, morphology and lift production are different from those derived here? This question can be examined by using the concept of marginal flight muscle ratios. If muscle mass-specific lift and mass-specific induced power output decrease in larger animals, then they should show higher marginal flight muscle ratios than those found here (0·16–0·18, Table 6). Pennycuick has described the Kori bustard, one of the heaviest extant flying animals (12 kg), as having marginal flight ability. Kori bustards need a taxiing run to take off, and make only short, laboured flights once airborne (Pennycuick, 1969). A Kori bustard that Pennycuick dissected had a flight muscle ratio of 0·164, which would enable only marginal takeoff ability, if that, in any of the birds, bats or conventional wingbeat insects that I studied. Thus, Kori bustards must produce a muscle mass-specific lift similar to that of the smaller animals tested here, or else they could not become airborne at all with a flight muscle ratio of 0·164.

Marginal flight muscle ratios can also be used to determine if muscle mass-specific lift decreases at extreme wing loadings. Wing loading varied from 0·4 to 53·8 N m^{-2} among the animals tested here, whereas wing loading reaches 245 N m^{-2} in some flying animals (Greenewalt, 1975; Livezey & Humphrey, 1985). Livezey & Humphrey (1985) made detailed studies of the flight ability and anatomy of steamer-ducks (Humphrey & Livezey, 1982), and found that one species, *Tachyeres patachonicus* (mean wing loading = 187–222 N m^{-2}), has marginal flight ability,

whereas three other *Tachyeres* species (mean wing loading $= 260$–$487\,\mathrm{N\,m^{-2}}$) are flightless. They concluded that the flightless *Tachyeres* species exceed the maximum wing loading for which flight is feasible. Livezey & Humphrey measured the mass of the pectoral muscles (pectoralis and supracoracoideus), but not total flight muscle mass (which includes a small amount of muscle from the scapula and wing bones), so flight muscle ratios cannot be directly obtained from their data. However, using data for a coot [*Fulica americana*, the bird in Hartman's (1961) study closest to steamer-ducks in wing and body form], I have calculated the mass of wing muscle that each of the four steamer-duck species should have. If the coot's wing area ($562\,\mathrm{cm^2}$) is expanded to the 1000–$1300\,\mathrm{cm^2}$ of steamer-ducks, then its wing muscle mass ($22{\cdot}5\,\mathrm{g}$) should increase to 54–$79\,\mathrm{g}$, based on two-thirds scaling of area and mass. I added these estimates to the measured pectoralis and supracoracoideus masses, then divided by body mass, to yield estimates of flight muscle ratios for Livezey & Humphrey's steamer-ducks. *T. patachonicus* should have a flight muscle ratio of approximately $0{\cdot}201$, whereas the three flightless species should have flight muscle ratios of $0{\cdot}153$–$0{\cdot}173$. A comparison of these ratios with my experimentally determined marginal flight muscle ratios for animals with less extreme wing loadings (Table 6), shows that the flightless species of steamer-ducks have muscle ratios that would make flight impossible, or very nearly so, for any conventional wingbeat animal, regardless of its wing loading. That most *T. patachonicus* can take off and fly with a flight muscle ratio of $0{\cdot}2$ suggests that they generate about $50\,\mathrm{N\,kg^{-1}}$ of muscle mass-specific lift, a value well within the range measured in my experiments (Figs 2–4).

The distribution of flight muscle ratios

The distribution of flight muscle ratios is poorly understood. Greenewalt (1962, 1975) reviewed the scaling of mass of the two large pectoral muscles in birds, but did not consider total flight muscle mass, flight muscle ratio, or interspecific variation in flight muscle ratio. Legal & Reichel (data given in Müllenhoff, 1885) and Hartman (1961) are the only studies to date that measured total flight muscle mass and flight muscle ratio; combined, they measured 425 bird species, but did not analyse their data statistically. Fig. 7 shows the distribution of flight muscle ratios among the birds sampled in those two studies. The marginal flight muscle ratios that I determined experimentally (Table 6, $0{\cdot}16$ for birds in particular) are an excellent predictor of the lower limit of flight muscle ratios seen in birds (Fig. 7). This agreement is a powerful corroboration of these experimental results.

