Outside JEB

FEEDING EFFICIENCY

THE COST OF WHALE GULPS: SIZE MATTERS!

From basic physiology texts to studies of consummate diving animals, the notion that diving capacity increases with body size follows intuitively from the fact that bigger bodies denote larger oxygen stores, but lower metabolic rates. Recent research by Jeremy Goldbogen at Cascadia Research Collective and collaborators in the US and Canada, however, demonstrates that in the most massive breath-hold divers, size matters in a different manner. Large rorquals (blue, fin and humpback whales) forage by lunge feeding, an extraordinary process by which these mammoths of the sea accelerate to high speed, engulf immense volumes of prey-laden water, and purge and filter their big gulps. Such exceptional feeding manoeuvres are not without consequence, however, as this technique requires high drag and incurs great energetic costs for these colossal creatures. Not surprisingly, these whales don't dive for as long as other large divers, including other whales that don't partake in lunge feeding. After generating a bounty of data on the foraging kinematics and energetics of baleen whales, Goldbogen and colleagues were inspired to take a closer look at the scaling of lunge-feeding performance in these titanic filter feeders. Bigger mouths mean bigger gulps for bigger whales, but as the energetic requirements of feeding are also predicted to increase with size, they hypothesized that the cost of a lunge might be disproportionately higher in large rorquals, thereby limiting their dive capacity.

The researchers compared diving and lunge-feeding performance among three species of rorquals foraging on krill, ranging in size from the (relatively!) modest humpback whale, to the mid-sized fin whale, and the heftiest animal on Earth, the blue whale. They gathered morphological data (body mass, length, etc.) and set out to derive parameters such as mouth and frontal body area, using geometric models and measurements like skull width and jaw length to estimate gulp size. Employing data from previously deployed acoustic tags and time–depth recorders, Goldbogen and colleagues obtained swimming speed, dive duration and depth, and dive and lunge profiles. Finally, they applied hydro-mechanical and energetic models to estimate the drag required for gulps and the energy exhausted during lunges.

The team revealed that not only is drag relatively higher in bigger whales, as a result of a larger mouth area, but also lunge speed increases with body size, further increasing drag in larger whales. Although maximum dive duration and depth were not different between the three species, the largest whales took longer to filter their mouthfuls. This means that humpbacks can lunge more per dive (and per minute of dive) than can fin or blue whales. Higher, sustained drag in larger rorquals requires more energy. When accounting for mass differences, the cost per gulp for blue and fin whales was three- and two-times higher, respectively, than for humpbacks. Despite a host of advantages stemming from the ability to make long dives (access to deeper waters, more time to search for and exploit prey, etc.), these behemoths forfeit enhanced diving capacity in favour of optimized gulps. This trade-off sets large rorquals apart from other true divers, probably allowing them to cash in on patchily distributed prey aggregations by taking gargantuan gulps.

10.1242/jeb.063842

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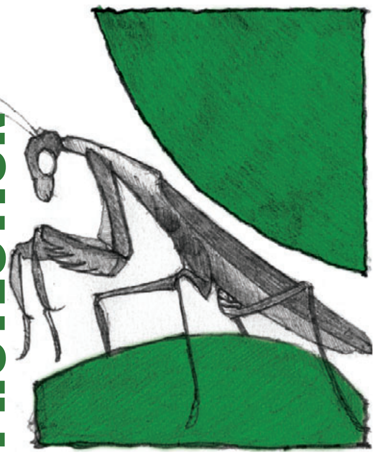
PROTECTION



INSECTS' INTESTINAL BARRIER AGAINST INFECTION

The enormously large and hence vulnerable surface of the vertebrate gastrointestinal tract is largely protected from pathogenic micro-organisms by a mucous matrix made of water, glycoproteins and antimicrobial substances. The gastrointestinal tract of insects is also exposed to many kinds of potentially harmful micro-organism, some of which are relevant to public health because they can be transmitted to humans through infected insect bites. However, insects do not secrete protective intestinal mucous. Instead, they produce a peritrophic matrix (PM) composed of a chitin mesh and glycoproteins, many of which have a chitin-binding domain to associate with chitin. As the PM lines the midgut epithelium, there was speculation about its potential function as a barrier to infection by pathogens residing in the gut content. Yet there was no clear evidence supporting this assumption until a team of Swiss scientists, led by Bruno Lemaitre, published the first genetic evidence for a protective role of the PM against bacterial infection in *PNAS*.

