either by changing the velocity at which their wings translate during each half stroke, which depends on stroke amplitude, stroke frequency and on alterations in lift coefficients during wing translation, or by changes in rotational circulation and wake capture at the end of each half stroke when the wings quickly rotate around their longitudinal axes (Dickinson et al., 1999; Ellington, 1984d; 1995; Ellington et al., 1996; Lehmann, 2000; Maxworthy, 1979; Nachtigall, 1979; Sane and Dickinson, 2001; Willmott et al., 1996). The production and control of aerodynamic forces, however, is also potentially limited by the fluid mechanical properties of the surrounding air and thus on Reynolds number that may change when an insect increases or decreases in body size.

Introduction

The limits of aerial performance in a flying insect are determined by a large variety of different factors including the ability of the flapping wings to produce aerodynamic lift. Although aerodynamic mechanisms may explain how insects stay in the air, they cannot alone explain the aerodynamics of flight behavior in these animals. Many insects must perform elaborate aerial maneuvers in order to avoid predators, feed, secure territories and mate. Even in less-elaborated forms of flapping flight, insects must modulate their flight forces to maintain maneuverability and flight stability during take off and landing. Insects can achieve these alterations in aerodynamic lift production either by changing the velocity at which their wings translate during each half stroke, which depends on stroke amplitude, stroke frequency and on alterations in lift coefficients during wing translation, or by changes in rotational circulation and wake capture at the end of each half stroke when the wings quickly rotate around their longitudinal axes (Dickinson et al., 1999; Ellington, 1984d; 1995; Ellington et al., 1996; Lehmann, 2000; Maxworthy, 1979; Nachtigall, 1979; Sane and Dickinson, 2001; Willmott et al., 1996). The production and control of aerodynamic forces, however, is also potentially limited by the fluid mechanical properties of the surrounding air and thus on Reynolds number that may change when an insect increases or decreases in body size.
Although the effect of Reynolds number on aerodynamic performance should be minimal in large flying animals, the case may be different in small animals such as fruit flies *Drosophila* with body masses ranging from 0.5 to 4.5 mg that fly in an intermediate Reynolds number domain ranging from approximately 50 to a several hundred. Small insects face a tremendous drag on both their body during forward motion and the moving wings due to the increase in viscous forces with decreasing Reynolds number. Viscous drag, also known as skin friction, is responsible for the steep increase in total wing drag at Reynolds numbers below 100 (Fig. 1A). Low Reynolds number during flight has two effects. First, high viscous forces in the fluid act against any acceleration of the fluid produced by the flapping wings. Thus fluid viscosity attenuates the development of aerodynamic net circulation and thus lowers the production of aerodynamic lift. Second, due to high viscosity the energetic costs to overcome the drag on the wings are large and insects that fly at lower Reynolds numbers should spend more mass specific energy on wing motion than their larger relatives. Smaller insects could cope with these constraints by reducing their flight costs which can be achieved either by (i) an increase in muscle efficiency, (ii) an increase in aerodynamic efficiency, in cases in which inertial power requirements for flight exceed aerodynamic power expenditures, (iii) employing elastic energy storage or (iv) reducing induced power requirements by decreasing stroke frequency while increasing stroke amplitude (Fig. 2, Lehmann, 2001). In small flies these potential alterations may compensate for the relative increase in viscous forces in order to maintain high flight performance within the entire range of intermediate Reynolds numbers.

To investigate how vital flight parameters such as flight power requirements, muscle and aerodynamic efficiency change with body size and thus Reynolds number, we have flown four different species of fruit flies *D. nikananu* Burly (*N* = 10), *D. melanogaster* Meigen (*N* = 27), *D. viridis* Sturtevant (*N* = 10) and *D. mimica* Hardy (*N* = 3) with mean body masses of 0.65 ± 0.06, 1.05 ± 0.13, 1.9 ± 0.19 and 3.25 ± 0.51 mg (means ± S.D.), respectively, while the tethered insects produced flight forces that were equal to their own body masses (hovering conditions). The coefficient was calculated using conventional aerodynamic theory that lumps all circulatory mechanisms during flight (wing translation, wing rotation, wake capture) into a single value.