Only 12 of the 425 bird species sampled to date (3%) have flight muscle ratios less than $0{\cdot}16$; they are shown in Table 7. These species generally fit into two broad categories: (1) common, aquatic and semi-aquatic birds (grebes, rails, coots, gallinules) that are obviously very weak fliers, some or all of which require taxiing runs to take off, and (2) reclusive, mostly neotropical birds inhabiting dense foliage, whose flight behaviour is little-known. These birds should be of special interest for future studies, to determine if and how they derive the necessary amount of lift from their relatively small flight musculature.
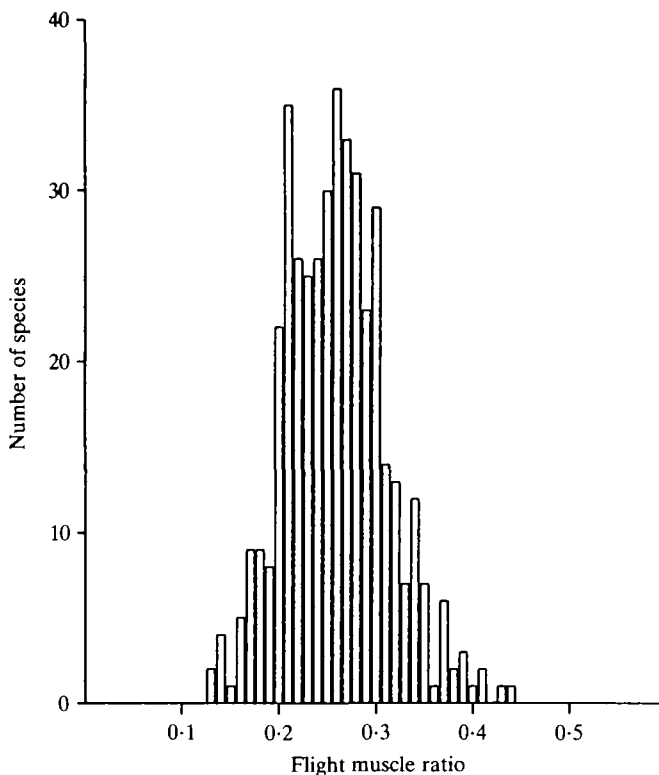
Fig. 7. Frequency distribution of flight muscle ratio among the 425 bird species for which total flight muscle mass has been measured (references given in text) ($\bar{x} = 0\cdot254$, s.d. $= 0\cdot053$, range $= 0\cdot115-0\cdot439$).

Unfortunately, there are no comparable data for flight muscle ratios of either bats or insects. Hartman (1963) measured only the ventral pectoral musculature, not total flight musculature of bats. All previously published values of flight muscle ratios in insects (reviewed in Greenewalt, 1962, 1975) are considerably lower than those of similar insect species I measured here, and are certainly erroneous due to incomplete dissection and/or desiccation during dissection. Bats in particular would be interesting to study in regard to flight muscle ratios because females carry their infants in flight, making weight loading especially important. Some bats are said to be unable to take off from the ground (e.g. Vaughan, 1978), and may have unusually low flight muscle ratios. Presumably, such bats always take off by dropping into the air, and thus avoid the more demanding situation of taking off from the ground in still air.

Wingbeat types

The only variable found to affect muscle mass-specific lift was wingbeat type. Clap-and-fling fliers achieved about 25 % more muscle mass-specific lift on average than did animals with other types of wingbeats. Weis-Fogh (1973) and Ellington (1984) have discussed reasons why clap-and-fling wingbeats should enhance lift.

