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INSECT FLIGHT TAKES OFF

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THE RESPIRATORY EXCHANGE OF THE DESERT LOCUST (*SCHISTOCERCA GREGARIA*) BEFORE, DURING AND AFTER FLIGHT

By the late AUGUST KROGH and TORKEL WEIS-FOGH

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(With Four Text-figures)

During the last two decades the knowledge of the physiology of heavy muscular work has increased considerably, and the high metabolic rate of flying insects has attracted particular attention. Jongbloed & Wiersma (1935), Chadwick & Gilmour (1940), and Davis & Fraenkel (1940) have reviewed the literature concerning the metabolic rate of flying insects. More recent investigations dealt mainly with the nature of the fuels combusted or with other aspects of insect flight. Most of the experiments referred to below dealt with measurements of the oxygen consumption of insects performing flight movements in a relatively small container. In this respect and because generally the animals were suspended and the natural locomotion was prevented the conditions of flight were abnormal. However, these limitations concerning the conditions of flight are probably of minor importance when we are interested mainly in the order of magnitude of the metabolic rate and in the nature of the fuels combusted, and with these limitations in mind, the present state of knowledge might be summarized:

(1) During flight the oxygen consumption is considerably increased and has been estimated at about 100 l. O_2/kg. body weight/hr. in bees (Jongbloed & Wiersma, 1935), flies (Davis & Fraenkel, 1940), and butterflies (Zeuthen, in Krogh, 1941). This means that the metabolic rate during flight in some insects increases 100 times or even more compared with the metabolism during rest. In an extensive and very interesting series of experiments Chadwick & Gilmour (1940) and Chadwick (1947) have demonstrated that various species of *Drosophila* consumed only 20 l. O_2/kg./hr., a figure which was indirectly verified by Williams, Barness & Sawyer (1943) and Wigglesworth (1949). In the above-mentioned papers by Chadwick, and a paper by Chadwick & Williams (1949), the metabolic rate was correlated with the wing-beat frequency.

(2) The respiratory quotient (R.Q.) during flight was measured in bees (Jongbloed & Wiersma, 1935, in *Apis*) and flies (Chadwick, 1947, in *Drosophila*). In both cases the R.Q. equalled unity, indicating the combustion of carbohydrates, and this interpretation seems to be correct, glucose and glycogen being utilized as fuels in *Apis* (Beutler, 1937) and *Drosophila* (Williams *et al.* 1943; Wigglesworth, 1949) respectively.

(3) After the cessation of flight a small oxygen debt was demonstrated in *Drosophila* (Chadwick & Gilmour, 1940). The debt was abolished in less than 2 min.

Raul Suarez and Jon Harrison write about August Krogh and Torkel Weis-Fogh's 1951 ground-breaking publication on insect flight physiology.

This 1951 JEB classic paper, written at the dawn of the Golden Age of biology by Viking physiologists August Krogh and Torkel Weis-Fogh, was a collaboration between two men at opposite ends of their careers (Krogh and Weis-Fogh, 1951). August Krogh, the only comparative respiratory physiologist to earn a Nobel Prize, mentored Weis-Fogh during the last years of his life, and died before the publication of this paper. Among biologists, Krogh is most famous for a concept that is widely applied even today (Editorial, *Nature Genetics* **34**, 345-346, 2003); that for a large number of problems, nature has provided an animal of choice on which it can be most easily studied. This was only Torkel Weis-Fogh's third paper in a series that have all become classics in the fields of flight physiology and biomechanics. Weis-Fogh (1949) had previously shown that it was possible to induce locusts to fly for long periods of time on a tether by stimulating sensilla on the head with a jet of air. The 1951 paper combined Weis-Fogh's tethered flight technique with August Krogh's expertise in respirometry to provide the first measures of metabolic rate and respiratory quotient in a flying locust. Weis-Fogh's research in Krogh's laboratory was made possible by a grant from London's Anti-Locust Research Center, demonstrating that then, as today, potential practical benefit can fuel basic research.