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**Fig. 1.** Force coefficients in biofoils change with Reynolds number. (A) Drag estimates on wings steeply increase at Reynolds numbers below 100. $C_{D_{\text{pro}}} = \frac{C_{D_{\text{pres}}} = C_{D_{\text{pro}}} + C_{D_{\text{sf}}}}{\sqrt{\text{Re}}}$. (B) Lift coefficient for wing translation increases with increasing Reynolds number. Data were measured in a 3-dimensional robotic wing moving on an average trajectory as described elsewhere (160 deg stroke amplitude, 45 deg angle of attack, Dickinson et al., 1999). (C) Mean force coefficient in flight of four species of fruit flies *D. nikanana* Burly (*N* = 10), *D. melanogaster* Meigen (*N* = 27), *D. viridis* Sturtevant (*N* = 10) and *D. mimica* Hardy (*N* = 3) with mean body masses of 0.65 ± 0.06, 1.05 ± 0.13, 1.9 ± 0.19 and 3.25 ± 0.51 mg (means ± S.D.), respectively, while the tethered insects produced flight forces that were equal to their own body masses (hovering conditions). The coefficient was calculated using conventional aerodynamic theory that lumps all circulatory mechanisms during flight (wing translation, wing rotation, wake capture) into a single value.
Scaling of aerodynamic performance

The dimensionless Reynolds number characterizes the flow of a fluid around an object and is defined as the ratio between inertial and viscous forces within the fluid. Inertial forces can be directly derived from Newton’s second law and are due to the momentum of a fluid volume that has been accelerated by the moving wings. In real fluids such as air, however, viscous forces will oppose the persistence of fluid motion and act against any alterations in fluid velocity. In flapping insect flight, Reynolds number is derived conventionally by the product of wing tip velocity, $u_t$, and mean chord of the flapping wing, $c$, divided by the kinematic viscosity of the fluid. Kinematic viscosity, $\nu$, is given by the dynamic viscosity of the fluid divided by its density (Ellington, 1984c). Thus Reynolds number, $Re$, can be written as:

$$Re = \frac{u_t c}{\nu}.$$  (1)

Wing tip velocity, in turn, depends on the product between mean stroke amplitude, $\Phi$, that characterizes the angle between the ventral and dorsal excursion of the wing within each stroke cycle, stroke frequency, $n$, and total wing length, $R$, defined as the distance between the wing base and the tip of the wing. Replacing wing tip velocity in equation 1 by these parameters, Reynolds number then yields:

$$Re = 2 \Phi n R c \nu^{-1}.$$  (2)

In contrast, the gross effects of body size on force production can be assessed by considering a conventional aerodynamic model, in which all circulatory mechanisms are lumped into a mean force coefficient, $C_f$ (Ellington, 1984c; Weis-Fogh, 1973). The mean force coefficient is a simple measure on how much aerodynamic circulation a wing produces when it sweeps through the fluid at a certain speed. According again to Newton’s second law, force production of a single wing, $F_t$, is thus proportional to the product between mean force coefficient, the fluid density, wing velocity squared and wing area and can be written as:

$$F_t = \frac{1}{2} \rho C_f^v (2 \Phi n R)^2 R e.$$  (3)

For an isometric group of animals, wing or body length is proportional to any linear dimension, $L$, and during hovering conditions flight forces are equal to the weight of the animal. Thus by replacing mean wing chord, $c$, and wing length, $R$, by $L$ and by incorporating equation 2 into equation 3 the above relationship can be reduced to:

$$C_f^v \propto R^{-0.5}. $$  (4)

Equation 4 suggests that in order for an animal to support its body weight at all sizes, mean force coefficient must scale with $L^{-1}$ or with the inverse square root of Reynolds number assuming that the product between stroke amplitude and stroke frequency is similar within the tested group of animals. We tested this prediction by comparing the mean force coefficient among four species of fruit flies: $D. nikanana$, $D. melanogaster$, $D. virilis$ and $D. mimic a$ covering mean Reynolds numbers from approximately 70 to 270. In a previous analysis, we have already shown that Reynolds number for wing motion linearly depends on body size in these four species of flies ($Re = 54.8 + 78.7x$, $r^2 = 0.91$, $P < 0.001$, Lehmann and Dickinson, 1998).

