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DISPATCH

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Flying animals expend considerable energy. A new study reveals that bats reduce their flight power requirements by nearly a third when flying in 'ground effect' close to the surface.

Flight is an energy demanding form of locomotion, particularly at slower speeds and when taking off from the ground or water. Consequently, aerodynamic mechanisms that can save energy and reduce flight power requirements are of key importance and likely to be under strong selection. Many flying animals take off and land from the ground or water, and many birds and bats forage (and drink) close to the water or ground surface. Examples include seabirds, such as black skimmers, frigate birds and albatrosses, that soar and forage over the ocean surface for days to months at a time [1-3], barn swallows that forage for aerial prey close to the ground [4], and many waterbirds, such as cormorants, mallards and oystercatchers, that commute by flying close to the water surface [5]. Also many species of echolocating bats fly close to the ground or water [6]. By doing so, these animals regularly experience a reduction in drag due to what is commonly referred to as the 'ground effect'. Now, in a recent study in *Current Biology*, Johansson and colleagues [7] report the first experimental measurements of how ground effect influences the drag and power requirements of flight by Daubenton's bats

(*Myotis daubentonii*) (Figure 1), which drink and forage for insects on or directly above the water surface.

When a bird or a bat flies close to the ground, the surface acts as an aerodynamic mirror reducing the downwash produced by the wing [8]. This may be observed by the interruption of vortices shed from the wingtips into the animal's wake. The surface effectively reflects a 'mirror-like' upwash of air vortices, which increases the pressure under the wings and, as a result, reduces the power requirements for flight close to a surface (Figure 2). Historically, the ground effect has been modeled using steady aerodynamic theory that applies well to fixed-wing aircraft and gliding birds, bats and insects. In general, aerodynamic theory indicates that ground effect will reduce flight power costs when flying at an altitude (h) that is within one wingspan (b) from the ground or water surface (i.e., when $h/b < 1$), with flight closer to the surface requiring progressively less power. Ground effect is well recognized by aircraft pilots during take-off and landing, with appropriate adjustments in wing angle of attack and engine flight power being required; power is increased when leaving ground effect on take-off and reduced when in ground effect upon landing; otherwise, a problematic case of floating over the ground for too long may occur, leaving insufficient runway to land safely. Indeed, ground effect was of concern in the early designs of helicopters [9], enabling them to achieve sufficient power and stability when taking off and subsequently losing the reduced drag benefits further away from the ground (in the case of helicopters, this occurs at altitudes greater than their rotor's diameter).

Johansson and colleagues [7] trained Daubenton's bats to fly in a wind tunnel (in itself a significant achievement) and used a technically sophisticated state-of-the-art approach (tomographic particle imaging velocimetry) to record the three-dimensional patterns of airflow shed by the bat's wings. By analyzing the shed wingtip vortices' subsequent interaction with the ground when flying in ground effect versus when flying out of ground effect ($h/b > 1$), they were able to quantify its influence on the bats' flight power requirements. Additionally, they cleverly created a treadmill surface within the wind tunnel flight section that moved at the bat's flight speed (4.5 m/s) to ensure that the bat's relative ground speed was matched, as it would be in nature. From their airflow recordings, Johansson and colleagues [7] show that the vortices shed from the bat's wingtips dissipate and are particularly weak when the wingtips complete their downstroke close to the ground. As expected, the dissipation of wingtip vorticity is not observed when the bats fly out of ground effect, as has been previously observed in other bats [10, 11]. In comparison to the energy savings predicted by models or fixed wings based on steady aerodynamic theory (reductions of 6.5% of total flight power for a gliding bat wing and a 14% reduction in total power for a flapping wing [12]), Johansson and colleagues's [7] direct airflow imaging analysis shows a substantially greater reduction of 29% in total power when flying in ground effect.

These substantive energy savings are likely to be a significant feature of the foraging, cruising and migrating costs of birds, bats and insects that regularly fly close to the surface, significantly reducing their daily energy budgets. Additionally, in contrast to the theoretically predicted increase in energy savings when animals fly progressively closer to a surface [8], Johansson and colleagues [7] found no evidence of an effect of altitude on reductions in flight power requirements of Daubenton's bats. This absence of an effect of altitude when flying within ground effect and the more substantial energy savings that Johansson and colleagues [7] find based on their direct experimental measurements are likely to reflect the dynamics of wing-shape change (wing morphing) and flapping kinematics that flying animals employ, but which are not captured in quasi-steady aerodynamics theory applied to gliding or fixed wings. Furthermore, the anhedral position of the bat's wingtips pointing down from the body at the end of downstroke, which places them closer to the surface, provides new insight for how flapping flight can achieve greater energy savings than predicted by theory. These results point to the need for future kinematic studies of wing motion and shape change in relation to varying flight conditions, linked to experimental aerodynamics measurements as reported here [7] and computational fluid dynamics modeling.

