Keeping track of the literature isn't easy, so Outside JEB is a monthly feature that reports the most exciting developments in experimental biology. Short articles that have been selected and written by a team of active research scientists highlight the papers that JEB readers can't afford to miss.

Outside JEB

PREDATION

THE HUNTING OF THE SHREW

When humans think 'fast predator', we typically think of charismatic megafauna (e.g. the cheetah, the shark, the eagle). Often times though, tiny predators are proportionally more impressive. One of the fastest mammalian predators is actually not the cheetah, but the very small and common American water shrew, *Sorex palustris*. Inhabiting streams across North America, these ferocious predators wake after sunset to go on the hunt, eating virtually any animal that they can overpower. Importantly, a big part of shrew cuisine consists of fish and other things that move really fast underwater. This is particularly impressive given the sorry state of the shrew visual system. Water shrews have terrible eyesight. So how does a virtually blind animal hunt so well in such a dark place? Ken Catania and colleagues recently addressed this question by bringing water shrews into the lab and filming them while they hunted.

In their first set of experiments, Catania and coworkers provided sound evidence that shrews hunt the same regardless of whether it's light or dark. The authors noticed that shrews appeared to respond to water currents generated by fish movements. To study this further, the team put individual animals in chambers ringed with controllable water jets and tested how the aquatic hunters oriented to puffs of water coming from different directions. Indeed, shrews launched predatory lunges with their 'mouths agape' in response to small pulses of water. These attacks were not random; the targets were clearly the offending water jets. Understandably, the shrews then interrogated the nozzles using a behavior (underwater sniffing) known to be involved in olfactory investigation. These observations argue that the little rodents cue in on water movements and smells while hunting.

Catania and colleagues next tested the idea that shrews also cue in on the shape of a potential prey item, not just how it moves or smells. To test this, they let hungry shrews loose in a tank with silicone 'prey' of various shapes. In amongst all the shapes was a fish replica cast in silicone. The little hunters were not fooled. After a brief search, they clearly attacked the 'fish shape' more often than the 'non-fish shape.' In addition, when presented with stationary objects of different shapes, shrews showed more interest in objects shaped like common prey items, and they did all of this in the dark. These results imply that shape detection by touch is a key component of underwater hunting behavior in water shrews.

The team found no evidence that shrews use other more sophisticated remote hunting techniques. Tests for electroreception or echolocation abilities came up negative. It appears the animals have evolved a foraging strategy that is based, instead, on detecting form and movement while continuously sampling odors under water.

It is important to note just how stunningly fast these shrews move while foraging. Seeing them in action leaves one breathless. These animals are going from raw sensory input to coordinated motor output in ~20 ms. This kind of speed is very rare among other vertebrates. We know very little about how the nervous system does this, but one thing is for sure: this animal's nervous system has evolved for speed.

This study highlights the fact that fast, fearsome predators come in all shapes and sizes and many of them live right in our backyards. This work is also notable because it started with a very simple natural history observation (shrews catch fish). Many of the great stories in animal behavior research have started out with just that kind of observation. It is inspiring to see that new work on a unique and beautiful animal can still be started in the same way.

10.1242/jeb.010983

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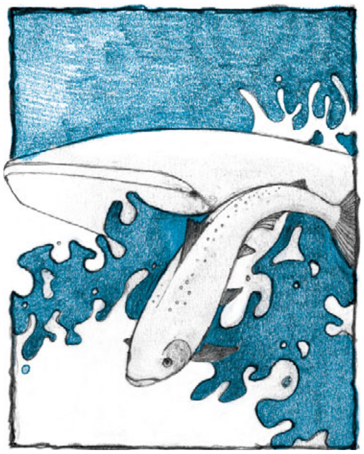
HIBERNATION



WINTER HIBERNATION FOR ANTARCTIC FISH

Many terrestrial animals save valuable energy reserves during icy winters by going into a state of dormancy or hibernation. While some fish show signs of reduced activity, feeding and growth during winter (all characteristics suggestive of hibernation), fish are thought to differ fundamentally from terrestrial hibernators. This is largely because metabolism is directly coupled to environmental temperature: any dip in metabolism is usually explained by a drop in temperature. But two key facts suggest that Antarctic fish might not have read the textbook. First, large variations in annual growth patterns occur in these fish, suggesting that they reduce their food intake; even when food is abundant, dramatic changes in growth are visible during the winter. Second, sea temperatures in the Antarctic, while chilly, are not particularly cooler in the winter than in the summer; these marine environments have relatively constant temperature. This indicates that potential dips in metabolism are probably not strictly temperature driven. So is it possible that Antarctic fish undergo hibernation in the wild?

