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INSIDE JEB

Slap keeps rushing grebes afloat

A western grebe and a Clark's grebe rushing. Photo credit: Susan Bissell

For true ballet aficionados, a snowy corps de ballet sailing across the stage in Swan Lake is one of the pinnacles of the classical cannon. But for ballerina Glenna Clifton, there is a duet that surpasses even the finest human performances. Recalling the remarkable 'rushing' behaviour of courting grebes – where the birds literally run across the surface of the water – Clifton describes the gravity-defying display as a beautiful pas de deux. Yet, little was known about the forces that maintain the birds above the water as they sail gracefully over the surface. Explaining that she was already interested in bird swimming, Clifton and her thesis advisor, Andrew Biewener, decided to unite her two passions and take a closer look at the birds' extraordinary courtship display. However, rushing is a natural behaviour that can only be seen in the wild, so instead of bringing the birds to Biewener's Harvard laboratory, Clifton relocated to the grebes' southern Oregon mating grounds.

Setting up a pair of high-speed cameras 40 m apart on the southern edge of the Upper Klamath Lake with field assistants Autumn Turner and Matthew Wysocki, Clifton soon became accomplished at predicting when a small number of the birds were about to rush: leaving the scientists as little as 8 s to accurately train both of the cameras on the birds to capture their manoeuvres in fine detail. And the fun and games didn't end there. Clifton explains that the team also filmed a short pole mounted on a remote control boat at the location where the grebes had just been moving, which they could use as a reference to reconstruct the 3D position of the grebes from the 2D movies. Eventually, after discarding hundreds of shots because of filming issues and even more after Ty Hedrick's help with the 3D calibration, Clifton was left with 100 reliable movies. Tracking the progress of the birds' beaks to measure their speed, Clifton could see that the grebes achieved speeds of up to 4 m s^{-1}, while their feet rattled along at insanely high step frequencies of up to 20 steps per second.

However, when she scrutinised the video in more detail, only two of the hard-won movies showed the movements of the birds' feet in sufficient detail to deconstruct the dainty footwork, allowing her to see all three forward-pointing toes splayed wide as the bird slapped its foot down onto the water. And when she analysed how they withdrew their feet at the end of a stride, she was surprised to see that they rotated the lower leg and pulled the foot out to the side. Clifton also noticed that the three front toes collapsed on top of each other as the foot withdrew from the water, forming a single streamlined super-toe to reduce drag.

Having revealed the movements that contribute to keeping the running birds afloat, Clifton turned to models of grebe feet to learn more about the forces that buoy them up. Plunging foot reconstructions into a bucket of water and measuring their velocity and deceleration traces as they hit the surface, Clifton calculated that the birds could generate up to 55% of the impulse required to remain above the water when they slapped the foot down. However, as she was unable to see what is going on beneath the water, Clifton is less certain about how grebes generate the additional force that is necessary to remain above the surface, but suspects that the birds sweep their feet like oars beneath the water to generate the additional lift required to keep them afloat.

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Clifton, G. T., Hedrick, T. L. and Biewener, A. A. (2015). Western and Clark's grebes use novel strategies for running on water. *J. Exp. Biol.* **218**, 1235-1243.

Kathryn Knight

Inside JEB highlights the key developments in The Journal of Experimental Biology. Written by science journalists, the short reports give the inside view of the science in JEB.

Ectotherms' cardiovascular upgrade for endothermic lifestyle

The ectothermic cane toad (*Rhinella marina*). Photo credit: Robert Drewes

Keeping warm has its advantages. Endotherms, which maintain a constant raised body temperature, keep going no matter how chilly their surroundings. Meanwhile, ectotherms are at the behest of the environment: many have to sit tight until they have absorbed enough warmth to function. But which physiological systems did our ectothermic ancestors have to upgrade for us to benefit from internal central heating? Stanley Hillman from Portland State University, USA, and Michael Hedrick from California State University East Bay, USA, explain that there are two competing theories: that ectotherms increased the number of mitochondria in muscle and modified the energy-producing organelles to upgrade to an endothermic lifestyle; or, our ancestors expanded the cardiovascular system to supply the additional oxygen required to fuel our costly, high-temperature way of life. With evidence stacking up on both sides, Hillman and Hedrick decided to review the differences between the cardiovascular systems of ectotherms and endotherms to find out whether expanding the cardiovascular system allowed endotherms to turn up the thermostat.

First, the duo scoured the literature for cardiovascular measurements from a wide range of exercising animals – from ectothermic fish and amphibians to endothermic birds and mammals – to put their theory to the test. But there was one glaring omission: 'a gap existed in the data for reptiles for [cardiac] flow and pressure during exercise', they say, before accepting – after contacting many colleagues – that the measurements have yet to be made. However, despite the setback, they interrogated the data to identify differences between the cardiovascular systems of exercising ectotherms and endotherms to find out just how hard the animals' hearts can work.

