JEB Classics

CARDIORESPIRATORY SUPPORT OF AVIAN FLIGHT
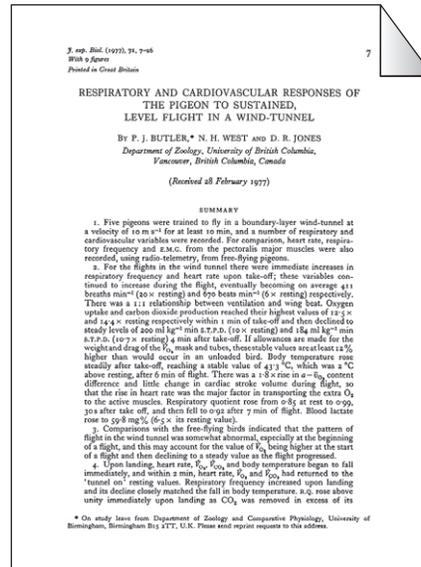
Bill Milsom discusses Pat Butler, Nigel West and Dave Jones' 1977 paper entitled 'Respiratory and cardiovascular responses of the pigeon to sustained, level flight in a wind-tunnel'.

A copy of the paper can be obtained from http://jeb.biologists.org/content/71/1/7.abstract

The ability of birds to fly has fascinated man and attracted the attention of scientists (not just biologists) throughout recorded history. Of significant note is that many of the pioneering and groundbreaking studies on bird flight have been published in *The Journal of Experimental Biology*. Indeed, two papers have already been written in the JEB Classics series on the studies of Colin Pennycuick (Pennycuick, 1968; Hedenström, 2009) and Vance Tucker (Tucker, 1968; Bundle, 2010) exploring the mechanical power requirements and metabolic power costs of flight, respectively.

These researchers, and subsequent others, found that birds expend much energy to stay airborne at slow flight speeds as well as to fly quickly. At intermediate speeds, however, flight costs are more economical. This gives rise to a U-shaped curve describing the relationship between metabolic cost and speed. The steepness of this curve varies across species as a function of wing beat frequency, wing movement and wing shape amongst other factors (Alexander, 1997). Even when measurements are taken from birds flying at optimal (i.e. the most energy efficient) speeds, however, the mass-specific rates of oxygen uptake by the pectoralis muscles of birds are among the highest known;

roughly twice those of the leg muscles of running mammals of equal size (Thomas et al., 1984). This cost also scales inversely with body mass, making the flight performance of small birds truly amazing.

This brings us to the classic *Journal of Experimental Biology* paper by Pat Butler, Nigel West and Dave Jones (Butler et al., 1977). Biologists have long been interested in what sets the limits to performance, for any individual, for individuals of a given species and for those species that comprise the elite of all animal athletes. Are the limits behavioural, mechanical or metabolic? With regards to metabolic constraints, for sustained performance 'what sets the limit to oxygen consumption?' Early studies revealed that the oxygen consumption of flying birds ranged from 5 to 14 times resting values. While these values are in the range of maximum aerobic performance measured in mammals, it must be remembered that these are measures of metabolic rate during sustained flight in birds, not maximum performance. For technical reasons, maximal oxygen consumption in birds has probably never been measured (Bundle et al., 1999). Our understanding of what determines the ability of birds to maintain the oxygen consumption rates required for sustained steady flight, begins (and almost ends) with the classic study of Butler and colleagues.

Up until this study, researchers had mastered techniques for measuring metabolic rate, deep body temperature, heart rate and breathing frequency from birds in flight in wind tunnels. These were impressive feats in and of themselves. Butler and colleagues took this a huge step further. Not only did they measure all of these variables, they also measured muscle EMG (to determine wing beat frequency) along with arterial and venous blood pressure, blood gas tensions, blood gas contents and blood lactate – all during active sustained flight! From the measures of metabolic rate and arterial and venous blood gas contents, they used the Fick equation for cardiovascular perfusion [oxygen consumption=cardiac output $\times$ (O_2 content of arterial blood–O_2 content of venous blood)] to calculate cardiac output. Based on this calculation and knowing heart rate they calculated the stroke volume of the heart (cardiac output=heart rate $\times$ stroke volume), and knowing arterial blood pressure they calculated the total vascular resistance of the circulatory system (total peripheral resistance=arterial blood pressure/cardiac output). When combined with their other measurements, this allowed them to explore the relative roles of

ventilation and perfusion (the two convective steps in the oxygen transport cascade), along with pulmonary diffusion, in oxygen delivery to the exercising tissues. This was a true tour-de-force: so much so that similar measures have only been obtained once in a study 28 years later (Peters et al., 2005)!

The data revealed several significant insights. The first was that at the onset of flight, the level of oxygen in arterial blood rose slightly while that of arterial CO_2 fell significantly. This was one of the early demonstrations that the massive increases in ventilation and heart rate associated with the onset of exercise were not driven by metabolically produced changes in blood gases but were part of a feed-forward mechanism that ensures that blood gases do not change in a manner that would constrain exercise. These same data also indicated that changes in ventilation were more than adequate to ensure sufficient gas exchange to power flight. Indeed, Butler and colleagues concluded that the high respiratory frequency during flight was related to the need to dissipate heat, not exchange gas. They also demonstrated the intriguing way in which this was done. Pigeons fly in a burst and glide fashion with bursts of wing beats interspersed with periods of gliding. During the flapping phase, wing beat frequency and ventilation frequency are coupled 1:1 (the birds take one breath for each complete wing beat cycle) (Tomlinson and McKinnon, 1957; Hart and Roy, 1966). Based on their EMG recordings, Butler and colleagues found that during the early part of a flight, breathing would slow during the glide phase, but late in the flight when body temperature was rising, ventilation would increase during the glide phase when it was not constrained by the wing flap frequency, to help dissipate heat.

Their calculations also allowed them to partition out the relative importance of changes in heart rate, cardiac stroke volume and tissue oxygen extraction to the increase in metabolic oxygen consumption. They found that the stroke volume of the heart changed very little and that the 10-fold increase in oxygen delivery was due to a 5- to 6-fold increase in heart rate and a doubling of the amount of O_2 extracted from the blood coursing through the tissue capillaries. Combined with data from subsequent studies (Bishop, 1997; Peters et al., 2005), it appears that the superior blood oxygen convection capabilities of pigeons over running mammals of equivalent size is attributable to the higher resting stroke volume (due to a larger heart) and larger exercise-induced increases in heart rate. These data contribute to the long-standing controversy that suggests that the limit to exercise performance in most mammals arises from limits to cardiac perfusion and tissue diffusion, and that one of the most important features distinguishing elite performers from average individuals within a population is the size of their heart and the cardiac stroke volume that an individual is born with (Wagner, 1996).

The results of this *Journal of Experimental Biology* classic are central to our understanding of avian cardiorespiratory physiology during flight and are the building block for current studies of the anatomical and physiological plasticity that underlies further avian adaptations to challenging environments. It certainly has had a profound influence on recent work from my colleagues and me on the bar-headed goose, which crosses the Himalayas on its biannual migration attaining altitudes as high as 9000 m. Meeting the metabolic demands of flight in the thin air at altitude, with its reduced O_2 content, is extremely challenging and appears to arise from further enhancements across the O_2 transport cascade (Scott and Milsom, 2006; Scott and Milsom, 2007; Scott et al., 2011). We are still unravelling the mechanisms that underlie this impressive feat, but our studies build on this pioneering study of 34 years ago.

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