In addition to flight in ground effect, it has become increasingly clear that flying animals regularly rely on energy saving mechanisms to reduce flight costs when foraging, commuting or migrating over longer distances. These include energy saving by means of formation flight, in which wingtip vortices shed by a leading bird's wing produce an upwash that may reduce the lift (weight-support) requirements of neighboring birds that trail the leading bird at an appropriate distance [13]. They also include energy extracted from wind shear gradients close to the ground or water that allow for dynamic soaring [2], as well as updrafts near cliff slopes [14].

Future studies that combine both field and experimental approaches to quantify animal flight performance will continue to yield new insight for evaluating existing aerodynamic theory, helping to improve the theory underlying variation in flight performance, as well as informing the engineering design of unmanned aerial vehicles. Finally, as Johansson and colleagues [7] note, the substantially reduced power requirements observed for Daubenton's bats when flying in ground effect provides new support for ground-up scenarios that have been proposed for the evolution of powered flapping flight in birds [15] and insects [16], and for the skimming flight behavior proposed for certain extinct pterosaurs [17].

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Figures.

Figure 1. The surface of the ground or water acts like an aerodynamic 'mirror' when animals fly close to the surface. Wingtip vortices that are normally shed and produce a downwash when

animals fly at higher altitude are dissipated and reflected upward by the ground, reducing the aerodynamic power requirements of flight.

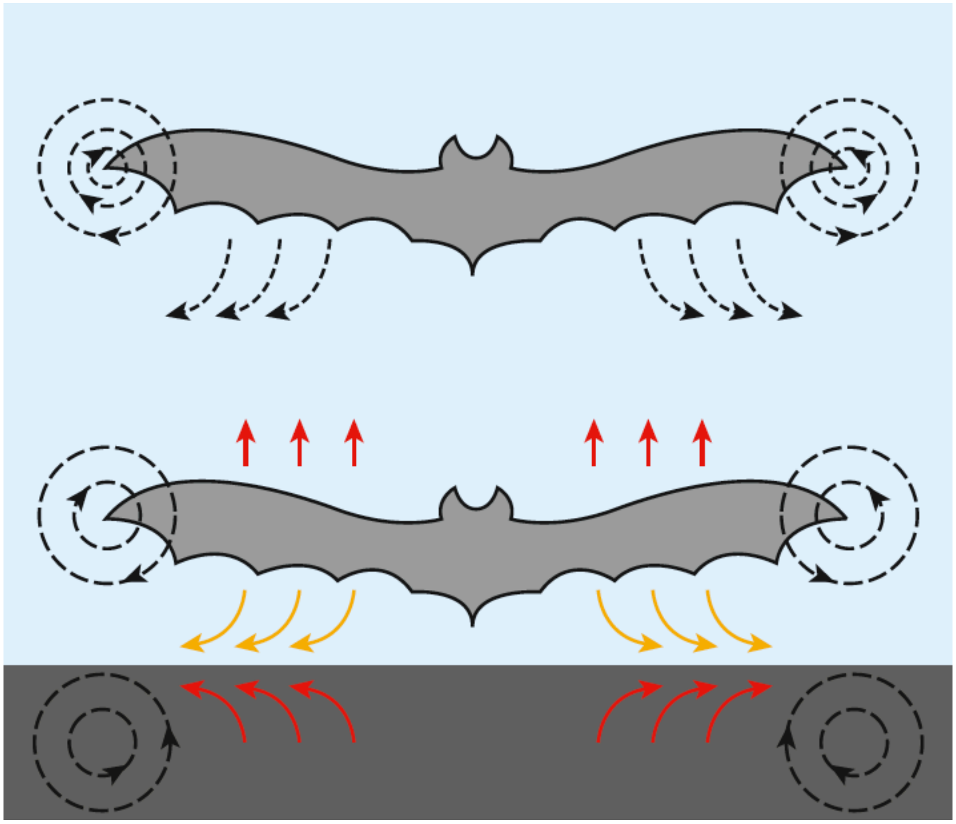

Figure 2. Daubenton's bat flying over water surface to catch a caddisfly. (Image © Paul van Hoof, courtesy of www:batconservationireland.org). NOT USED