Hamish Campbell and Stuart Egginton, of the University of Birmingham, and their collaborators Keiron Fraser, Lloyd Peck and Charles Bishop at the British Antarctic Survey and the University of Bangor in Wales joined up at Rothera Research Station in Antarctica to tackle this intriguing question. Working on the notothenoid fish, *Notothenia coriiceps*, Campbell and the team investigated the fish's behavioural and metabolic strategies over a complete annual cycle using three approaches. First, they monitored growth and feeding in immature adult fish by capture–recapture techniques and found that whilst growth was higher than in temperate fish during summer months it was negative during winter. Second, the activity of fish was monitored remotely by implanting acoustic radio-transmitters. These data clearly showed a 20-fold reduction in activity and a 6-fold reduction in home range during winter compared with summer. Third, they estimated metabolic rate in the field and in the laboratory to establish whether metabolism dropped in winter and, if so, whether this change is controlled by environmental temperature variation.

To estimate metabolic rate in the wild, the team surgically implanted individual fish with a tiny data logger. However, because these loggers only record heart beats, the team needed to calibrate heart rate frequency with metabolic rate. After laboratory trials on a number of fish, and with the relationship between heart rate and metabolic rate established, the team then used fish with implanted loggers to quantify typical summer and winter energy consumption.

The total cost of living in the wild (field metabolic rate) showed a clear 58% drop from 3.59 to 1.48 mg O_2 100 g^{-1} h^{-1} between summer and winter. In the laboratory, respirometry experiments showed a seasonal 29% dip in standard metabolic rate (the resting cost of physiological processes), and reversing summer and winter water temperatures produced no significant change in standard metabolic rate. This indicates hibernation, rather than temperature-dependent metabolic rate variation. But the final proof that hibernation occurred in these fish was that SCUBA divers visiting the fish during the middle of winter found them unresponsive to handling. By contrast, simply catching these fish by hand in summer was nearly impossible.

Therefore, Campbell and co-workers have neatly demonstrated that *N. coriiceps* can in fact enter a hibernation-like state in Antarctic winters. Furthermore, the team propose that this state might be induced by changes in photoperiod characteristic of the onset of winter in polar environments. Finally, they suggest this sort of energy-saving metabolic strategy may have contributed to the remarkable success of these fish in the Southern Ocean.

10.1242/jeb.010967

Campbell, H. A., Fraser, K. P. P., Bishop, C. M., Peck, L. S. and Egginton, S. (2008). Hibernation in an Antarctic fish: on ice for winter. *PLoS One* **3**, e1743.

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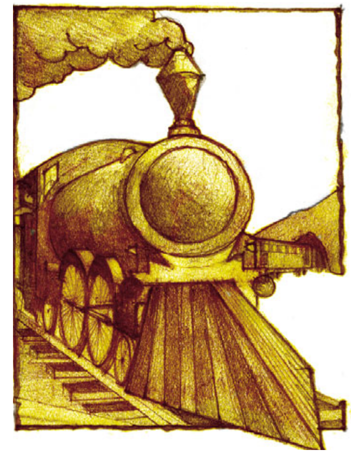
GLIDING



NOT FALLING BUT GLIDING

Measuring anything about a nocturnal mammal as it glides from tree to tree through the steamy, cluttered Singaporean forest is quite a daunting prospect, best tackled by a team of dedicated field biologists, electronic wizardry and superglue. But this was the challenge that Greg Byrnes, Norman Lim and Andrew Spence were well prepared to rise to. They pooled their skills, and succeeded in attaching backpacks containing accelerometers, data-loggers and radio telemetry tags to six wild colugos (aka 'flying lemurs'), allowing them to study gliding under truly wild conditions.