Table 7. *Bird species from Hartman (1961) and Legal & Reichel (data in Müllen-hoff, 1885) that had flight muscle ratios less than 0·16*

Species	Flight muscle ratio
Podicpes dominicus Least grebe	0·143
Podilymbus podiceps Pie-billed grebe	0·115
Ixobrychus exilis Least bittern	0·139
Aramides cajanea Gray-necked wood rail	0·159
Laterallus albigularis White-throated rail	0·120
Porphyrula martinica Purple gallinule	0·137
Fulica americana American coot	0·135
Piaya cayana Squirrel cuckoo	0·136
Todirostrum cinereum Common tody-flycatcher	0·157
Thryothorus modestus Plain wren	0·157
Larus ridibundus Black-headed gull	0·133

A strictly dichotomous grouping of wingbeat types may be somewhat artificial in that air flow patterns around the wings vary between different clap-and-fling fliers, and conventional wingbeat fliers may also create beneficial unsteady aerodynamic effects between opposite wings (Ellington, 1984). However, variation in wingbeat patterns among the animals I tested appeared to be more discrete than continuous, that is they either had extensive contact between opposite wings, or they had very little contact. The designation of two wingbeat groups in this study simply reflects that fact and explores its consequences. The validity of this dichotomous grouping is best demonstrated by comparing muscle mass-specific lift between damselflies and dragonflies, and between sphinx moths and other Lepidoptera (Table 5). Each of these comparisons is between groups with similar build and taxonomy, but different wingbeat types, and shows a consistent effect of wing contact in enhancing lift when other variables are held fairly constant.

One animal that was difficult to classify in this scheme was the pigeon. During takeoff, pigeons' wings make an audible clap at both extremes of the wing stroke. However, the pigeon tested here achieved a muscle mass-specific lift of $63 \cdot 2 \, \text{N kg}^{-1}$, nearly identical to the mean value for birds ($62 \cdot 3 \, \text{N kg}^{-1}$, Table 5). I grouped the pigeon with conventional wingbeat fliers to avoid breaking up the grouping scheme, and because it did not show enhanced lift. Why this pigeon failed to achieve more lift

is unclear, but it is possible that pigeons do generally achieve enhanced lift and that my small sample of one pigeon failed to detect it.

Another group of animals with an ambiguous wingbeat pattern was the hesperiid butterflies (skippers), whose opposite forewings appeared to come into contact from about midway along their length to their tip, rather than from base to tip as did wings of other clap-and-fling insects. The two hesperiids tested here achieved 68·8 and 68·0 N kg^{-1} of lift, values about halfway between the mean for butterflies (72 N kg^{-1}) and the mean for conventional wingbeat fliers (59 N kg^{-1}). This result, although based on a very small sample, indicates that the extent of wing contact may determine how much lift enhancement occurs. Ellington (1984) predicted that partial clap-and-fling wingbeats should yield partial lift enhancement.

Implications about flight mechanics

It is tempting, but risky, to try to ascertain what the results presented here indicate about finer details of the mechanics of animal flight in still air. Near-constancy of maximum still-air muscle mass-specific lift and induced power output may indicate that the animals had equal muscle mass-specific power output (as has frequently been assumed, e.g. Weis-Fogh & Alexander, 1977; 250 W kg^{-1}), of which a constant fraction was required for inertial and profile power. However, and perhaps more likely, these power components may have varied among animals, but in such a way that increases in muscular power output were offset by increased inertial or profile power requirements, so that mass-specific induced power output remained fairly constant.

The prediction that maximum mass-specific induced power output should scale inversely as the square root of wing disk loading (see earlier references) was based on the assumption that longer wings accelerate a given mass of air through the wing disk at a lower velocity than shorter wings, creating an energetic saving. This model holds true for propellers and helicopters (e.g. Johnson, 1980), for which the model was originally derived. However, in applying the model to animal flight, adequate consideration has not been given to the fact that animal wings use oscillatory rather than circular motion. Because of this difference, animals experience large inertial costs of accelerating and decelerating their wings (e.g. Casey, 1981), especially during hovering and takeoff when wingbeat amplitude is maximal. Thus, even though shorter wings necessitate a greater induced velocity to achieve a given mass flow of air, they may be less expensive to beat. My observation that muscle mass-specific lift was independent of wing and disk loading may indicate that the cost/benefit relationship between inertial power and induced power may be nearly constant over a broad range of wing sizes.