As shown in Fig. 1C, the smallest species of fruit flies $D. nikanana$ fly at Reynolds numbers ranging from 70 to approximately 100. In this domain of intermediate Reynolds numbers, the mean force coefficient for aerodynamic lift production measured at a flight force that balances the animal’s body weight, varies between approximately 1.7 and 2.7. These values are 2–3 times higher than the steady-state value for Drosophila wings of roughly 0.8 that was measured in a 2-dimensional wind tunnel indicating that non-steady state aerodynamic mechanisms are involved in the generation of flight force (Zanker and Götz, 1990). Recent data suggest that a prominent leading edge vortex during the up and down stroke (Ellington et al., 1996), circulation due to wing rotation and wake capture (Dickinson et al., 1999) are likely to be the primary mechanisms for this phenomenon. Mean force coefficient in the two larger species $D. virilis$ and $D. mimic a$ amounts to values ranging from 1.0 to 1.5 that were measured at Reynolds numbers between approximately 200 and 260 suggesting a two-fold difference in aerodynamic circulation between the smallest and the largest species (Fig. 1C). The mean force coefficient for $D. melanogaster$ lies somewhere between both extremes.

The previous paragraph has indicated that aerodynamic performance in tethered flying fruit flies increases with decreasing Reynolds number. Surprisingly this result runs counter to predictions of both 2-dimensional aerodynamic theory based on Reynolds number and results derived from direct force measurements in a dynamically-scaled robotic wing during 3-dimensional wing translation at which the velocity of each wing blade element is increasing with increasing distance to the wing hinge (Ellington, 1984a,b; Dickinson et al., 1999). Figure 1B shows the small but significant decrease in translational lift coefficient, $C_l$, of the 3-dimensional robotic wing with decreasing Reynolds number, which agrees with
aerodynamic theory of viscous fluids (linear regression fit, \( C_L = 1.92 + 4.6 \times 10^{-5} Re, r^2 = 0.75, P < 0.0001, N = 16 \)). However, if the production of translational circulation due to conventional and leading edge vorticity can not explain the high force coefficients in small fruit flies, how do small animals increase their aerodynamic performance compared to their larger relatives? It might be that rotational circulation or wake capture contribute more relative lift at low Reynolds number due to the higher fluid viscosity stabilizing vortex shedding. However, measurements in the robotic wing suggest that even total lift coefficients based on translational and rotational aerodynamic mechanisms (rotational circulation and wake capture) tend to decrease with decreasing Reynolds number (data not shown). Thus we may exclude the possibility that an increase in efficiency of rotational mechanisms can explain the increase in total force coefficient in small fruit flies. Two alternatives remain to justify this discrepancy. First, smaller fruit flies might use different stroke kinematics (excluding stroke amplitude and stroke frequency) that produce higher force coefficients. For example, it has been shown that higher rotational speeds and an advanced timing of wing rotation at the end of each half stroke may enhance flight forces and thus total lift coefficient (Sane and Dickinson, 2001). These parameters are not covered by conventional aerodynamic theory and potentially are powerful enough to explain part of the measured increase in \( C_L \) with decreasing body size. However, assuming that smaller fruit flies increase their force coefficients during flight by more ‘efficient’ kinematic maneuvers during wing rotation or by alterations in their wing velocity profile during the up and down stroke, it remains the question why larger fruit flies do not use the same kinematic strategies? The answer to this puzzling problem might lie in other constraints (or mechanisms) on aerodynamic force production such as force enhancement by wing-wing interaction, which potentially favors high force production in small species of fruit flies.

