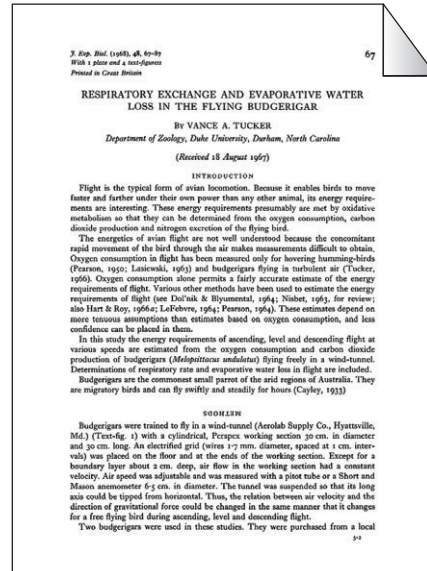


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JEB CLASSICS

OXYGEN UPTAKE OF FLYING BUDGERIGARS BY V. A. TUCKER



Matthew Bundle discusses Vance Tucker's 1968 paper entitled 'Respiratory exchange and evaporative water loss in the flying budgerigar'.

A copy of the paper can be obtained from <http://jeb.biologists.org/cgi/content/abstract/48/1/67>

In studies of animal movement, few questions have provided more understanding of an organism's functional morphology and comparative physiology than asking, what are the rates of metabolic energy required to sustain motion and how do these rates of energy liberation change when the speed of locomotion is altered? Addressing these fundamental questions has provided powerful insight to cellular metabolism, the contractile dynamics of working muscle, the design and function of the respiratory system, and the economy of movement. A number of methods are available for contemporary biologists to investigate these and similar questions but the gold standard in studies of whole animal energy release remains the measurement of oxygen uptake during locomotion. The long established technological capacity to achieve reliable measurements of oxygen and carbon dioxide fractions and the broad implications of these measures has resulted in many of the early oxygen consumption studies remaining well known today.

Prior to Vance Tucker's pioneering research program to document the rates of oxygen uptake during bird flight, published in his 'classic' *The Journal of Experimental Biology* paper (Tucker, 1968) and a preliminary, comparatively lesser known, report (Tucker, 1966), very little was

known about the physiology of flight. Previous experimental investigations of avian respiratory and locomotor physiology during flapping flight were extremely limited, and included measurements obtained from hummingbirds remaining aloft within 1 gallon containers (e.g. Lasiewski, 1963), estimates of carbon dioxide production in pigeons during unrestrained flights (e.g. LeFebvre, 1964), the weight lost during lengthy, potentially non-stop, migrations (e.g. Nisbett et al., 1963) and measurements of cardio-vascular physiology from birds remaining aloft for less than 15 s (e.g. Eliason, 1963). For mostly methodological reasons the conclusions that could be drawn from these early studies were few. First, on the afternoon of LeFebvre's experiments, thunderstorms forced most of the pigeons to land, limiting the ability of these results to provide clear insight to the metabolic rates or cost of transport required of flight. Second, studying animals hovering in small enclosures permits metabolic measurements but disrupts the mechanisms of weight support (e.g. Rayner, 1994). Third, the short bursts of instrumented flight possible within hallways and laboratories are too brief to allow the bird's respiratory and circulatory systems to reach a steady state and offer meaningful and repeatable measurements.

An apparent route to progress was to borrow a strategy long employed by investigators focusing on terrestrial and aquatic forms of locomotion, i.e. enable the animal to engage in locomotion but also remain stationary within the laboratory. A wind tunnel would allow a researcher to use traditional lab-based measuring equipment to study bird flight rather than being forced to fly behind the animals in a small aeroplane (Raspert, 1960), or to develop miniaturized sensors for the birds to wear in the wild. Although the use of wind tunnels to study animal flight predated Tucker's experimental endeavors by over 40 years, their use had been limited to investigations of the aerodynamics of stuffed and model birds, and a single previous study focused on hummingbird wingbeat kinematics (Greenewalt, 1960). Tucker's initial attempt (Tucker, 1966) to measure the metabolic rate-flight speed relationship was hampered by turbulence within the test section of his first wind tunnel, and the resulting metabolic measurements were difficult to interpret.