Colugos are not mere squirrels with small flaps of skin between the legs. In fact, they are closely related to primates (diverging only 87 million years ago), and have extremely elongate, slender limbs, supporting a huge area of skin – they truly are dermopterans (literally 'skin wings'). But how often do our close relatives actually glide in the wild? How good a glide can they perform? (And how bad a glide do they habitually survive?) Impossible questions for traditional laboratory or field studies to answer, but now approachable with advances in lightweight sensors and data-loggers.

In some respects, the project sounds simple enough: catch six animals, glue on a backpack, let the animals do their thing for 2 to 6 days, then use the telemetry tags to find where the backpacks fell off so that the data loggers can be recovered. However, the logistics required to achieve this goal are impressive: the whole backpack weighed less than 30 g, less than 4% of the animal's body weight and far less than the load they carry when gliding with their young (Greg has observed gliding culogos carrying young weighing 400 g!); the data loggers held a total of 430 h of data, recording 222 glides; all but one logger was recovered. And afterwards, the animals are at liberty to roam free unharmed.

So, what can be deduced from all these 3D accelerometry data? For a start, the team measured glides lasting up to 15 s. Take a moment to consider just how impressive a 15 s glide is. I would hit the ground within 5 s if I fell out of the tallest tree in the world, so these mammals' ability to remain airborne is quite remarkable. The team also analysed the accelerations during the leap and landing to determine peak take-off and landing forces, and the velocity when coming in to land. Unsurprisingly, glides of longer duration were initiated with bigger leaping impulses. More interestingly, landing after brief glides included the highest forces. It appears that, once the animal has been gliding for more than 4ish seconds, it can use aerodynamics to control its landing speed and forces. Just as for parachutists, it may be the jump from a low height that presents the greatest risk of injury, as the aerodynamic surfaces take time to be deployed and develop lift and drag.

The next step – or should that be giant leap? – is to incorporate miniature gyroscopes or magnetometers in order to get a dynamic measure of orientation throughout the glides. When and how much do they pitch to control their landing? How much can they steer? How stable – or manoeuvrable – are they? Further extending this work to trustworthy measurements of velocity and displacement for glide periods exceeding 15 s will present a considerable technical challenge – and another significant milestone. And at this stage it will be possible to really understand the performance envelope of these extreme gliders.

10.1242/jeb.010959

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PARASITES WITH BENEFITS

Throughout evolution, plants and insects have exploited each other in mutually beneficial relationships where two or more parties benefit from essential ecological interactions. For example, insects act as plant pollinators while plants act as hosts providing food or housing for insect offspring. Such partnerships often require a delicate balance of give and take. Recently, a group from Imperial College of Science, Technology and Medicine (London) led by James M. Cook questioned the intrinsic risk of such cooperative relationships. They investigated the relationship between fig trees and pollinator wasps, with the intention of finding what keeps one partner from taking advantage of the other.

Conditions favoring one partner over the other constantly threaten to erode the balance in mutually beneficial relationships. For example, when a female pollinator wasp pushes her way into a fig blossom, pollinating the tree while depositing her eggs, the tree loses one seed. The sacrifice is offset for the tree by the fact that each egg laid produces the offspring that will emerge and eventually disperse that tree's pollen. Still, what keeps the wasp from taking advantage of the host and destroying the tree's entire crop?

As is often the case, there are more than two players in this relationship. The fig tree also plays host to small parasitic wasps that attack pollinator wasp larvae in the fruit. Cook and his colleagues wondered whether the parasitic wasp, previously thought to be harmful to both parties, may contribute to the stability of the fig tree and pollinator wasps' relationship by keeping the pollinator larvae in check.

Suspecting that that the pollinator wasp is under selective pressure to deposit her eggs in the flower's innermost real estate where her larvae are less likely to be killed, the team collected fig flowers from six different sites in Queensland, Australia, brought them back to the lab and sliced them open. They measured the distance from the wall to the inner cavity of the fig flower, taking note of the precise position where the pollinator eggs were deposited inside the flower. They also assessed the offspring survivorship and found that the larval eggs deposited in the flower's innermost folds were more likely to survive compared with eggs deposited near the flower's outer layers. The researchers determined that parasitic wasps are able to attack the pollinator offspring only if the pollinator eggs are deposited in the outer layer of the fig flower ovule (the 'small egg' within the flower that will develop into a seed) and that larvae buried deep in the flower bud were almost parasite free.