A fascinating result from these experiments is that insects, birds and bats achieved nearly identical muscle mass-specific lift, despite their tremendous physiological differences. Detailed physiological studies will be necessary to determine the proximate causes of this constancy. The ultimate reason for this constancy is probably that the evolution of flying animals has converged on the maximum

obtainable lift and aerodynamic power production per unit muscle mass. This convergence in performance has not necessitated convergence in morphology; the tremendous morphological diversity of flying animals represents a great variety of ways in which different animals have achieved the best solution to the common problem of producing lift in still air, while maintaining specializations for their other modes of flight.

It is curious that all animals do not use clap-and-fling wingbeats, which enhance still-air lift production by about 25 %. The reason for this may be that animals with clap-and-fling wingbeats are at a relative disadvantage in some aspect of flight performance not measured in this study. For example, clap-and-fling fliers may achieve lower maximum forward speed due to excessive drag on their large flat wings.

Limitations to these findings

Results and conclusions from these experiments cannot be generalized to all flight situations. In forward flight, drag on the wings becomes an important consideration, and wings of different sizes and shapes experience different drag forces. In forward flight, wingbeat amplitude decreases and the inertial cost of beating the wings may become relatively unimportant, making longer wings advantageous for lift, production and induced power output.

Power requirements for horizontal flight are a U-shaped function of forward speed (Pennycuick, 1968; Tucker, 1968; Carpenter, 1985), so steady forward flight can be accomplished at a fraction of the animal's maximum power output capability. Presumably, animals with high flight muscle ratios recruit only a fraction of their muscle fibres during steady forward flight. Thus, a high flight muscle ratio is of no advantage during flight at the minimum power or maximum range speed, and in fact can be considered a disadvantage, for it should be more beneficial for animals to transport non-muscular loads (such as eggs, 'fuel', water, etc.) from one place to another, rather than excess, mostly unused muscle. High flight muscle ratios should occur in animals that frequently need maximum power output for lifting loads, capturing prey, avoiding predators or competing aerially for territories and mates.

The experimental technique used here required that animals briefly lift attached weight loads, and no attention was given to how long they could sustain such flights. It is possible that additional variation in muscle mass-specific lift could be explained by variation in the fractional myofibrillar content of muscle. Animals with lower fractional mitochondrial volumes in their flight muscles, primarily using anaerobic metabolism, may have achieved more muscle mass-specific lift because they had more myofibrils per unit muscle mass. I am currently testing this hypothesis.

