The U, J and L of bird flight

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Respirometric measurements of the power needed for birds to fly at various speeds have been at odds with aerodynamic theory. Direct experiments confirm theory, but loose ends remain.

Aircraft need a lot of power to fly slowly and a lot to fly fast, but fly more economically at intermediate speeds. So a graph of power against speed is U-shaped, both for fixed-wing aircraft and for helicopters (Fig. 1a). The same must be expected to be true for birds and other flying animals, yet respirometric measurements of the oxygen consumption of animals in flight have usually shown little dependence of power on speed, giving graphs that are almost flat or slightly J-shaped[1].

Oxygen consumption is not a direct measure of mechanical work, however; it indicates how much food is burned aerobically as fuel, but may not be a good indicator of work performance if muscles work with variable efficiency. Dial and his colleagues, writing on page 67 of this issue[2], now describe how they have made direct measurements of the work done by a flying bird. They find that, as for aircraft, much more power is needed to fly slowly than to fly at intermediate speeds.

Dial *et al.* determined the work done by the principal wing muscle of a magpie, flying in a wind tunnel. To do this, they needed to know the length changes of the muscle, and the force it exerted, at each stage of the wing-beat cycle. They calculated the length changes from the wing movements seen in cine film. To measure the forces, they used a tiny strain gauge, implanted surgically on the crest of the humerus where the muscle attaches to it. The forces and length changes were used to calculate the work done in a wing-beat cycle, and this was multiplied by the frequency of the wing beat to obtain the mechanical power. The resulting graph of power against speed is shown in Fig. 1b. The power required for flight is high at low speeds, low at intermediate speeds and rises only slightly at high speeds. The graph is perhaps better described as L-shaped than as U-shaped.

In Fig. 1b, the graph obtained from these experiments is compared to a theoretical curve calculated for the same species using a theory devised by Pennycuick[3]. The theoretical curve runs parallel to the empirical one, but shows somewhat higher power requirements. This comparison is less than ideal, because Pennycuick's theory is designed to apply only to the faster of the two 'gaits' that birds commonly use in flight (the continuous vortex gait). Magpies[4], like many other species with rounded wings[5], seem to use the slow (vortex ring) gait even when flying at maximum speed. Rayner[6] has shown how power requirements can be calculated for this gait. No results from his theory have been published for magpies, but Fig. 1b includes his theoretical curve for a pigeon. This curve is U- rather than L-shaped, showing power requirements increasing steeply as the bird approaches its maximum speed. A later model[5] predicts power requirements for the continuous vortex gait. It also produces markedly U-shaped graphs of power against speed.

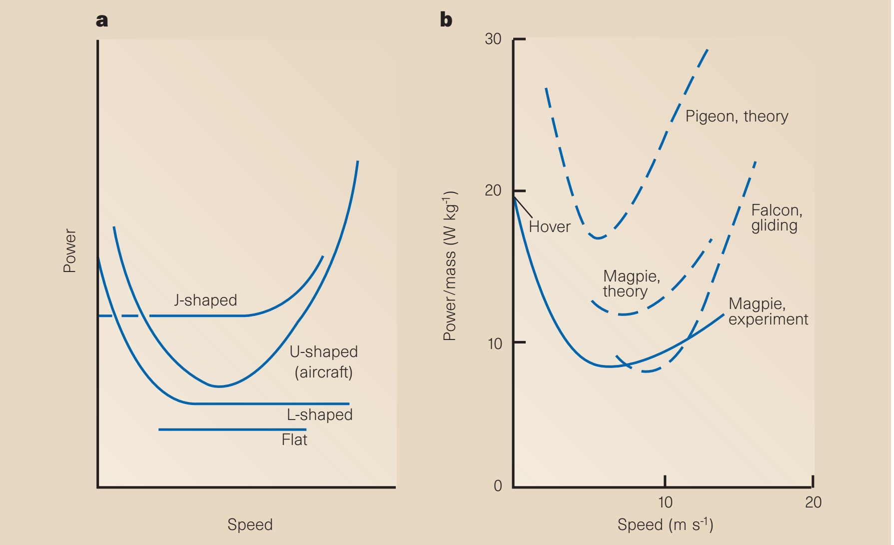

Figure 1 **Power for flight at different speeds.** a, **Schematic graphs of power against speed, showing various possible shapes.** b, **Graphs of the mechanical power exerted in flight, against speed. The continuous line is the empirical graph for magpies which results from the experiments by Dial *et al.*[2] discussed here. Dashed lines show theoretical graphs for a magpie[3] and a pigeon[6], and a graph for a falcon calculated from its observed gliding performance[7].**

Observations of gliding offer another approach. Gliding is flight powered by gravity, so a graph of the rate of loss of potential energy, against speed, is in effect a graph of power against speed. Such a graph[7] is included in Fig. 1b. Like the theoretical graph for the pigeon, it shows power increasing steeply at high speeds.

Observations of gliding and calculations using Rayner's models[5,6] both show power requirements increasing steeply as birds approach their maximum speeds. In contrast, Dial and colleagues'[2] experiments on magpies show that, at the highest speed at which they could be persuaded to fly, the power requirement was well below the power they exerted in hovering.

Measurements of oxygen consumption can only tell us about metabolic power requirements in the range of speeds that can be sustained by aerobic metabolism. Hummingbirds are the only birds known to be able to hover aerobically; surprisingly, they have been found to have J-shaped curves, using oxygen no faster when hovering than when flying at moderate speeds[1]. It has been suggested[5] that this result could be an artefact of using an open-jet wind tunnel, which may have increased the power requirement at moderate speeds.

Several questions remain. Well-established aerodynamic arguments lead us to expect U-shaped graphs of power against speed. The L-shaped graph of mechanical power for magpies may be a U truncated at the right-hand side, but why is it truncated? If the power required at 14 m s^{-1} (Fig. 1b) is less than the power that the magpies exert when they hover, what is there to prevent a magpie from flying faster? The relatively flat graphs of oxygen consumption that have been obtained for various birds may be interpreted as fragments from the bottoms of U-shaped graphs, but can the J-shape of the hummingbird graph be dismissed as an artefact? □

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1. Ellington, C. P. *J. Exp. Biol.* **160,** 71–91 (1991).
2. Dial, K. P., Biewener, A. A., Tobalske, B. W. & Warrick, D. R. *Nature* **390,** 67–70 (1997).
3. Pennycuick, C. J. *Bird Flight Performance* (Oxford Univ. Press, 1989).
4. Tobalske, B. W. & Dial, K. P. *J. Exp. Biol.* **199,** 263–280 (1996).
5. Rayner, J. M. V. *Contemp. Math.* **141,** 351–400 (1993).
6. Rayner, J. M. V. *J. Exp. Biol.* **80,** 17–54 (1979).
7. Tucker, V. A. & Parrott, G. C. *J. Exp. Biol.* **52,** 345–367 (1970).