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Inside JEB

WHY BIG PEOPLE WALK MORE ECONOMICALLY THAN SMALL PEOPLE

Any parent that takes their kid out for a walk knows that children tire more quickly than adults, but why is that? Do kids and small adults walk differently from larger people or do they tire faster for some other reason? Peter Weyand from Southern Methodist University, USA, is fascinated by the effect that size scaling has on physiological function. ‘This goes back to Max Kleiber’s work on resting metabolic rates for different sized animals. He found that the bigger you are the slower each gram of tissue uses energy,’ explains Weyand, who adds, ‘It’s interesting to know how and why metabolism is regulated that way.’ Intrigued by the question of why smaller people use more energy per kilogram body mass than larger individuals when walking, Weyand teamed up with Maurice Puyau and Nancy Butte, from the USDA/ARS Children’s Nutrition Research Center at Baylor College of Medicine, and undergraduate Bethany Smith. Together they decided to measure the metabolic rates of children and adults, ranging from 5 to 32 years old, weighing between 15.9 kg and 88.7 kg and ranging in height from 1.07 m to 1.83 m, to try to find out why big people are more economical walkers than smaller people (p. 3972).

First Weyand and colleagues filmed male and female volunteers as they walked on a treadmill at speeds ranging from a slow 0.4 $m\,s^{-1}$ up to 1.9 $m\,s^{-1}$. Meanwhile, they simultaneously measured the walkers’ oxygen consumption and carbon dioxide production rates to obtain their total metabolic rate. Next the team calculated the amount of energy that each person used for walking by subtracting the basal metabolic rate (energy required to maintain the body’s basic metabolic functions) from the total metabolic rate. Finally, the team compared the way each person walked, measuring the walkers’ stride lengths, stride durations and the proportion of each stride they spent in contact with the ground (duty factor) to find out if large and small people walk differently.

Analysing the walkers’ styles, the team found that all of them moved in exactly the same way regardless of their height. Essentially, if you scaled a 5 year old up to 2 m, the giant child would walk in exactly the same way as a 2 m tall adult. So large people are not more economical because they walk differently from smaller people.

Next the team calculated the metabolic cost of a stride as each walker moved at their most economical pace and they discovered that walkers use the same amount of energy per stride regardless of their height. So, big people do not become more economical because they walk in a more economical style. Something else must account for their increased economy.

Finally, the four scientists plotted the walkers’ heights against their minimum energy expenditure and they were amazed when they got a straight line with a gradient of almost –1. The walkers’ energy costs were inversely proportional to their heights, with tall people walking more economically than smaller people because they have longer strides and have to take fewer steps to cover the same distance. So smaller people tire faster because each step costs the same and they have to take more steps.

Based on this discovery the group derived an equation that can be used to calculate the energetic cost of walking. ‘The equation allows you to take your height and weight and plug it in and say if I walk this far and I’m this tall and I weigh this much here’s how many calories I burn,’ says Weyand. The team is also keen to extend the equation to calculate metabolic costs at any speed. ‘This has clinical applications, weight balance applications and the military is interested too because metabolic rates influence the physiological status of soldiers in the field,’ explains Weyand.

10.1242/jeb.052902

Weyand, P. G., Smith, B. R., Puyau, M. R. and Butte, N. F. (2010). The mass-specific energy cost of human walking is set by stature. *J. Exp. Biol.* **213**, 3972-3979.

ROBOFIN PRODUCES THRUST WHEN OTHER FINS DRAG

Bluegill sunfish have an agility that human engineers can only marvel at. Their repertoire includes hovering, reversing and spinning around, and they achieve all this with deft moves of their fins. James Tangorra from Drexel University, USA, explains that bluegill sunfish pectoral fins are particularly remarkable because they generate forward thrust even when they are swept forward against the flow. Intrigued by the fin's remarkable ability to generate thrust when other fins produce drag, Tangorra and his colleagues, George Lauder, Ian Hunter, Rajat Mittal, Peter Madden and Meliha Bozkurttas, decided to build a robotic fin to see if they could replicate the fish's remarkable fluid dynamics and thrust characteristics (p. 4043).

First the team analysed the fin's complex manoeuvres. Tangorra explains that the fin is composed of 14 rays spanned by a membrane, so Lauder and Madden digitised 300 points on the surface of swimming fish fins to define the fin's movements. Then, Mittal and Bozkurttas analysed the kinematics and calculated the fluid flows over the surface to find out how the fin generated thrust. Having identified key aspects of the fin's motion, the team realised that they could simplify its structure down to five key rays to reproduce the fin's complex motion. Next, Tangorra and Hunter built a series of seven robot fins where they varied the taper and flexibility of the rays in an attempt to reproduce the fin's flowing movements. Sewing flexible polyester/elastane weaves between the rays to reproduce the membrane, Tangorra programmed each of the rays to replicate the sunfish's complex movements as the fin flapped. Then the team measured the forces on the rays and visualised the spinning vortices generated by the fin pushing against the water as they 'swam' the fin in still and flowing water.