Using a wind tunnel with more laminar airflow, Tucker's classic *The Journal of Experimental Biology* manuscript was the first to measure an identifiable relationship between flight speed and the metabolic power required. He obtained these results by training two budgerigars (*Melospiza melanocephala*)

undulates) to fly at different speeds, while wearing a lightweight acetate mask (Fig. 1) designed to capture the birds expired gases. After several minutes of continuous flight the expired gases were analyzed for oxygen and carbon dioxide content, permitting quantification of the rate of oxygen consumption and metabolic energy liberation. Tucker found that his birds required high rates of energy release at both fast and slow flight speeds but at intermediate speeds flight costs were more economical. In addition to the power curve for level flight, he measured a series of similarly U-shaped power curves by tilting the wind tunnel and forcing the birds into either climbing or descending flights.

The agreement between Tucker's metabolic power measurements and the mechanical power estimates that were published later that same year in another classic *The Journal of Experimental Biology* article (Pennycuick, 1968; Hedenström, 2009) created a short-lived harmony between the understanding of the energetics and mechanics of bird flight. As a result, throughout the original literature and physiology textbooks, the budgerigar U-shaped power curve was widely considered to be representative of birds in general. However, subsequent studies of flight metabolism in other species, including one conducted by Tucker (Tucker, 1972), generated essentially flat metabolic power curves, suggesting that some birds require little change in metabolic power in order to fly across a wide range of speeds. The disagreement between these subsequent physiological measurements and classical aerodynamic expectation has come to dominate the avian flight literature for nearly 40 years (e.g. Alexander, 1997). More recently, experimental evidence from several independent lines of research appears to have identified Tucker's initial U-shaped power curve as the likely archetype for birds in general (e.g. Tobalske et al., 2003; Askew and Ellerby, 2007; Bundle et al., 2007). Although, despite an array of experimental methods used to address this issue, the variety of study

species has been unfortunately narrow. As a result, a satisfactory explanation for the numerous flat metabolic power curves has not been forthcoming.

The scientific contributions of Tucker's 1968 study are not limited solely to providing the first empirical measurements of the metabolic requirements of flight, and this manuscript would not have been cited nearly 300 times from follow-up studies attempting to resolve the controversy that arose from the two qualitative types of avian power curves. The mass-specific rates of oxygen uptake that Tucker measured indicate that during flight the pectoralis of the budgerigar is among the most metabolically active tissues known. For many years, these results provided some of the strongest experimental support for the assertion that the avian lung's cross-current gas exchanger was likely to support greater maximal rates of oxygen flux than the mammalian design. When working with flying birds, it is often unclear whether a particular animal or species is unable to generate higher power outputs due to behavioral, mechanical or metabolic limitations. As a result, clear measurements of maximal aerobic power during flight have not been obtained (Bundle et al., 1999). Accordingly, the budgerigar's high rates of oxygen uptake have been used as an estimate for the upper functional limit to the avian respiratory system in the extensive literature relating the form and function of the respiratory cascade.

Tucker's results have also been critically important in understanding the energetics of bird migration. Many investigators have relied on these results as the experimental support from which to generate predictions for the energy expended during long distance flights by assuming the species of interest will require similar increases in metabolic rate at equivalent flight speeds. These estimates of the daily energy budget can inform our understanding of feeding and refueling strategies, timing of

departures and general life history strategies for a trait that remains logistically difficult to study directly.

The scientific contributions of Tucker's work with budgerigars extend beyond the elegance of a simple question that is of central importance to avian biology. For instance, other investigators had asked similar questions but these efforts lacked the innovation and experimental skill that allowed Tucker to successfully quantify the metabolic energy used during flights across a wide range of speeds. For example, this work would not have been possible without either the calorimetry protocols he developed for this study and that continue to be cited or the ability to train birds to wear a mask and fly for sufficient durations to achieve a metabolic steady state. The results of these classical experiments remain central to our understanding of avian flight biology and their importance is unlikely to diminish in the near future.

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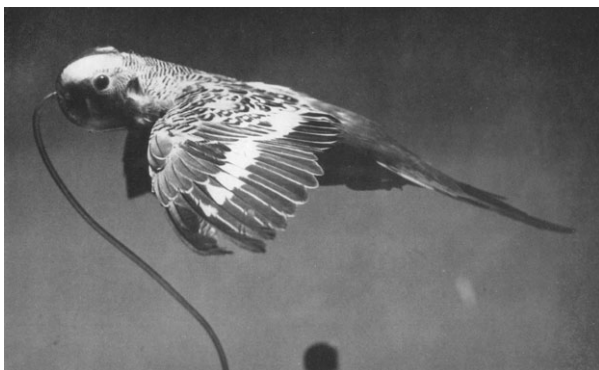


Fig. 1. One of Tucker's budgerigars flying at 35 km h⁻¹ in a wind tunnel while wearing a mask to capture the expired metabolic gases for analysis