Calculating the vascular conductance, cardiac power and work done per heart beat (stroke work), Hillman and Hedrick found that endotherms' hearts pumped blood at a higher pressure (17.1 kPa vs 3.3 kPa for the ectotherms) and at a higher heart rate (~5 beats s^{-1} compared with the ectotherms' ~1 beat s^{-1}), allowing the exercising endotherms to produce higher exercise cardiac power. And when they compared the relative size of the endotherms' and ectotherms' hearts, they found that the endotherms' larger hearts enabled them to increase their blood pressure. They say, 'A major difference between ectotherms and endotherms is the large increase in blood flow rates', which is largely due to their higher heart rates and allows endotherms to increase the oxygen supply to the power-hungry muscles that keep them warm. However, the duo also found every mW of cardiac power supports a remarkable 158 mW of aerobic power output (which is only 0.6% of the exercise aerobic energy expense) regardless of the animal's lifestyle, showing that the cost of circulation is low for endo- and ectotherms alike.

Focusing on the cardiac changes that were essential for ectotherms to warm up, Hillman and Hedrick explain that our ancestors had to remove the cardiac shunts – which allow amphibians and reptiles to mix oxygenated and deoxygenated blood – to increase oxygen transport. They also had to increase their heart rates by developing the sarcoplasmic reticulum – which controls the calcium levels in muscle that regulate muscle contraction – to increase the heart rate. And finally, endotherms had to increase their cardiac muscle mass relative to the body mass of similarly sized ectotherms to produce the higher blood flow rates that are essential for a metabolically demanding endothermic lifestyle.

The duo says, 'These results suggest that a key step in the support of endothermy was the greatly enhanced ability of the cardiovascular system to deliver oxygen which accounted for the approximately ten-fold increase in aerobic scope between endotherms and ectotherms'.

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Hillman, S. S. and Hedrick, M. S. (2015). A meta-analysis of *in vivo* vertebrate cardiac performance: implications for cardiovascular support in the evolution of endothermy. *J. Exp. Biol.* **218**, 1143-1150.

Kathryn Knight

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Fish-eating myotis pay metabolic cost of protein diet

Most animals don't think twice about the cost of dragging a large digestive tract around, but for tiny bats and birds the costs can be substantial. Kenneth Welch, from the University of Toronto Scarborough, Canada, and colleagues Aída Otálora-Ardila, Gerardo Herrera and José Flores-Martínez from the Universidad Nacional Autónoma de México, explain that flying vertebrates tend to have much shorter digestive tracts than similarly sized land-based animals. However, the bat's reduced digestive system may restrict the animal's ability to fuel their costly aerial lifestyle. Puzzled by the apparent paradox, Welch and his colleagues began investigating how one bat, the fish-eating myotis (*Myotis vivesi*) from the Sea of Cortés deals with shrimp meat meals.

Feeding the minute mammals (∼28 g) 1.5 g and 3 g shrimp banquets (∼5% and ∼10% of their body mass), the team measured the bats' O_2 consumption and CO_2 production rates for up to 5 h, and found a massive increase in their O_2 consumption within 20 min of tucking in. O_2 consumption rocketed by 3 times after the 1.5 g meal and soared to 4.3 times the resting metabolic rate while the bats were digesting the enormous 3 g meal. Could the immense metabolic investment accelerate digestion to cut their overall energy costs? However, when the team tracked how long it took the tiny animals to process the meals, they were surprised to see that instead of extracting the goodness faster, the bats were taking up to 5 h to digest the largest meal. And when the team analysed the ratio of CO_2 production to O_2 consumption, they were surprised to see that instead of rising (as a result of the increased levels of bicarbonate in the blood associated with acid production for digestion), the ratio inexplicably fell.

So, fish-eating myotis pay a high metabolic price for their protein diet, and the team says, 'The rate of prey digestion may limit food intake rate'. They also add that the cost of digestion may vary seasonally as the bats switch diet from lipid-rich fish in the autumn to almost total reliance on crustaceans in winter, so the team hopes to learn more about the complex interactions between the ecology and physiology of these tiny animals.

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Welch, K. C. Jr, Otálora-Ardila, A., Herrera M., L. G. and Flores-Martínez, J. J. (2015). The cost of digestion in the fish-eating myotis (*Myotis vivesi*). *J. Exp. Biol.* **218**, 1180-1187.

Kathryn Knight
Kathryn@biologists.com

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