In a previous study, Lemaitre and his team examined the immune response in the *Drosophila* gut and made the exceptional observation that a gene for a putative eye lens protein called Drosocrystallin (Dcy) is strongly up-regulated in the gut of adult flies in response to oral infection with pathogenic bacteria. As this protein contains a chitin-binding domain, they went on to test the possibility that Dcy might be a component of the fly's PM. Indeed, when they looked for Dcy in the insect's gut using anti-Dcy antibodies they found that the protein localizes to the PM. Next, they analysed a *Drosophila* strain that lacks a functional version of the Dcy protein and found that the insect's life-span was significantly reduced. And when they took a closer look at the mutant's intestine, the scientists observed that the thickness of the PM was significantly reduced and its permeability was increased. Being immunologists, they wondered whether flies lacking the *dcy* gene would be more susceptible to oral bacterial infections than wild-type flies.

To test this, they fed dietary solutions containing pathogenic bacteria to *Drosophila* and monitored the flies' mortality at different time points. The mutant flies lacking the fully formed PM were more susceptible to bacterial infection. The scientists also observed increased mortality when they fed solutions of bacterial toxins to the flies, leading them to conclude that the PM detains bacterial toxins – especially pore-forming toxins – to prevent them from damaging intestinal cells.

By analysing mutant flies defective in the *dcy* gene, Lemaitre and his colleagues have provided the first genetic evidence that the PM plays a pivotal role in defence against enteric bacteria in *Drosophila* by limiting the effect of bacterial toxins. Certainly, we are in the early stages of discovering the role of the PM in innate immunity; however, Lemaitre's team's discovery will doubtless inspire future studies to reveal the precise function of individual PM proteins in fighting infections caused by bacteria and other micro-organisms. The old idea of the PM as an attractive target for insect control may yet be resurrected in order to develop novel integrated pest management strategies.

10.1242/jeb.064006

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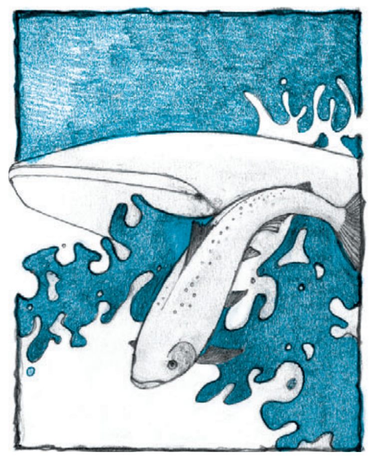
SOUND PRODUCTION



HELIUM BREATHING SHOWS DOLPHINS DON'T WHISTLE

We've all been at a party where someone has inhaled the helium from a balloon to make their voice go squeaky. Rarely do we consider this to be a useful scientific tool for determining how animals produce their characteristic sounds, but that's what Peter Madsen, of Aarhus University, Denmark, and his team have done. In a new paper published online in *Biology Letters*, Madsen and co. use heliox breathing to determine the mechanism by which dolphins produce their 'whistles'. Dolphins use tonal whistles for communication but it is unclear how they achieve consistency in a challenging underwater environment where they encounter a great range of hydrostatic pressures, which could dramatically alter the sounds that they produce just by virtue of their depth. Are their cries true whistles, produced by air flows in their complex nasal system, or are they the result of a vibrating structure?

When humans speak, vibrations from the vocal chords cause the air in the throat to vibrate. When we breathe helium, our vocal chords still vibrate at the same frequency but, because sound travels faster in helium than in air, there is a shift in timbre. Timbre describes the quality of a sound and enables us to distinguish between different sounds; for example, if you play the same note at the same volume on a piano and a clarinet, you can hear the difference between the instruments because the timbre is different. Our voice sounds squeaky after inhaling helium because of the resulting change in the resonance frequency of the vocal tract. This enhances the higher frequencies while attenuating the lower frequencies so that we sound a bit like Donald Duck. Dolphins could have a similar problem, sounding squeaky at the surface and more sonorous at depth if their calls are produced by whistling. This is because the air volumes of the dolphin nose are reduced when they dive and so the resonance frequency of them increases.

Madsen and his team made use of this phenomenon to test whether the dolphin's whistle is actually a true whistle or a misnomer by analysing the sounds produced by a dolphin in heliox and normal air. If the 'whistles' are produced by an airflow (true whistle), the fundamental frequency would change during heliox breathing; if they are produced by a vibrating structure (not a true whistle), there would be no change in frequency. Having access to recordings made by Sam Ridgway and Donald Carder in the 1970s of sounds produced by a bottlenose dolphin (*Tursiops truncates*) inhaling first a heliox mixture (80% helium and 20% oxygen) and then normal air, the team decided to analyse the calls to find out whether dolphins whistle.