The team also noticed that that pollinator larvae, parasites and seeds are relegated to different neighborhoods over the entire tree, which appear to be determined by flower length. Cook's research shows that longer flowers provide the pollinators' larvae with plenty of 'enemy-free space' at the fruit's centre because the parasitic wasps prefer to invade shorter flowers alone. So the female pollinating fig wasp actively selects regions of the tree with long flowers, relegating the parasitic wasps to tree zones covered in shorter blooms.

Whether the fig tree controls its own fate by producing variable length flowers for the wasp to 'choose' from when depositing her eggs, or the parasitic wasp determines the territorial layout for the tree, the end result is the same. A portion of the fig tree seeds will come to fruition. This led Cook and his colleagues to suggest that the parasitic wasp, previously designated a harmful opportunist, helps to ensure that a fraction of the tree will bear seeds and thus may contribute to the stability of the pollinator–fig beneficial relationship by keeping the pollinator wasp in check.

10.1242/jeb.019919

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CARDIAC FUNCTION

THE SECRET OF SHUNTING?

The primary role of the vertebrate cardiorespiratory system is to deliver oxygen to tissues and transport carbon dioxide and other wastes of metabolism to the body's excretion sites (i.e. the lungs, gills, skin, kidneys). To efficiently accomplish this, birds and mammals have evolved a divided circulatory system in which the left side of the heart pumps blood to the systemic circulation and the right side pumps blood to the pulmonary circulation. The divided system allows for the generation of high systemic blood pressures without high pulmonary pressures (which can damage the vasculature of the lungs) and prevents the mixing of oxygen-rich and oxygen-poor blood. In contrast, other amniotic vertebrates (i.e. lizards and turtles) do not possess a divided circulatory system. Rather, in these animals, the circulatory system is undivided, meaning that the potential exists for a mixing of oxygen-rich and oxygen-poor blood. However, amniotes with an undivided circulatory system have the ability to reduce blood flow to the lungs and divert it back to the systemic circulation; a phenomenon termed a right-to-left shunt.

The reasons underlying why some groups of amniotes possess a completely divided circulation whereas others do not, as well as the physiological function(s) of the right-to-left shunt, has garnered much scientific investigation. Nevertheless, clear answers to these questions have yet to emerge. Recently, a team of researchers from the University of Utah set out to investigate this curious cardiopulmonary feature and devised a series of experiments to test the hypothesis that the shunt is important for digestion. The team explains that the creation of the gastric acid required for digestion is dependent on the partial pressure of CO_2 in the blood. Therefore, a right-to-left shunt should retain CO_2 in the body, allow for its transport to the gastrointestinal system and ultimately aid in digestion.

To test this hypothesis, the team first examined whether shunting occurred during digestion. Indeed, the team found that American alligators (*Alligator mississippiensis*), instrumented with blood flow probes to monitor changes in cardiovascular status, shunted blood past the lungs after eating. Next, the team examined the contribution of the shunt to digestion. The team surgically disabled the ability of some alligators to shunt and then compared a variety of indices of digestion efficiency with another group of animals that were sham operated. By inserting a pH electrode orally into the alligators' stomach after feeding, the researchers discovered that the maximal rate of gastric acid secretion was significantly less in animals surgically prohibited from shunting than those able to shunt. Further, the researchers found that digestion was slower in the disabled animals. Repeated X-ray imaging over 23 days of a piece of bone introduced into the stomach revealed that the dissolution of the bone was slower in non-shunting animals.

The team argues that when combined, their data indicate that shunting of blood from the lungs to the systemic circulation facilitates digestion. The shunt retains CO_2 and transports it to the gastrointestinal tissues where it allows for increased gastric acid production, which facilitates digestion. Thus, the role of the shunt in digestion may explain some of the novel and curious features of the undivided circulation of some amniotes.