Morphology and lift data for each animal tested

Taxon	Body mass (g)	Flight muscle mass (g)	Wing area (cm²)	Wing span (cm)	Maximum lift force (N×10²)
BIRDS					
Passer domesticus (House sparrow)	33	7·1	80	21	49·2
Columba livia (Pigeon)	267	59·0	486	57	372·9
Chiroxiphia lanceolata (Lance-tailed manakin)	17	4·4	99	23	29·9
Spinus psaltria (Dark-backed goldfinch)	11	2·3	32	15	15·8
Amazilia tzacatl (Rufous-tailed hummingbird)	6	1·8	17	12	10·5
Melanerpes rubricapillus (Red-crowned woodpecker)	45	11·4	112	24	60·1
Mimus gilvus (Tropical mockingbird)	71	13·9	197	31	103·9
Turdus grayi (Clay-coloured robin)	65	17·6	188	28	103·9
Turdus grayi (Clay-coloured robin)	67	19·9	221	36	106·8
Thraupis episcopus (Blue-gray tanager)	29	8·4	108	23	47·6
BATS					
Artibeus watsoni	15	4·7	102	26	27·9
Artibeus watsoni	18	5·4	102	26	27·8
Artibeus jamaicensis	41	10·6	266	46	64·9
Artibeus jamaicensis	45	11·6	293	48	70·6
Micronycteris megalotis	6	1·7	73	22	11·0
Micronycteris megalotis	6	1·7	73	22	11·4
Micronycteris megalotis	6	1·4	73	22	9·9
INSECTS					
Lepidoptera					
Danaidae					
Danaus plexippus	0·417	0·146	32	10	1·1
Danaus plexippus	0·526	0·191	35	11	1·4
Danaus plexippus	0·544	0·196	40	11	1·5
Danaus plexippus	0·509	0·200	37	11	1·1
Danaus plexippus	0·422	0·152	33	10	1·0
Pieridae					
Pieris rapae	0·043	0·017	10	5	0·14
Pieris rapae	0·052	0·020	10	5	0·14
Pieris rapae	0·033	0·011	8	5	0·08
Pieris rapae	0·042	0·016	8	5	0·13
Pieris rapae	0·039	0·016	9	5	0·09
Pieris rapae	0·049	0·016	9	5	0·11

Morphology and lift data for each animal tested

Taxon	Body mass (g)	Flight muscle mass (g)	Wing area (cm^2)	Wing span (cm)	Maximum lift force (N$\times10^2$)
Pieris rapae	0·037	0·015	9	5	0·10
Pieris rapae	0·042	0·016	9	5	0·10
Phoebis argante	0·184	0·077	25	8	0·58
Phoebis argante	0·202	0·075	22	7	0·62
Nymphalidae					
Heliconius cydno	0·154	0·048	20	9	0·28
Heliconius erato	0·053	0·014	9	6	0·11
Heliconius erato	0·105	0·026	15	8	0·26
Parides sesostris	0·314	0·096	26	9	0·71
Papilionidae					
Papilio sp.	0·149	0·059	21	7	0·51
Hesperiidae					
Unidentified sp. 1	0·115	0·049	7	5	0·33
Unidentified sp. 2	0·184	0·065	8	5	0·45
Lycaenidae					
Unidentified sp.	0·200	0·078	15	7	0·41
Noctuidae					
Ascalapha odorata	1·32	0·428	50	14	3·32
Ascalapha odorata	1·72	0·586	64	16	4·50
Saturniidae					
Rothschildia lebeau	0·930	0·270	78	16	1·86
Rothschildia lebeau	1·26	0·342	86	17	2·50
Titaea tamerlan	1·31	0·380	87	18	2·73
Sphingidae					
Xylophanes tersa	0·403	0·143	8	7	0·84
Xylophanes tersa	0·410	0·146	8	8	0·87
Xylophanes tersa	0·711	0·162	9	8	1·29
Xylophanes sp. 1	0·905	0·294	15	9	1·89
Xylophanes sp. 2	0·470	0·144	8	7	0·86
Xylophanes sp. 2	0·529	0·182	9	7	1·22
Xylophanes sp. 2	0·552	0·199	10	8	0·95
Manduca sp.	1·87	0·628	27	12	3·26
Pachylia ficus	1·93	0·637	21	11	4·17
Pachylia ficus	4·57	0·976	37	15	6·80
Enyo sp.	1·17	0·294	8	7	1·80
Agrius cingulatus	1·69	0·416	18	10	2·82
Unidentified sp. 1	0·829	0·271	16	10	1·98
Unidentified sp. 2	1·16	0·505	16	9	2·54
Unidentified sp. 2	2·23	0·753	27	12	4·56
Unidentified sp. 2	3·18	1·010	31	14	6·23
Unidentified sp. 3	1·40	0·512	12	9	2·92
Unidentified sp. 3	1·47	0·439	15	10	2·34
Unidentified sp. 3	2·04	0·347	15	9	2·77
Unidentified sp. 4	0·921	0·332	12	8	2·21
Unidentified sp. 5	0·573	0·157	12	8	1·14
Odonata					
Anisoptera					
Sympetrum sp. 1	0·074	0·030	7	6	0·18
Sympetrum sp. 1	0·123	0·069	6	5	0·36
Sympetrum sp. 1	0·092	0·035	6	5	0·19

