

AN EXPERIMENTAL DETERMINATION OF THE
RELATIONSHIP BETWEEN LIFT AND AERODYNAMIC
POWER IN *CALLIPHORA ERYTHROCEPHALA* AND
PHORMIA REGINA

By JAMES WOOD*

Department of Regulatory Biology, University of Connecticut, Storrs, Connecticut

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INTRODUCTION

Detailed calculations of insect aerodynamic power output during flight have been made only for the locust *Schistocerca gregaria*, and these calculations depend on the assumption that steady-state aerodynamic theory applies to insect flight. Jensen (1956) calculated the total mechanical power (aerodynamic and inertial) transmitted to the wings of the locust for several hypothetical values of thoracic elasticity. For two individuals the mechanical power was 7.1 and 11.2 kcal/kg h if total elasticity were assumed, and 12.0 and 13.7 kcal/kg h if a completely inelastic system were assumed. The net aerodynamic power of less than 5 kcal/kg h is within the range of aerodynamic powers calculated for birds and insects by several different theories of bird and insect flight (Weis-Fogh, 1961). The review of Weis-Fogh & Jensen (1956) should be consulted for a consideration of these theories. All calculations assume the applicability of conventional steady-state aerodynamics to the rapid velocity changes encountered in insect flight. Later, Weis-Fogh (1964) showed that for the locust, lift and metabolic rate varied almost linearly. He pointed out that for the locust, the theories of von Holst & Kuchemann (1941) and Walker (1925, 1927) predict a nearly linear relationship between lift and aerodynamic power.

Osborne (1951) calculated aerodynamic power as a function of mass for several insects, based on Magnan's (1934) data. He found that power and mass showed an approximately linear relationship for many different insects in spite of large differences in wingbeat frequency, wing geometry, and size. The calculated aerodynamic power was usually greater than 9 kcal/kg h with the Diptera studied, falling generally between 10 and 30 kcal/kg h. Other calculations of aerodynamic force and power are reviewed by Chadwick (1953), Weis-Fogh & Jensen (1956) and Weis-Fogh (1961).

This paper describes a study to determine experimentally the relationship between aerodynamic power and lift in *Calliphora erythrocephala* and *Phormia regina*. Alternative assumptions are made which make it possible to determine the limits of the calculated ratio of aerodynamic power to aerodynamic force for the animals used. It is not assumed that steady-state aerodynamics apply as has been assumed in earlier calculations. This method also differs from most earlier work in that force and power are calculated from measured air velocities.

* Present Address: Mental Health Research Institute, University of Michigan, Ann Arbor, Michigan 48104.

METHODS

Flies were suspended in the working section of a low-turbulence wind-tunnel, and the instantaneous velocity distributions over a plane parallel to their wingbeat plane and 0.5 cm behind the wingbeat plane were determined (Fig. 1). Velocities were measured by hot-wire anemometry at points on an imaginary grid behind one wing at 2 or 3 mm intervals as a function of time after the start of the downstroke. Further details of the measurement procedure and the criteria for choosing the animals to be studied can be found in an earlier paper (Wood, 1970). Results from four *Calliphora* and four *Phormia* were used in these calculations.

Calculations of force and power were made from the momentum and energy equations, both of which may be validly applied to velocities which vary periodically about a mean (von Mises, 1945). Because lateral velocities (U_y) were large enough to introduce significant error into measurement of anterior-posterior velocities (U_x) by the technique used in this study (Wood, 1970), both lift and power were calculated in two ways. One method assumed that U_x was not increased during flight and that $U_y = 0$. It is important to note that both of these assumptions decrease the calculated aerodynamic power as well as the calculated lift. Furthermore, calculated power, which depends on the cube of velocity, was decreased more than calculated force by these assumptions. A second calculation of lift and power was made treating the measured horizontal velocity ($U_x + 1.4|U_y|$) as U_x and calculating lift and power from these numbers. This should maximize the calculated ratio of power to lift. U_y , which contributes to the power term, is increased by a factor of 1.4. The dependence of power on the cube of velocity makes this value increase more rapidly with increasing U_x than the calculated lift, which depends on the square of velocity. These calculations make it possible to set limits to the power/force ratio and are of interest because they provide a check on calculations provided by workers who used steady-state assumptions. In both cases lift (F_z) and power (P) were calculated from approximations of the equations

$$F_z = \rho \int_S \overline{U_n U_z} dS \quad \text{and} \quad P = \rho \int_S (\overline{U_n U^2/2}) dS$$

(von Mises, 1945), where ρ is air density (1.15×10^{-3} g/cm³), U_n is velocity normal to the control surface S enclosing the animal at the point of interest, and U is the magnitude of the velocity. Actual calculations were carried out with an IBM 360 computer. For each of 16–20 equally separated instants over one wingbeat cycle the instantaneous values of $\overline{U_n U_z}$ and $\overline{U_n U^2/2}$ were calculated. These values were averaged and the averages for each point were multiplied by ρ and ΔS , the rectangular area of measurement plane between four adjacent probe positions (0.04 or 0.09 cm²). A second face of the measurement plane was assumed to exist anterior to the insect and at this face U_z was assumed equal to zero, with U_x equal to the wind-tunnel velocity. For calculating power one-half the product of ($\rho U_n \Delta S$) and the wind-tunnel velocity squared was subtracted from the previously formed sum. Total power was obtained by summing the values calculated for each point in the measurement plane.