Analysing the power distribution in each call, Madsen and his colleagues showed that although there was less energy in the fundamental frequency (the lowest frequency) in the heliox calls, there was no significant difference in other frequency variables between the two conditions. This suggests that, although there is an indication of some air effect on timbre, the fundamental frequency is consistent and therefore produced by tissue vibrations. If the sound was produced by whistling, the team would have found a change in frequency. This means that the term 'whistle' is not technically correct as the calls are not produced by resonating air volumes but by vibrating structures that are the nasal equivalent of the vocal chords of humans and other mammals.

Madsen and colleagues' results showing that these sounds are produced by vibrating structures, rather than vibrating air columns, enable a better understanding of how dolphins communicate information and signal identity regardless of depth.

10.1242/jeb.063834

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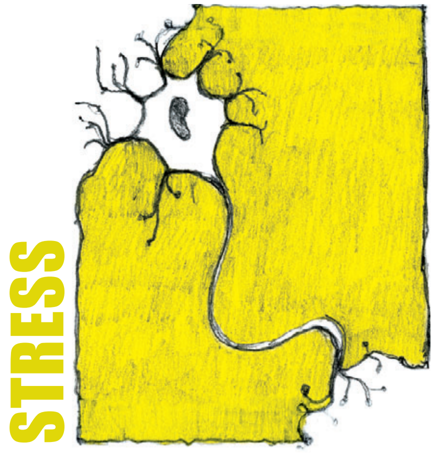

NO MOM, NO PEACE FOR RHESUS MONKEYS

Stress at an early age can have important consequences on the behaviour and brain development of an animal. For example, in their 2000 publication in *Primates*, Drago and Thierry found that when baby Tonkean Macaques were separated from their mothers they became aggressive and depressed. Early adversity also has long-term effects on the hypothalamus–pituitary–adrenal axis; a neural system that, through the release of cortisol, prepares the body to deal with stressful situations. However, when adversity is sustained for prolonged periods of time the initial cortisol high fades and is followed by abnormally low levels of cortisol release. So, what happens when, after early misfortune, life resumes its normal course? Can the consequences of early adversity on behaviour and brain development be reversed? A study recently published in *PNAS* by a group of Chinese researchers led by Xiaoli Feng reveals that the behavioural and neurological consequences of mother separation at birth will last for at least 3 years, but probably for life, after the initial stress.

The scientists examined the behaviour and cortisol levels in 22 Rhesus monkeys that had been reared by their moms and 13 that had been separated from their mothers at birth. The babies were taken from their mothers because they were at risk if they had stayed with their moms. For example, some of the mothers were very inexperienced and incapable of properly caring for the baby, some others did not produce enough milk and in the case of a few babies, cold rainy weather at the time of birth threatened their health. Then, after a few months, all the mother-reared and mother-separated monkeys were moved to a communal indoor–outdoor facility with no adults simulating the primates' normal social environment.

To investigate the long-term effects of mother separation on cortisol secretion and behaviour, Feng and her team analysed the levels of cortisol from hair samples taken from the monkeys and evaluated different types of behaviour at 2 and 3.5 years of age. In addition, the researchers investigated cortisol secretion induced by sudden stress by analysing cortisol levels in the blood of the monkeys during the first 30 min after capture.

The cortisol levels in the monkeys that had been separated from their moms at birth were low even after 3 years of normal social life; this was consistent with the low cortisol production observed in animals exposed to prolonged stress. In addition, the mother-separated monkeys had a delayed response to sudden stress, in that the peak of cortisol present in the blood occurred later than in the mother-reared monkeys; this may be disadvantageous when the animal is trying to cope with imminent threat. The monkeys that had been separated from their mothers at birth also showed behavioural signs of anxiety, such as sucking on their digits, pacing and grasping parts of their own body, and were less prone to sit along side their peers. Furthermore, these monkeys were less likely to move than their mother-reared counterparts.

The results from this study are unique in that they show that the effects of stress at an early life stage cannot fully be reversed by subsequent exposure to a normal 'unstressful' life and that early adversity can have long-lasting consequences on the physiology and behaviour of an animal. The good news is, the better we understand how psychiatric problems develop, the better equipped we will be to deal with them.

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