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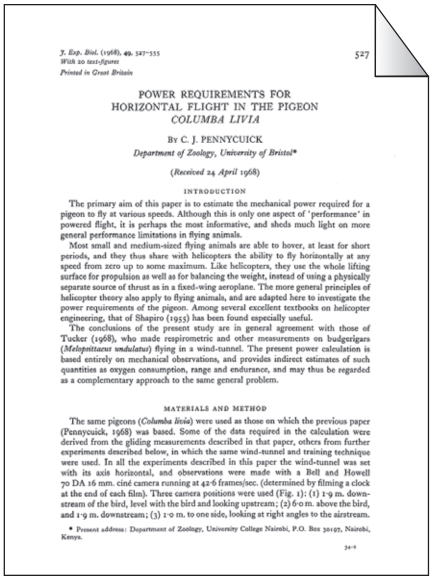
MECHANICS OF BIRD FLIGHT: THE POWER CURVE OF A PIGEON BY C. J. PENNYCUICK



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POWER REQUIREMENTS FOR
HORIZONTAL FLIGHT IN THE PIGEON
COLUMBA LIVIA

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INTRODUCTION

The primary aim of this paper is to estimate the mechanical power required for a pigeon to fly at various speeds. Although this is only one aspect of 'performance' in powered flight, it is perhaps the most informative, and sheds much light on more general performance limitations in flying animals.

Most small and medium-sized flying animals are able to hover, at least for short periods, and they thus share with helicopters the ability to fly horizontally at any speed from zero up to some maximum. Like helicopters, they use the whole lifting surface for propulsion as well as for balancing the weight, instead of using a physically separate source of thrust as in a fixed-wing aeroplane. The more general principles of helicopter theory also apply to flying animals, and are adapted here to investigate the power requirements of the pigeon. Among several excellent textbooks on helicopter engineering, that of Shapiro (1955) has been found especially useful.

The conclusions of the present study are in general agreement with those of Tucker (1968), who made respirometric and other measurements on budgerigars (*Melopsittacus undulatus*) flying in a wind-tunnel. The present power calculation is based entirely on mechanical observations, and provides indirect estimates of such quantities as oxygen consumption, range and endurance, and may thus be regarded as a complementary approach to the same general problem.

MATERIALS AND METHOD

The same pigeons (*Columba livia*) were used as those on which the previous paper (Pennycuick, 1968) was based. Some of the data required in the calculation were derived from the gliding measurements described in that paper, others from further experiments described below, in which the same wind-tunnel and training technique were used. In all the experiments described in this paper the wind-tunnel was set with its axis horizontal, and observations were made with a Bell and Howell 70 DA 16 mm. ciné camera running at 42·6 frames/sec. (determined by filming a clock at the end of each film). Three camera positions were used (Fig. 1): (1) 1·9 m. downstream of the bird, level with the bird and looking upstream; (2) 6·0 m. above the bird, and 1·9 m. downstream; (3) 1·0 m. to one side, looking at right angles to the airstream.

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Anders Hedenström discusses Colin Pennycuick's 1968 paper entitled 'Power requirements for horizontal flight in the pigeon *Columba livia*'.

A copy of the paper can be obtained from http://jeb.biologists.org/cgi/content/abstract/49/3/527

The ability of certain animal groups to fly by themselves has always stirred our imaginations. Even in the 15th century Leonardo da Vinci was famously inspired to try to build bird-like ornithopters. However, it was not until the 19th century that the nature of aerodynamic lift was understood, and it is a little more than 100 years since it was successfully applied to achieve flight by an aircraft. The key to success, as previous attempts to mimic animal flapping flight had failed (sometimes fatally), was to separate lift and thrust generation, so that aircraft wings provide lift while a propeller generates thrust. But animals generate lift and thrust by flapping their wings, which continuously change shape and deform elastically throughout the wingstroke. An analytical solution of Navier–Stokes equations (the general differential equations arising from applying Newton's second law to viscous fluid motion), which describe the aerodynamic forces that keep fliers aloft, would, in principle, solve the problem of how birds fly, but a solution to these equations defies scientists to this day. However, there is some light at the end of the tunnel. In a landmark paper from 1968 published in *The Journal of Experimental Biology* (Pennycuick, 1968b), Colin Pennycuick combined aerodynamic (helicopter) theory with ingenious wind tunnel experiments using a trained pigeon *Columba livia* to derive a quantitatively accurate mechanical model of bird flight. In a companion paper Pennycuick also estimated some basic properties for the bird in steady gliding flight in a tilted wind tunnel (Pennycuick, 1968a), including how the profile drag coefficient varies in relation to the lift coefficient and the magnitude of the parasite drag coefficient of a bird. Pennycuick used this information about wing lift and drag from the body and wings to develop his classic 'momentum jet' model of flapping flight mechanics (Pennycuick, 1968b).

The 'momentum jet' component of the model, which Pennycuick borrowed from helicopter theory, considers the bird as an 'actuator', a circular disc of diameter equal to the wingspan. The actuator generates a downward deflected uniform jet (which is why this model is also called the 'momentum jet' model of flight). The rate of momentum acquired by this jet must balance the bird's weight in steady level flight, while the fact that the wings are flapping and generating a pulsed wake is ignored by this model.