10.1242/jeb.010942

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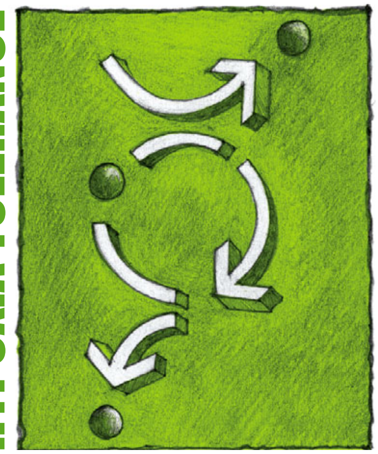
HYPOXIA TOLERANCE



REPROGRAMMING BASAL METABOLISM PROTECTS CELLS FROM HYPOXIA AND ISCHEMIA

As a rule, animal cells require molecular oxygen to support mitochondrial energy production, and have thus evolved elaborate mechanisms to sense and respond to changes in ambient oxygen concentrations. The HIF prolyl hydroxylases (PHD1–3) are enzymes that use molecular oxygen as a substrate, and thus their activity is dependent on the availability of oxygen, which makes them highly sensitive oxygen sensors. When oxygen is high, these enzymes hydroxylate proline residues on the Hif-1α and Hif-2α proteins, which marks these proteins for degradation and thus keeps their activity low. When oxygen becomes limiting, hydroxylation is inhibited, which leads to Hif protein stabilization and the subsequent activation of the HIF-1 transcription factor. HIF-1 activates the transcription of a number of genes that collectively initiate a cellular response to hypoxia. Julián Aragonés and colleagues investigated the role of Phd1 in regulating metabolism and the cellular response to hypoxia in their 2008 *Nature Genetics* paper.

To investigate the function of Phd1, the group created a *Phd1* knockout ($Phd1^{-/-}$) line of mice. They then characterized a battery of physiological, metabolic and biochemical parameters in skeletal muscle tissue and isolated myofibers from these mice including oxygen consumption, glucose utilization, levels of oxidative stress and hypoxia tolerance. The team hoped to find a link between oxygen sensing and the changes in metabolism that are associated with survival of hypoxia.

They found that loss of Phd1 function caused a reduction in oxygen consumption in cells exposed to normal levels of oxygen. This decreased oxygen consumption was associated with decreased oxidation of glucose, while oxidation of lipids was not affected. In addition, anaerobic utilization of glucose increased in *Phd1*$^{-/-}$ mice, indicating a shift towards increased anaerobic capacity even under aerobic conditions. Taken together, these findings suggest a reorganization of basal metabolism in mice lacking the *Phd1* gene.

The group also discovered that isolated myofibers from *Phd1*$^{-/-}$ mice were protected from damage normally associated with a lack of blood flow (ischemia) and exhibited an increased tolerance of hypoxia. These traits are probably due to changes in basal metabolism that are mediated by activation of two potent transcription factors Pparα and Hif-2α due to the loss of Phd1. Increased tolerance of hypoxia in *Phd1*$^{-/-}$ mice was associated with decreased oxygen consumption, reduced oxidative stress and reduced mitochondrial damage compared with hypoxic wild-type myofibers. Importantly, the muscle fibres of mice lacking the *Phd1* gene were able to continue producing ATP at low oxygen levels when ATP production failed in normal mice. Interestingly, *Phd1*-deficient mice showed a reduced exercise endurance compared with wild-type mice when forced to run uphill on a treadmill, indicating that increased hypoxia tolerance may come at the cost of decreased exercise performance.

Loss of Phd1 activity appears to pre-adapt myofibers for increased tolerance of hypoxia. These findings are the first report of a mechanistic link between cellular oxygen sensing and the rate of oxygen consumption in cells. This reprogramming of metabolism and the associated increase in hypoxia tolerance may help to explain changes in metabolism associated with metabolic dormancy in a variety of animals, and the baseline differences in the metabolism of hypoxia-tolerant and -intolerant species. In addition, this study establishes the possibility that inhibition of Phd1 may be one avenue for reducing damage during ischemic events in mammalian tissues.

10.1242/jeb.010975

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