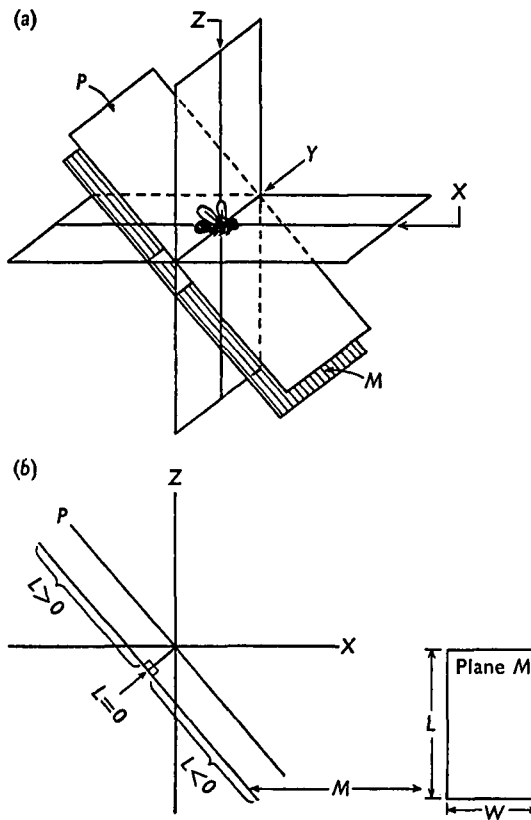


Fig. 1. (a) The planes and co-ordinate systems used in recording air velocities. The origin of the XYZ axes is at the fly's wing articulation. Values of U_x are positive from anterior to posterior. U_y is positive laterally from the wing hinge, and U_z is positive from dorsal toward ventral. Plane P, the wingbeat plane, is shown cutting the Y axis with the measurement plane M where velocity recordings were made parallel to it. (b) Side view of the planes and axes of (b). The co-ordinate system of the measurement plane is illustrated. $W = 0$ is in the ZX plane. W is parallel to Y and positive in the same direction.

Table 1. Calculated lift and the ratio of power to lift using (1) wind-tunnel velocity as U_x and $U_y = 0$ and (2) $U_x + 1.4|U_y|$ as U_x

	Assuming no increase in U_x or U_y		Treating $U_x + 1.4 U_y $ as U_x	
	Lift (mg)	Power/lift (kcal/kg h)	Lift (mg)	Power/lift (kcal/kg h)
<i>Phormia</i>	4.4	2.3	20.5	10.9
	4.7	2.4	4.5	19.1
	6.7	2.5	10.0	22.2
	17.6	3.7	30.2	29.1
<i>Calliphora</i>	3.1	4.7	9.8	19.5
	4.3	3.9	4.9	11.9
	8.7	6.1	10.8	27.9
	11.1	3.4	16.6	26.1

RESULTS

The sum of $1.4|U_y|$ and the increase in U_x above the wind-tunnel velocity is of the same order of magnitude as U_w (Fig. 2). Ratios of power to lift, calculated assuming no increase in U_x or U_y , differ by an order of magnitude from ratios calculated treating $U_x + 1.4|U_y|$ as U_x (Table 1). The relationship between calculated power and calculated lift does not differ greatly from linearity (Fig. 3) on the basis of either assumption.