Morphology and lift data for each animal tested

Taxon	Body mass (g)	Flight muscle mass (g)	Wing area (cm²)	Wing span (cm)	Maximum lift force (N×10²)
Sympetrum sp. 1	0·121	0·048	6	5	0·28
Sympetrum sp. 1	0·125	0·062	7	5	0·37
Sympetrum sp. 1	0·080	0·033	7	6	0·18
Sympetrum sp. 1	0·111	0·045	7	5	0·28
Anax junius	0·913	0·397	22	10	2·45
Anax junius	0·955	0·400	23	10	2·44
Anax junius	0·945	0·416	23	10	2·61
Anax junius	0·980	0·420	23	10	2·54
Anax junius	1·083	0·411	23	10	2·61
Aeshna canadensis	0·612	0·243	20	9	1·58
Aeshna canadensis	0·600	0·253	19	9	1·61
Aeshna canadensis	0·605	0·212	19	9	1·44
Aeshna canadensis	0·605	0·245	19	9	1·68
Aeshna sp.	0·357	0·180	15	8	0·99
Libellula pulchella	0·422	0·223	19	9	1·20
Libellula pulchella	0·513	0·281	16	9	1·53
Libellula pulchella	0·463	0·238	16	9	1·35
Libellula pulchella	0·556	0·198	12	7	1·11
Libellula pulchella	0·407	0·202	15	8	1·29
Libellula pulchella	0·364	0·192	15	8	1·16
Libellula pulchella	0·473	0·240	16	9	1·55
Libellula pulchella	0·386	0·197	16	8	1·18
Libellula pulchella	0·399	0·199	14	8	1·05
Libellula pulchella	0·536	0·282	15	9	1·53
Libellula pulchella	0·431	0·228	15	8	1·35
Libellula sp.	0·320	0·150	17	9	1·07
Zygoptera					
Megaloptera sp.	0·233	0·076	24	12	0·57
Mecistogaster sp. 1	0·149	0·045	13	10	0·32
Mecistogaster sp. 1	0·217	0·063	18	12	0·51
Argia chelata	0·037	0·017	3	4	0·15
Argia chelata	0·035	0·016	3	4	0·11
Argia chelata	0·024	0·011	2	4	0·09
Argia chelata	0·022	0·010	2	4	0·09
Argia chelata	0·030	0·013	2	4	0·15
Argia chelata	0·039	0·018	3	5	0·17
Argia chelata	0·046	0·015	3	4	0·13
Argia chelata	0·035	0·016	2	4	0·13
Argia chelata	0·019	0·008	2	4	0·07
Argia chelata	0·042	0·018	3	4	0·17
Argia chelata	0·055	0·020	3	5	0·15
Argia chelata	0·036	0·015	3	4	0·17
Hymenoptera					
Sphecidae					
Pepsis sp. 1	0·449	0·118	5	6	0·67
Pepsis sp. 1	0·598	0·139	7	7	0·90