**Scaling of flight power requirements and muscle efficiency**

In flapping flight, the mechanical power output of the flight muscle must support at least three different requirements: inertial, profile and induced power assuming hovering conditions (Fig. 2, Casey and Ellington, 1989). Inertial power, \( P_{\text{acc}} \), is needed to accelerate real and virtual mass of the wing for each
stroke and is equal to the kinetic energy of the wings at mid-stroke divided by the quarter-stroke acceleration period (Ellington, 1984c). The virtual wing mass is the mass of the fluid cylinder around the wing that varies with aerodynamic circulation. Wing inertia also depends on wing shape and the wing tip trajectory with respect to time during the stroke. Wings that move sinusoidal, for example, produce 1.37-fold higher inertial costs compared to wings moving on a saw tooth trajectory at the same cycling frequency (Lehmann and Dickinson, 1998). Mean inertial costs depend on stroke amplitude and stroke frequency, squared respectively. In contrast to inertial power, wing aerodynamic power represents the costs that are associated with the aerodynamic mechanisms acting on the beating wing (Ellington, 1984c). The aerodynamic costs for flight are thus composed of induced power and profile power.

Profile power, \( P_{\text{pro}} \), is determined by the product of profile drag and the velocity of the wing in the relative stroke plane which is defined as the plane parallel to the shed vortex loops and perpendicular to the axis of the wake. Conventional profile drag is typically estimated from the instantaneous linear velocity of the wing during the up- and down stroke assuming quasi-steady flow conditions. This approach, however, ignores any contribution of drag that results from unsteady aerodynamic mechanisms such as delayed stall and rotational circulation and is thus thought to represent a lower estimate of total wing drag. Moreover, profile drag depends on pressure drag and skin friction (Fig. 1A). The relative contribution of skin friction to profile drag increases with increasing viscosity of the fluid so that the mean profile drag coefficient is typically given as a function of mean Reynolds number or mean wing tip velocity (\( C_D = 7 \text{Re}^{-0.5} \), Ellington, 1984c). However, force measurements in the dynamically-scaled robotic wing suggest that in the fruit fly \textit{D. melanogaster} (\( \text{Re} = 134 \)) mean profile drag might be 3.5 times higher than the value based on Reynolds number (Dickinson et al., 1999). Thus in this study, we derived \( C_D \) as the product between both values that gave 3.5 times higher profile power requirements in flight than using Ellington’s conservative approach.

Induced power, \( P_{\text{ind}} \), is the cost to generate an air momentum that keeps the insect airborne. This measure can be derived as the product between the Rankine-Froude estimate for induced power and a factor that characterizes temporal and spatial corrections for the wake periodicity and circulation profile during the stroke, respectively (Ellington, 1984c). Rankine-Froude power is equal to the minimum power requirements for flight and can be derived from the product between momentum flux and the fluid velocity within the wake. Mean induced power depends on the product between stroke amplitude raised to the power of 2.5 and the cube of stroke
frequency. Aerodynamic power requirements for flapping flight, however, are not simply the sum of induced, profile and inertial power (Fig. 2). In cases in which inertial costs exceed the sum of induced and profile power, insects may reduce total flight costs by elastically storing kinetic energy of the moving wings during the second part of each half stroke (Dickinson and Lighton, 1995). The inertial energy yielded by wing deceleration at the end of each half stroke can then be released during the first part of the following half stroke when the wings are accelerated from rest.

Figure 3A shows, however, that this seems not to be the case in different sized fruit flies. Assuming an increase in drag coefficient by a factor of 3.5 compared to the conventional estimate as suggested by Ellington (1984c), muscle mass specific profile power exceeds inertial power in all four species during hovering flight. Under these conditions no elastic energy storage is required to minimize flight costs because inertial costs can serve as a power source to overcome profile power at the end of each half stroke. While muscle mass specific induced power tends to increase only slightly with increasing body mass, \( m_b (P_{\text{ind}}^*= 21.4 m_b^{0.035}, r^2 = 0.09, P = 0.03, N = 50, \text{Fig. 3A}) \), inertial power estimates increase more steeply \( (P_{\text{acc}}^* = 60.3 m_b^{0.48}, r^2 = 0.41, P < 0.0001, \text{Fig. 3A}) \). Due to the small scaling exponent of profile power \( (P_{\text{pro}}^* = 120 m_b^{0.20}, r^2 = 0.16, P = 0.004, \text{Fig. 3A}) \) compared to inertial power, aerodynamic power requirements (the sum between induced and profile power) and inertial power requirements are thought to be equal when body weight of the insect reaches approximately 4 kg.

