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Inside JEB

BIRDS 'FLAP RUN' TO SAVE ENERGY


Brandon Jackson

Why don't you ever see baby pigeons? For the same reason you don't see many chicks: they can't fly. It can take months for their partially developed wings and flight muscles to become airworthy, and by then the youngsters are almost fullygrown. However, long before their maiden flight, pigeon chicks probably put their developing wings to use, flapping as they run up steep branches. Brandon Jackson from the University of Montana, USA, explains that Ken Dial and his son first noticed this strange behaviour when filming chuckar chicks negotiating obstacles: instead of flying over, the birds ran up the object flapping their wings. And when Dial discussed this behaviour with local ranchers and hunters, some described adult chukars flapping to run up cliffs. So why do adult birds flap and run up steep objects when they are perfectly capable of flying? Jackson, Dial and their colleague Bret Tobalske wondered whether pigeons might use 'flap running' to save energy, so they decided to measure the amount of power generated by the flight muscles of flap running and flying birds (p. 2354).

First, the team familiarised the birds with the ramps they were to ascend and trained them to fly to a perch so that they could compare the muscle power output from the flight muscle as the birds 'flap ran' and as they flew up at the same angle. Then they implanted sensors into the birds' wing and flight muscle to measure the power output and muscle activity. Finally, the team filmed the birds as they flap ran up an almost vertical ramp (85 deg) and a steep ramp at 65 deg, and flew at various take-off angles to the perch.

Watching the muscle activity trace as the birds flap ran up the 65 deg incline, the team could barely see any electrical activity in the flight muscle. 'We thought, "It's flapping, there must be activity," so we zoomed in on the computer screen and there was the signal, it was just over an order of magnitude smaller in amplitude,' recalls Jackson. The birds seemed to be using hardly any power to flap their wings as they ran up the slopes. And when the trio calculated the power produced by the flapping flight muscle, it was less than 10% of the power required for the bird to fly at the same angle. The flap running birds were making significant power savings in their flight muscles by flap running up slopes. The team also realised that the adults only increased their flight muscle power output by small increments as the slope angle increased.

'The basic story comes out that once you can run up a nearly vertical substrate your muscle and wings are ready to control your descent. They are ready even to fly on the level,' says Jackson. So, by building up slowly from flap running up shallow inclines to ascending steeper slopes, flap running could be an essential stage in chicks learning to fly, allowing them to build up their muscles gradually before the first take off. Jackson also adds that flap running could have been a key stage in the evolution of flight.

'At some point birds came from bipedal dinosaurs with small forelimbs that evolved into small wings,' explains Jackson. Knowing that archaeopteryx's flight muscles were probably too small to power flight, he suggests that they may have been large enough to help it flap run up steep obstacles. So, just as flap running appears to be a key stage in learning to fly, it could also have been a major breakthrough in the evolution of flight.

10.1242/jeb.061309

Jackson, B. E., Tobalske, B. W. and Dial, K. P. (2011). The broad range of contractile behaviour of the avian pectoralis: functional and evolutionary implications. *J. Exp. Biol.* **214**, 2354-2361.

Kathryn Knight

CARBONIC ANHYDRASE SHORT-CIRCUIT COULD RELEASE ROOT HAEMOGLOBIN OXYGEN

If you've ever tried scuba diving, you'll know just how tricky regulating your buoyancy is, yet fish do it with ease. So how do they suddenly inject oxygen into their buoyancy-adjusting swim bladders when the pressure exerted on them by the water can exceed tens of atmospheres? Jodie Rummer from the University of British Columbia explains that fish have a specially adapted oxygen-carrying haemoglobin that can suddenly dump all its oxygen when the conditions are highly acidic; and the swim bladder has an acid-producing gland that provides the perfect conditions. However, there is one catch: the specially adapted haemoglobin evolved 270 million years before this type of swim bladder appeared, so why did this so-called ‘Root effect’ haemoglobin evolve?

This is the question that puzzled Rummer and principle investigator Colin Brauner. They suspected that this adaptation must have evolved to deliver oxygen to muscle. But there was another catch: haemoglobin’s low affinity for oxygen under acidic conditions would make it impossible to pick up oxygen at the gill, making it almost useless as a regular oxygen deliverer. Rummer and Brauner realised that there must be some fast-acting acid switch that could trigger the sudden release of oxygen at the tissues but rapidly return the pH to neutral in the red blood cell before the blood passed back through the gills.

After months of brainstorming, Rummer and Brauner hit on an ingenious scheme that could allow the specialised haemoglobin to release oxygen in normal tissue (p. 2319). According to Rummer, stressed fish have a safety mechanism that stops their red blood cells becoming too acidic when the muscle works hard and is producing high levels of carbon dioxide that is converted into acidic protons and bicarbonate. The pair also knew that a hormone called noradrenaline switches on a pump that pumps protons out of the cell and into the plasma to maintain a neutral pH in the red blood cell so that the haemoglobin it carries is ready to pick up oxygen when it returns to the gill. The duo realised that fish could short-circuit this protection mechanism and send the red blood cell pH plummeting, but only if there was an enzyme called carbonic anhydrase in the plasma to recombine the acid protons and bicarbonate into carbon dioxide that could quickly diffuse back into the red blood cell. This would drop the red blood cell pH instantaneously to cause an acidosis and release the oxygen.