Analysing movies of the robofin movements, the team could see that the most flexible rays produced the most realistic swimming action, while the fins with stiffer rays move more rigidly. And when the team compared the forces generated by the fins, they found that fins with the most flexible rays produced thrust even when the fin was being swept forward, while stiffer fins produced drag as they were swept forward. Tangorra explains that the fin's flexibility, coupled with the cup shape that it forms as it sweeps forward, produces thrust when other fins generate drag. Finally, when the team visualised the fluid flowing over the robofins, they found that the robots produced realistic fluid flows, replicating the spinning vortices that Lauder had seen when looking at the swimming fish.

Thinking about the ways that fish adjust thrust production as they move, Tangorra says, 'It was really nice to see how this fin structure got tuned… you can stiffen it up and the forces change drastically'. He adds, 'Sunfish have a way of modulating the mechanical properties of the fin so that when they want to swim forward and have a continuous thrust, they are able to do so, and we are now able to do the same with this robotic system.' Considering how the fish control thrust production from an engineering perspective, Tangorra points out that fish produce this remarkably fine control with remarkably low power controls – central pattern generators – and concludes, 'I think that this is a model that engineers are fascinated by and want to learn from.'

10.1242/jeb.052910

Tangorra, J. L., Lauder, G. V., Hunter, I. W., Mittal, R., Madden, P. G. A. and Bozkurttas, M. (2010). The effect of fin ray flexural rigidity on the propulsive forces generated by a biorobotic fish pectoral fin. *J. Exp. Biol.* **213**, 4043-4054.

DIVING LEATHERBACKS REGULATE BUOYANCY

Leatherback turtles are remarkably versatile divers. Routinely diving to depths of several hundred metres, leatherbacks are occasionally known to plunge as deep as 1250 m. The animals probably plumb the depths to avoid predators, search for prey and avoid heat in the tropics. However it wasn't clear how these mammoth reptiles regulate their buoyancy as they plunge down. Sabrina Fossette from Swansea University explains that no one knew how the turtles descended so far: do they swim down or become negatively buoyant and plummet like a stone? Curious to find out how nesting leatherbacks dive, Rory Wilson and his long time collaborator, Molly Lutcavage, decided to deploy data loggers containing triaxial accelerometers on leatherback females as they nested on beaches on St Croix in the US Virgin Islands (p. 4074).

'When you first see a leatherback turtle coming out of the water, it's like a dinosaur, it's really impressive,' says Fossette, having just returned from collecting data in the Indian Ocean. Three members of the team, Andy Myers, Nikolai Liebsch and Steve Garner, attached accelerometers to five females as they laid their eggs, and then waited 8–12 days for the reptiles to return to the beach to lay more eggs. Retrieving the accelerometers, the team found that only two of the five had collected usable data, but the data loggers that functioned showed 81 dives that the team could analyse, ranging from 64 m down to 462 m.

Back in Swansea, Fossette, Wilson and their colleagues Adrian Gleiss and Graeme Hays analysed the temperature, pressure and acceleration data collected by the loggers. Describing the accelerometer data, Fossette says, 'You can almost see the animal swimming. It's the first time we could see the locomotor activity during those deep dives.'

Extracting the acceleration data that showed the leatherbacks' movements, the team could see that the turtles dived deeply at an average angle of 41 deg as they began their descent. Initially the turtles swam with each flipper stroke lasting 3 s, but as they descended further they swam less hard until they stopped swimming altogether, became negatively buoyant and began gliding down. At the bottom of the dive, the turtles began swimming as they headed to the surface and continued swimming until they regained buoyancy near the surface and began gliding again.