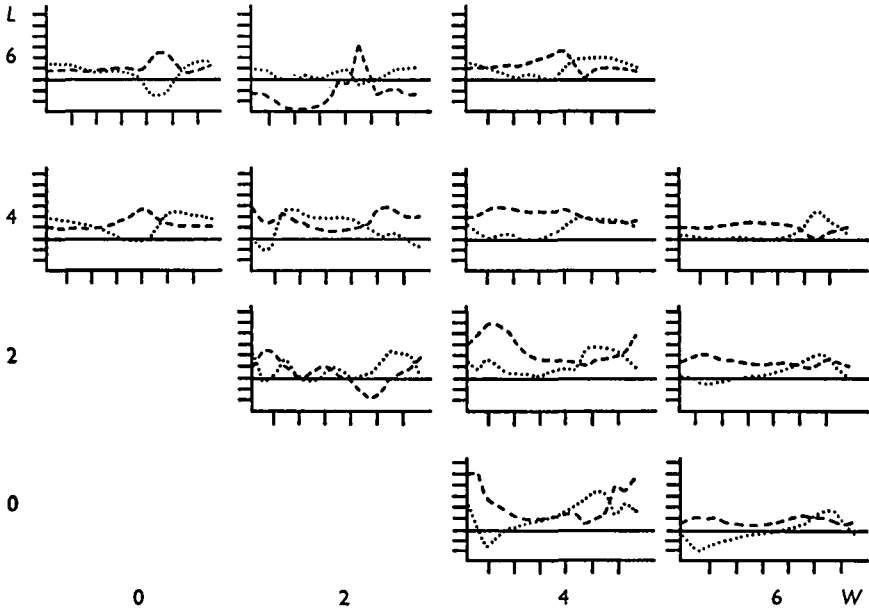


Fig. 2. The distribution of vertical and horizontal velocities in the measurement plane of one *Phormia*. Dashed line: $U_x + 1.4|U_y|$. Dotted line: U_x . Ordinate: 1 division = 3 cm/sec. Abscissa: 1 division = 1 msec. The solid horizontal line is zero cm/sec.

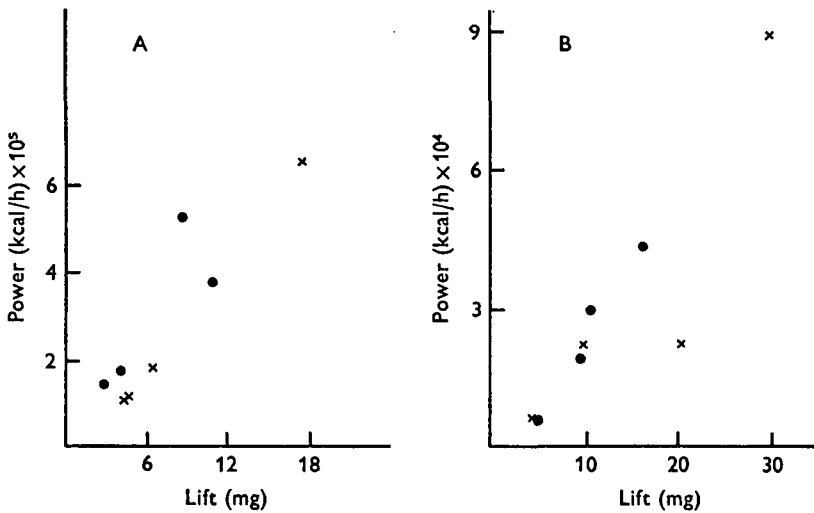


Fig. 3. The relationship between aerodynamic power and lift for four *Phormia* and four *Calliphora*. x, *Phormia*; ●, *Calliphora*. (a) Assuming $U_y = 0$ and U_x is not increased above wind-tunnel velocity. (b) Treating $U_x + 1.4|U_y|$ as U_x .

DISCUSSION

The minimum ratio of aerodynamic power to lift is 2–6 kcal/kg h when lift and power are calculated on the assumption that there is no increase in either U_x or U_y . This lower range of aerodynamic powers is slightly lower than those calculated by Osborne (1951) for a variety of insects and includes the ratio calculated by Weis-Fogh (1964) for the locust. Maximum power-to-lift ratios calculated by treating $U_x + 1.4|U_y|$ as U_x range from 10 to 30 kcal/kg h. The range 2–30 kcal/kg h includes the range of power-to-lift ratios calculated for many animals using steady-state assumptions (Weis-Fogh, 1961). It is interesting to compare the ratios of lift to power for the locust and for the Diptera which have been studied. A standard locust with lift equal to its body weight has a metabolic rate of approximately 70 kcal/kg h. Its aerodynamic power is of the order of magnitude of 5 kcal/kg h (Weis-Fogh, 1964). Aerodynamic power for the locust therefore represents between 5% and 10% of the metabolic rate. For *Lucilia*, which is similar in size and wing-stroke frequency to *Calliphora* and *Phormia*, Davis & Fraenkel (1940) found average oxygen consumptions of slightly less than 100 cc/g h. Assuming the oxygen to be used entirely in metabolizing carbohydrates, the metabolic rate is about 20 kcal/kg h. If the metabolic rates of *Lucilia* and the Diptera studied here are comparable, then the lowest calculated aerodynamic power represents about 10% of the metabolic rate of these insects, and the ratio of aerodynamic power to lift is similar for both the locust and these Diptera. A metabolic rate of 20 kcal/kg h would exclude the higher aerodynamic powers calculated here, but the possibility remains that 20 kcal/kg h does not represent the maximum metabolic rates of *Calliphora* or *Phormia*.

In either case calculations of aerodynamic power and lift from measured air velocities indicate that the aerodynamic power of *Calliphora* and *Phormia* is between 2 and 30 kcal/kg h, a range which agrees well with figures calculated on the assumption that steady-state aerodynamics can be applied to insect flight.

SUMMARY

Lift and aerodynamic power were calculated for *Calliphora* and *Phormia* using assumptions which maximized and minimized the ratio of aerodynamic power to lift.

The ratios of aerodynamic power to lift calculated by these methods, which do not rely on the assumption that steady-state aerodynamics applies to insect flight, are in agreement with results calculated by others using steady-state aerodynamics.

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