In retrospect, what is perhaps most impressive about this paper is that the authors were able to collect data that have stood the test of time with gas analysis instrumentation that was 100–10,000 times less sensitive than what we have today. For those who have not had the pleasure of using the Haldane method of O_2 and CO_2 analysis, it is a tricky, toxic business, in which samples of air are trapped within a volumetric syringe behind mercury, and the O_2 and CO_2 gas fractions calculated from the changes in gas volumes after they are solubilized by ferricyanide and NaOH, respectively. Measuring the gas exchange of a flying insect is more challenging than for a vertebrate, as the many spiracles preclude the use of a respiratory mask. To overcome the low-sensitivity of their gas analysis method, the Vikings devised a respirometry chamber equipped with a home-built pump that recirculated air onto the tethered locust's head, providing the stimulus for flight. For the short time-interval studies of respiratory quotient in post-flight locusts, they allowed acidified water to flow in around the locust as they extracted the entire chamber volume, providing them with maximum sample from an animal maintained in the minimum possible volume. With these techniques they reported resting and flight metabolic rates very similar to those measured later with modern gas analyzers (Armstrong and Mordue, 1986; Greenlee and Harrison, 2004).

The composition of metabolic fuels is such that the oxidation of a given amount of carbohydrate produces the same amount of CO_2 as the O_2 consumed, while fat oxidation yields a ratio of CO_2 to O_2 of 0.7. Thus, the ratio of the steady-state rate of CO_2 production to O_2 consumption by animals, i.e. the respiratory quotient, can be used as an index of the nature of the fuel(s) used. Another important scientific finding reported in this paper was that, unlike all prior studies of insect flight, the respiratory quotient of flying locusts was less than 1, and tended to decline with time in flight. Up to the publication of this paper, respiratory quotient had only been measured for bees and fruitflies, which had been shown to utilize carbohydrates as the primary fuel for flight. This paper provided the first evidence (later confirmed, by Jutsum and Goldsworthy, 1976) that fat was the primary fuel in long-term locust flight. Since then, many investigators have used respirometric and biochemical methods to study temporal changes in fuel use by insects and the diversity of fuel use among species. The fact that the fuel used to support flight seems to vary more with phylogenetic history than ecology/life history remains an understudied problem in this field.

Equally interesting is the, as yet, unresolved finding in this paper of elevated gas exchange rates for 1–2 h after flight. The study of 'oxygen debt' was popular when this paper was published, and new insights into this topic continue to emerge (Pinz and Portner, 2003). In the 1951 paper, Krogh and Weis-Fogh referred to this elevated post-exercise oxygen consumption as 'oxygen debt', but suggest that it is not due to lack of oxygen in the flight muscle. However, subsequent work has confirmed that flight metabolism is completely aerobic in sustained insect flight. This elevated post-flight gas exchange is unlikely to be due simply to passively declining thoracic temperature, which should occur a few minutes after landing. Are we observing the slow removal of neurohormonal factors (e.g. octopamine; Orchard et al., 1993) that elevate tissue metabolic rates, and perhaps spontaneous behavior? What portion of these represent the costs of resynthesizing the fuels catabolized in the previous flight? More than half a century later, these data could still provide grist for a grant application!

Studies of animal flight continue to address fundamental problems and remain one of the most vibrant areas of experimental biology. Biomechanists use high-speed video, physical models and advanced theory to understand how animals fly and steer (Sherman and Dickinson, 2004; Usherwood and Ellington, 2002); this area now seems poised to provide the biological inspiration for engineers to design minute flying robots. Muscle physiologists are now able to go into insect thoraxes to directly measure stress, strain, frequency and oxygen consumption, allowing the estimation of power input, output and efficiency of active muscles (Josephson et al., 2001). Pathway flux rates and mitochondrial electron transfer rates in individual flying insects have been examined to yield insights into how insects achieve the highest metabolic rates known in the animal kingdom (Suarez et al., 2000). A whole arsenal of molecular techniques is now available to study the flight muscle contractile machinery as well as membrane ion channels and pumps (Vigoreaux, 2001). The evolution of insect flight itself is being examined (Marden and Thomas, 2003). The great experimental biologists, August Krogh and Torkel Weis-Fogh provided large shoulders on which many must stand well into the future.

A PDF file of the original paper can be accessed online: http://jeb.biologists.org/cgi/content/full/207/19/3251/DC1

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