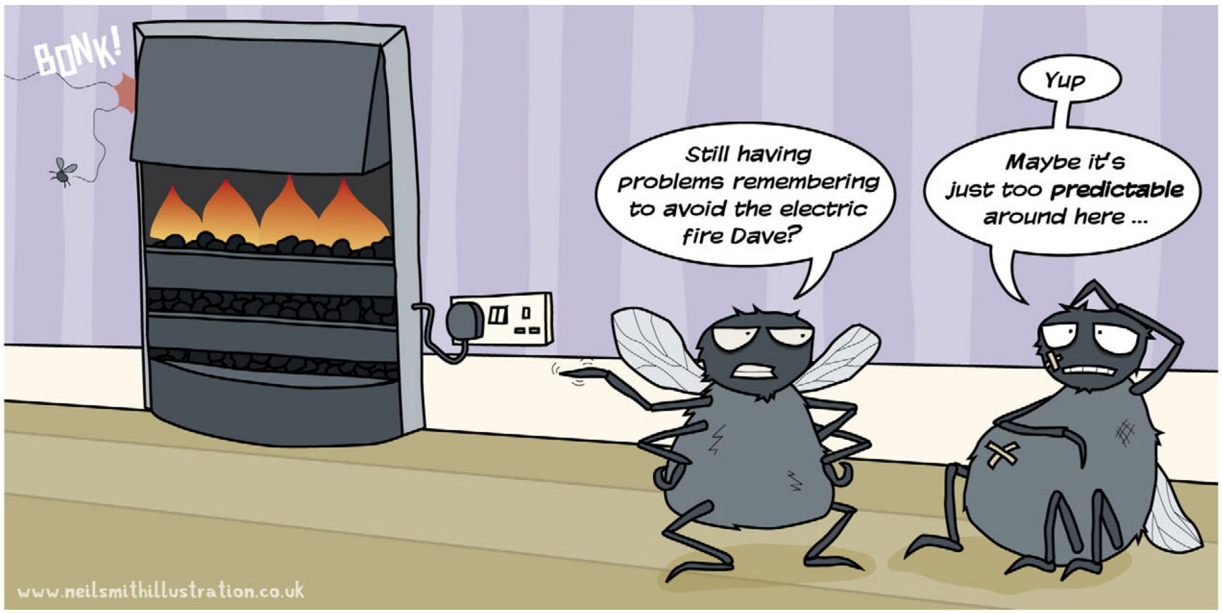
Fossette explains that many diving animals exhale before they leave the surface to minimise the risk of decompression sickness; however, leatherbacks do not. They dive carrying a lungful of air. Curious to find whether leatherbacks vary the amount of air that they inhale to regulate their buoyancy, Fossette and Gleiss compared the depths at which the turtles became negatively buoyant with the maximum depth that they reached. The team found that the deepest divers remained buoyant the longest and started gliding at deeper depths. So the turtles probably regulate their buoyancy before diving by varying the amount of air they inhale. Fossette also says, 'The nesting turtles may glide for 80% of the dive's descent to optimise their energetic reserves, which is crucial for the production of eggs.'

The team is now keen to look at the diving patterns of leatherbacks in their foraging grounds in the North Atlantic. Fossette explains that nesting turtles lose weight while foraging turtles are gaining weight and this could affect their buoyancy and diving behaviour. However, tagging a 400 kg turtle in the ocean is a much bigger problem than tagging them on a beach.

10.1242/jeb.052928

Fossette, S., Gleiss, A. C., Myers, A. E., Garner, S., Liebsch, N., Whitney, N. M., Hays, G. C., Wilson, R. P. and Lutcavage, M. E. (2010). Behaviour and buoyancy regulation in the deepest-diving reptile: the leatherback turtle. *J. Exp. Biol.* **213**, 4074-4083.

UNPREDICTABILITY HELPS FLIES REMEMBER TO AVOID HEAT



Having a good memory can save your life, and smart creatures that learn to avoid bad situations (or home in on good ones) do better than animals that don't. However, life is unpredictable and it isn't always possible to base memories on established patterns. Divya Sitaraman and Troy Zars from University of Missouri, USA, explain that heat kills and *Drosophila* remember to avoid hot places better after random doses of heat. However, it wasn't clear whether it was the high temperature that enhanced the insect's memory or the unpredictable pattern. Sitaraman and Zars tested two groups of insects, one that had control over the thermostat and another that did not, to find out whether the high temperature or random temperature fluctuations primed the insect's memory (p. 4018).

First the team exposed one group of insects to a predictable pattern of high temperature fluctuations that the flies controlled by moving to one end of the arena, and a second group of insects to the same temperature fluctuations as the first, but with no control over the pattern, so that it occurred randomly as far as the insects were concerned. Having exposed both groups of insects to heat fluctuations, the team trained the insects to avoid one end of the arena by raising the temperature when the insects ventured there. Finally, the team tested the insects' memories by seeing whether they would remember to avoid the area that caused the temperature to rise, to see if the unpredictable pre-training heat pattern or just exposure to high temperatures had improved the insects' memories.

Amazingly, the memories of the flies that had experienced an unpredictable pre-training temperature pattern were twice as good as the flies that experienced a predictable pre-training temperature pattern: they were better at avoiding the end of the arena. So unpredictability enhanced memory formation in the flies. Sitaraman and Zars suspect that the flies store the unpredictable information in a 'buffering system'. When the insects receive more accurate information about threatening temperatures the buffering system is released, improving the insects' memories.

10.1242/jeb.052936

Sitaraman, D. and Zars, T. (2010). Lack of prediction for high-temperature exposures enhances *Drosophila* place learning. *J. Exp. Biol.* **213**, 4018-4022.

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