Pennycuick's main focus was to derive how the total mechanical power required to fly varies across a range of airspeeds (*U*). To do so he divided the total power into three components, each of which varies with airspeed but in different ways. The three components are induced power due to lift generation (declines with *U*), parasite power due to the drag of the body (called parasite because it originates from non-lifting parts, increases with *U*), and profile power due to drag of the wings. Determining how profile power varies across speed was the most difficult task, but due to diverging processes Pennycuick concluded that it remains almost constant in the mid-range of natural flight speeds, although eventually it will increase, as speeds get very high. The wind tunnel experiments allowed Pennycuick to assign values to the three power components, which added together yielded the famous U-shaped power curve of animal flight (Fig. 1). With this curve in hand Pennycuick could predict how fast a bird should fly in different situations, what the feasible speed range is for sustained flight, and at what rate flight fuel is consumed, etc.

Pennycuick's 1968 papers sparked a new era in his own, and others', research, leading to amendments and extensions of the theory, which were summarized in another 'flight classic' published as a book chapter (Pennycuick, 1975). This paper included tables and diagrams that allowed anyone to calculate potential flight ranges

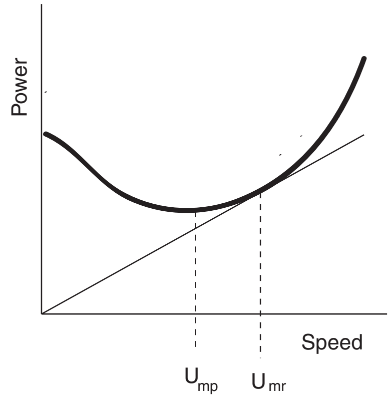

Fig. 1. The relationship between mechanical power and forward airspeed of a bird in flapping flight. The U-shaped curve immediately suggests the existence of two optimal flight speeds, U_{mp} for minimum power and U_{mr} for maximum range.

in migratory birds given only the fuel load (expressed as a fraction of take-off mass) and a minimum of morphological parameters. Ever since the early days Pennycuick has remained faithful to the field of animal flight by dissecting and improving on various components of his flight mechanics theory. Importantly, Pennycuick has greatly facilitated the use of his model by distributing computer programs that calculate bird flight performance, such as optimal flight speeds and flight range. His 1989 book (Pennycuick, 1989) had a floppy disk on the inside cover and his most recent book, 'Modelling the Flying Bird' (Pennycuick, 2008), is also centred on the flight performance programs (current versions available at http://www.bio.bristol.ac.uk/people/pennycuick.htm).

A crucial factor to the success of Pennycuick's approach to animal flight was his theoretical angle of attack, and that the calculations of the flight performance thereby could be generalized and applied to any bird. The theory also implied the existence of certain optimal flight speeds (U_{mp} – speed of minimum power; U_{mr} – speed of maximum range), which the bird should choose depending on its task. That birds actually select their speeds in different ecological contexts, as if they knew Pennycuick's theory, is a remarkable endorsement (Hedenström and Alerstam, 1996).

Because of its general implications nearly all research on animal flight must relate to Pennycuick's flight theory in one way or another, but it has not been without controversy. The prescribed U-shaped power curve (Fig. 1) has been tested many times. Initially researchers measured flight metabolic rate by attaching a respirometry mask to birds flying in wind tunnels. The theory predicts the relationship for mechanical power output, while whole-animal metabolism (as measured by respirometry) measures power input. If the conversion efficiency is constant across speeds the metabolic measurements should reflect the U-shaped function, and indeed this is what Vance Tucker found in budgerigars *Melopsittacus undulats* (Tucker, 1968). However, other studies, both old and recent, have obtained rather flat power curves across airspeeds, while others obtained the characteristic U-shape. This has certainly caused some confusion and even criticism, suggesting that 'Pennycuick is wrong'. More recently new methods have been used that attempt to measure more directly the work rate of the flight muscles, which should reflect mechanical power more closely, and the power curves that come out show the expected U-shape (Tobalske et al. 2003; Askew and Ellerby, 2007).

In the 1968 paper Pennycuick also derived the 7/6 law, which says that mechanical power required to fly increases as (body mass)$^{7/6}$, which combined with scaling of power available from muscles ($\propto$mass$^{2/3}$) suggests that there is an upper size limit for self-powered vertebrate flight of about 12 kg. Another important application of flight mechanical theory is its application to migration ecology. Pennycuick developed the basic ideas about migration range, optimal flight speed, effect of wind and body size in another influential paper (Pennycuick, 1969). The fundamental range curve, as derived from flight mechanical principles, served as an important point of departure for what is now called optimal bird migration theory (see Alerstam and Lindström, 1990).

When I was still a PhD student my thesis advisor Thomas Alerstam landed a sizeable grant to set up a new wind tunnel at Lund University to be dedicated to research on animal flight. Pennycuick was instrumental from the design stage to the final use of this tunnel facility, and until very recently the original computer and instrumentation, all of which were designed and installed by Pennycuick, still monitored the air flow in the tunnel. Ever since 1994 this wind tunnel has been the focus of my own research, but we now use different methods to study the aerodynamics of bird and bat flight. Although we now know that the momentum jet model developed by Pennycuick (Pennycuick, 1968b) is an unrealistic simplification of the true geometry of the wake of a flying bird, it captures enough detail about the physics of animal flight to still make it a very useful tool for analysing bird flight performance.

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