Although this estimate is based on fruit fly kinematics, it might imply that elastic energy storage cannot minimize energetic costs in flapping insect flight in general. However, this conclusion strongly depends on the actual scaling of stroke kinematics, body morphology, and drag coefficients with changing Reynolds number. For example, to prevent wings from stalling at higher Reynolds numbers, the angle of attack and thus the drag coefficient during wing translation should decrease with increasing body size. Our predictions of profile power might thus greatly overestimate profile power costs in larger animals and elastic energy storage might be already beneficial in medium sized insects. Nevertheless, this analysis shows the importance of an accurate estimate in profile power requirements for our understanding on flight energetics and thus on how flapping flight in insects may have evolved.

As mentioned earlier, flying insects may limit their energetic expenditures during flight by increasing muscle and/or aerodynamic efficiency. Muscle efficiency is the ratio between mechanical power output of the thoracic flight muscles and the total metabolic costs neglecting parasite metabolic power due to other respiratory requirements such as an increase in heart beat or contractions of abdominal and leg muscles during flight (Fig. 2, Ellington, 1984c; Zanker, 1988a, b). In hovering Drosophila, muscle mechanical power must meet total aerodynamic power requirements for flight, \( P_{\text{aero}}^* \), which increase with increasing body size \( (P_{\text{aero}}^* = 141 m_b^{0.18}, r^2 = 0.17, P = 0.003, N = 50, \text{Fig. 3B}) \). In contrast, flight muscle mass specific metabolic rate, \( P_{\text{CO}_2}^* \), in flying fruit flies significantly decreases with increasing body weight \( (P_{\text{CO}_2}^* = 692 m_b^{0.19}, r^2 = 0.25, P = 0.0003, N = 50, \text{Fig. 3B}) \) which results in an increase in muscle efficiency with increasing body size (Fig. 3C). Due to the high profile drag estimates, muscle efficiency, \( \eta_m \), of the asynchronous flight muscle during hovering conditions yields 20–25% in small animals (D. nikanani) and is up to 40% in larger species of fruit flies (D. melanogaster, D. virilis and D. mimicosa), linear regression fit, \( \eta_m = 7.04 +1.33 m_b, r^2 = 0.28, P < 0.001, N = 50 \). This increase in efficiency could result from the change in magnitude or rate of strain in the asynchronous power muscles in larger flies. During flight in fruit flies, the asynchronous power muscles undergo cyclic length changes (2–4% of their length) within one contraction and relaxation cycle (Chan and Dickinson, 1996). As a consequence, flight muscles in larger flies should have higher absolute strain amplitudes during flight that in turn might enhance the efficiency of cross bridge cycling and thus muscle efficiency. A broad comparison among many different invertebrates and vertebrates suggests that this relationship between muscle length/size and efficiency follows a general trend within the animal kingdom (for data see Lehmann, 2001). However, it remains surprising that this trend is even visible within a small 6-fold range of different body sizes in the fruit fly Drosophila.