The duo had to test the idea. ‘We have these three elements that have to happen: we have to have blood that is acidified, is exposed to noradrenaline and the plasma must be exposed to carbonic anhydrase,’ explains Rummer. So she incubated trout blood with carbon dioxide to produce acidic conditions, switched on the protective acid-extracting pump with an analogue of noradrenalin and then added carbonic anhydrase to see if the haemoglobin would release its oxygen.

Amazingly, it did. The carbonic anhydrase short-circuited the protective pump, creating the acidic conditions that would release the oxygen from the red blood cell’s haemoglobin. And Rummer calculates that the drop in red blood cell pH could release 25 times more oxygen than if the pH remained neutral. The team also found that there could be other acid-pumping systems on the red blood cell membrane that could enable oxygen delivery by the specialised haemoglobin even at moderate activity levels.

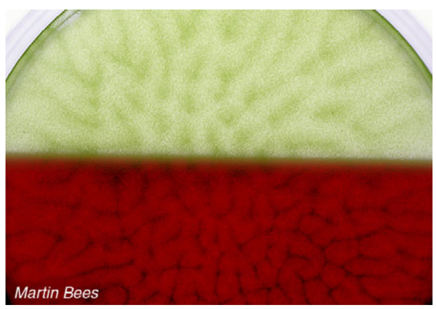
So, having found that the fish’s specialised haemoglobin could – in theory – have evolved to deliver oxygen to exercising muscles, Rummer and Brauner are keen to find out if fish do this in practice.

10.1242/jeb.061291

Rummer, J. L. and Brauner, C. J. (2011). Plasma-accessible carbonic anhydrase at the tissue of a teleost fish may greatly enhance oxygen delivery: *in vitro* evidence in rainbow trout, *Oncorhynchus mykiss*. *J. Exp. Biol.* **214**, 2319-2328.

Kathryn Knight

HOW ALGAE RESPOND TO DIM AND BRIGHT LIGHT



At first glance, you might think that a well-stirred vat of *Chlamydomonas augustae* algae was simply a suspension of inert green goo; but you’d be wrong. Swimming away from bright light, toward dim illumination and against gravity, the algae eventually set up bioconvection flows. They form intricate swirling patterns that allow light to penetrate deep in the suspension and promote nutrient and gas mixing to keep the algae well supplied. But no one had systematically investigated the effect that different light intensities and illumination orientation had on the algal distributions. Rosie Williams and Martin Bees from the University of Glasgow explain that finding optimal algal growth conditions is essential for industries that hope to exploit algae for biofuels and vegetable oil production. So, they decided to illuminate algae to find out how light influences the distribution of algal suspensions (p. 2398).

Varying the concentration of algae exposed to white light and analysing the mottled distributions, the team saw that the more concentrated algal suspensions formed patterns more quickly than the dilute samples. Also, the pattern formed by the concentrated algae was much finer and more tightly packed than the relatively diffuse pattern formed by the dilute algae. In addition, the duo found that the algae did not respond at all to red light, producing patterns on the same scale regardless of the light’s intensity. ‘This lack of response implies that illumination by red light is equivalent to practically no illumination,’ say Williams and Bees.

Focusing on the effect of white light intensity on the algal distribution, the duo illuminated algal suspensions from below with light intensities ranging from a dim 645 lx to a bright 4780 lx. They saw that the patterns became tighter as the intensity increased to 2020 lx. Then, as the intensity increased to 2710 lx, the pattern’s distribution became more sparse and, although each pattern was distinct, they all reformed on the same scale when the experiments were repeated at the strongest light intensities.

However, when the duo illuminated the algae from above, the algae behaved differently. This time the pattern became more diffuse as the intensity rose from 645 lx to 1330 lx, before tightening again as the illumination became brighter.

‘To explain these results, we recall that there is a competition between bottom-heavy induced upswimming (gravitaxis), gyrotaxis due to viscous and gravitational torques and phototaxis towards/away from weak/bright light, distinguished by the critical light intensity,’ the duo says. They also add that their observations agree qualitatively with theoretical predictions, although they admit that making comparisons between theoretical and experimental observations is difficult. Ultimately, Williams and Bees hope to be able to refine their measurements to obtain better estimates of the critical light intensitys at which the algae are no longer attracted to or repelled by light.

10.1242/jeb.061317

Williams, C. R. and Bees, M. A. (2011). A tale of three taxes: photo-gyro-gravitactic bioconvection. *J. Exp. Biol.* **214**, 2398-2408.

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