Morphology and lift data for each animal tested

Taxon	Body mass (g)	Flight muscle mass (g)	Wing area (cm^2)	Wing span (cm)	Maximum lift force (N×10^2)
Apidae					
Bombus affinis	0·150	0·045	0·8	3	0·27
Bombus affinis	0·098	0·032	0·6	3	0·18
Bombus affinis	0·141	0·043	0·7	3	0·24
Bombus affinis	0·151	0·042	0·7	3	0·22
Bombus affinis	0·091	0·031	0·6	3	0·14
Bombus affinis	0·172	0·036	0·7	3	0·24
Bombus affinis	0·100	0·033	0·7	3	0·16
Bombus affinis	0·141	0·034	0·6	3	0·20
Bombus affinis	0·078	0·025	0·6	2	0·14
Bombus affinis	0·074	0·022	0·5	2	0·12
Bombus fervidus	0·182	0·060	0·9	3	0·31
Bombus fervidus	0·164	0·047	0·8	3	0·24
Bombus fervidus	0·169	0·052	0·8	3	0·28
Bombus fervidus	0·209	0·058	0·9	3	0·33
Bombus fervidus	0·173	0·053	0·9	3	0·30
Bombus fervidus	0·151	0·045	0·8	3	0·23
Bombus fervidus	0·144	0·046	0·9	3	0·24
Bombus fervidus	0·129	0·046	0·9	3	0·22
Bombus terricola	0·142	0·040	0·7	3	0·24
Xylocopa veripuncta	0·517	0·170	2·4	5	1·01
Xylocopa veripuncta	0·574	0·230	2·7	5	1·37
Xylocopa veripuncta	0·578	0·162	2·3	5	0·96
Xylocopa veripuncta	0·793	0·234	2·6	5	1·24
Xylocopa veripuncta	0·362	0·137	1·9	4	0·72
Xylocopa veripuncta	0·428	0·172	2·1	5	0·87
Xylocopa veripuncta	0·704	0·222	2·5	5	1·04
Xylocopa veripuncta	0·480	0·141	1·8	4	0·77
Xylocopa veripuncta	0·854	0·243	2·7	5	1·20
Xylocopa veripuncta	0·435	0·163	2·4	5	0·87
Xylocopa sp. 1	1·26	0·380	3·7	6	2·05
Xylocopa sp. 1	1·41	0·363	3·8	6	2·03
Coleoptera					
Scarabaeidae					
Dichotomius carolinus	2·11	0·455	8·0	8	2·62
Curculionidae					
Unidentified sp. 1	0·259	0·056	1·6	4	0·31
Unidentified sp. 1	0·297	0·074	1·6	4	0·39
Unidentified sp. 1	0·575	0·127	2·4	5	0·69
Unidentified sp. 2	0·880	0·206	4·3	6	1·03
Hemiptera					
Pentatomidae					
Unidentified sp.	0·442	0·084	2·9	4	0·55
Lygaeidae					
Unidentified sp. 1	0·171	0·051	1·8	3	0·31
Unidentified sp. 1	0·225	0·062	2·2	4	0·37
Unidentified sp. 1	0·205	0·055	1·9	4	0·33

Morphology and lift data for each animal tested

Taxon	Body mass (g)	Flight muscle mass (g)	Wing area (cm²)	Wing span (cm)	Maximum lift force (N×10²)
Unidentified sp. 1	0·208	0·050	2·0	4	0·35
Unidentified sp. 1	0·192	0·052	1·7	3	0·27
Unidentified sp. 1	0·195	0·052	1·9	4	0·30
Unidentified sp. 2	0·138	0·029	1·4	3	0·19
Diptera					
Asilidae					
Unidentified sp. 1	0·173	0·065	1·0	4	0·44
Unidentified sp. 1	0·179	0·068	1·5	4	0·46
Unidentified sp. 1	0·200	0·073	1·3	4	0·38
Unidentified sp. 1	0·208	0·082	1·5	4	0·47
Unidentified sp. 1	0·276	0·109	1·8	4	0·64
Syrphidae					
Unidentified sp.	0·117	0·038	0·5	2	0·18
Orthoptera					
Mantidae					
Tenodera aridifolia	0·305	0·064	13	7	0·36
Tenodera aridifolia	0·387	0·096	14	7	0·47

The units of measure have been changed from the SI units used in the text in order to minimize zeros. These values have been rounded off and do not yield statistical values given in the text.

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