Scaling of aerodynamic and total efficiency

Flying insects may limit their energetic expenditures during flight by increasing the efficiency with which the flapping wings produce aerodynamic lift. Aerodynamic efficiency is defined conventionally by the ratio between the Rankine-Froude estimate of induced power and the sum of induced power and profile power requirements in an insect (Ellington, 1984c, 1985). Aerodynamic efficiency thus indicates how much muscle mechanical energy is lost in the wake behind the animal during flight. We have already seen that larger fruit flies may limit their energetic...
expenditures during flight owing to increased muscle efficiency (Fig. 3C). The benefit of this increase with respect to total flight efficiency, however, depends on how aerodynamic efficiency scales with body size because total flight efficiency is simply the product between muscle and aerodynamic efficiency. Moreover, muscle, aerodynamic and total flight efficiency significantly vary within the working range of the thoracic flight motor of a single fruit fly *Drosophila melanogaster* (Fig. 4). Fruit flies that are flown in a virtual reality flight arena vary their force production in response to the vertical motion of a stripe pattern displayed in the arena by changing stroke amplitude and stroke frequency. At a force that is equal to the body weight of the animal (hovering conditions) stroke frequency and muscle mechanical power output reach maximum values (Lehmann and Dickinson, 1997). To produce flight forces in excess of hovering force, fruit flies decrease stroke frequency while increasing stroke amplitude that produces the puzzling relationship between both kinematic measures. Interestingly, fruit flies achieve maximum total flight efficiency (Fig. 4C) around hovering conditions by balancing two opposing trends: muscle efficiency is increasing with increasing force production (Fig. 4A) whereas aerodynamic efficiency is decreasing with increasing force production (Fig. 4B). It remains uncertain whether this small advantage in total efficiency during hovering flight was shaped by evolutionary factors or results from functional constraints on both the production of mechanical power by the indirect flight muscles and the unsteady aerodynamic mechanisms in flapping flight.

Figure 5 eventually shows how aerodynamic and total efficiency scale at hovering conditions in flying fruit flies. The data suggest that small fruit flies tend to produce aerodynamic lift more efficiently than do their larger relatives. In the smallest species (*D. nikananu*) we measured a maximum mean aerodynamic efficiency, $\eta_a$, of 16%, a value that quickly tends to decrease with increasing body size in the three larger species (linear regression fit, $\eta_a = 12.0 - 0.50 m_b$, $r^2 = 0.02$, $P = 0.325$, $N = 50$, Fig. 5A). Since muscle efficiency significantly increases but aerodynamic efficiency tends to decrease with increasing body size, total flight efficiency, $\eta_t$, increases only slightly within the 6-fold change in body size (linear regression fit, $\eta_t = 2.81 + 0.46 m_b$, $r^2 = 0.19$, $P = 0.0015$, $N = 50$, Fig. 5B). Mean total efficiency averaged over all flies amounts to 3.4 ± 0.72% (mean ± S.D., $N = 50$ flies). This value is very similar to efficiency estimates based on conventional drag coefficients ($C_D = 7 \, Re^{-0.5}$).
suggesting that total flight efficiency is broadly independent of different profile power estimates in flapping flight of insects (Lehmann, 2001).

**Conclusions**

Body size may potentially limit aerodynamic force production in flying insects. Small insects have to cope with a relative increase of viscous forces within the fluid that attenuates aerodynamic lift production and increases drag. In contrast, large insects face an increase in inertial power requirements due to the increase in wing length. If inertial costs exceed aerodynamic power requirements for flight, larger insects may limit their energetic costs by elastic energy storage. We have investigated these constraints on insect flight performance by comparing four different species of fruit flies flying in a virtual reality flight arena.

Surprisingly, small animals that fly at low Reynolds numbers yield higher total force coefficients than larger fly species which seems to require subtle differences in stroke kinematics between the four species. Moreover, re-analyzing profile power requirements for flight using recent drag coefficients suggests that within the entire range of body sizes mass specific inertial power is always smaller than aerodynamic power requirements. Thus in many small and medium sized insects the benefit of elastic energy storage might be minor. The elevated performance of mechanical power output and muscle efficiency match the extraordinary properties and morphology of the asynchronous flight muscle in insects. The low density of sarcoplasmic reticulum typically found in the insect flight muscle has freed space for additional contractile filaments and mitochondria (Josephson and Young, 1987). On the one hand, this arrangement seems to enhance muscle mechanical power output. On the other hand, the low content of sarcoplasmic reticulum makes it difficult to control the power output of these muscles by the nervous system. Thus to maintain maneuverability, flies employ tiny steering muscles on each side of the body that twitch synchronously with each nerve spike allowing the animal to control wing kinematics and aerodynamic forces within each single stroke (Götz, 1983; Heide, 1971a, b; Lehmann, 1994; Zolaker, 1947).

**References**


