

## OUTSIDE JEB

## From pinnipeds to people: divers have elastic arteries



Upon submersion, mammalian divers invariably exhibit a characteristic ‘dive reflex’: the heart slows and the peripheral vessels, supplying blood to muscles and non-vital organs, constrict, thereby prioritising blood flow to the brain. This stereotyped response, dubbed ‘the master switch of life’ by Per Scholander following his pioneering work, imposes unusual demands on the major arteries. The slowed heart rate results in greater cardiac filling between beats, meaning the volume pumped per contraction (stroke volume) increases. However, this large volume of blood is driven against a high resistance generated by the peripheral vasoconstriction, thus putting strain on the central vessels.

Seals are particularly adept divers, and as revealed in Scholander’s classic work, exhibit a pronounced dive reflex. In a recent paper, Arnoldus Blix and his colleagues explored how the outflow of the seal heart is adapted to their diving lifestyle. In a post-mortem investigation, the Norwegian team investigated both the mechanical properties and the detailed anatomy of the hooded seal aorta.

It had been previously established that the seal aorta exhibits an unusual ballooning, referred to as the ‘aortic bulb’. Blix and his colleagues isolated the bulb and measured pressure as they loaded it with saline. The vessel was extremely elastic; it could comfortably accommodate the estimated diving stroke volume with

minimal changes in pressure. During dives, the aorta thereby functions as an elastic reservoir, or ‘windkessel’, that cushions the circulation from dangerous pressure fluctuations.

Given its vital role, Blix and colleagues next investigated the microanatomy of the aortic bulb. Many large arteries are nourished by blood vessels (vasa vasorum), but they are traditionally reputed to remain superficial. However, in the thick aortic bulb of seals, a rich arborisation of blood vessels clearly penetrated the entire wall. These vessels provide the oxygen necessary to maintain the integrity of the elastic wall. It is possible that the surprising extent of this vasculature is unique to the peculiar bulb in seal arteries, but the authors speculate that similar vasa vasorum may have simply been overlooked in the vessels of other animals, including humans.

In an independent article, published in the same journal, Hirofumi Tanaka and colleagues studied arterial stiffness in another group of expert divers: the Ama people of Japan. Ama women free dive in pursuit of pearls and may dive over 100 times per day. To investigate whether this is reflected in arterial adaptations, the team assessed arterial stiffness in pearl divers in comparison to both physically active and inactive non-divers. This involved a suite of techniques, including measuring arterial blood pressure and taking ultrasound images of the carotid artery in resting individuals.

Tanaka and colleagues demonstrated that both divers and physically active non-divers generally had less-stiff arteries than sedentary individuals. However, in several key parameters, for example the profile of the pressure waves in the arteries, the divers clearly stood out. Much like those of seals, the divers’ arteries were better adapted to buffer the pressure changes between heartbeats.

These two studies demonstrate that in marine mammals and humans, the distinct cardiovascular challenges imposed by diving are alleviated by similar mechanisms. The elastic arteries of seals

have been sculpted by millions of years of natural selection, whilst in the Japanese divers this adaptation is a direct result of a lifetime of pearl collecting.

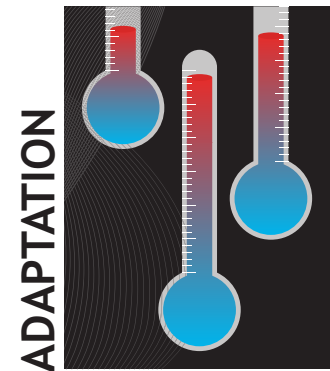
10.1242/jeb.130278

**Blix, A. S., Kuttner, S. and Messelt, E. B.** (2016). The ascending aorta of hooded seals with particular emphasis on its vasa vasorum. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* doi:10.1152/ajpregu.00070.2016.

**Tanaka, H., Tomoto, T., Kosaki, K. and Sugawara, J.** (2016). Arterial stiffness of lifelong Japanese female pearl divers. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **310**, R975-R978.

**William Joyce**  
Aarhus University  
william.joyce@bios.au.dk

## Hot fish hit concrete temperature ceilings



We’ve all heard the boiling frog cautionary tale: place a frog in hot water and it will immediately jump out. Gradually heat the water and the frog will bask in the warmth until it’s too late. This story is used to advise people against the dangers of ignoring small, but consistent changes that can lead to disastrous outcomes. The parallels with climate change are obvious. Ironically, many experiments investigating the effects of warming on organisms use short-term exposures to high temperatures, akin to dropping the frog into a boiling bath. Understanding the consequences of long-term heating due to climate change requires experiments more like the long exposure, slowly boiled frog scenario. But, finding a study site that’s experienced artificially warmed conditions over decades is not trivial. Luckily, Erik

Sandblom and Fredrik Jutfelt from the University of Gothenburg knew of one such spot in their native Sweden and assembled a team to test whether slow-cooked fish really are worse off.

A region of water on the east coast of Sweden, known as the Biotest enclosure, receives heated water from a nearby power plant, which keeps the temperature 5–10°C warmer on average than the surrounding Baltic Sea. Fish have lived in these warmed waters for the past 30 years, enough time for individuals to acclimate and, potentially, for generations to adapt. The team wanted to know whether this life-long warming produces more heat-tolerant fish. They first compared the lower and upper cardiorespiratory performance (metabolic rate, heart rate and cardiac output), or physiological ‘floors’ and ‘ceilings’, of European perch (*Perca fluviatilis*) collected from the warmed Biotest waters and the cooler Baltic Sea, as well as Baltic Sea fish acutely warmed to Biotest temperatures for 24 h. They then calculated each group’s thermal tolerance, essentially performing the ‘frog in the slowly heated water’ experiment, by gradually increasing the water temperature in the aquaria, measuring how hot it got before each fish lost its balance, and then subtracting each individual’s environmental temperature from the temperature at which they toppled over.

The team found that lower cardiorespiratory performance ‘floors’ had adapted over generations to accommodate life in hot water: the Biotest fish, which had experienced long-term warming, showed lower resting metabolic rate and heart rate compared with the Baltic Sea perch that had been acutely warmed to Biotest temperatures for 24 h. However, there were only limited adjustments to the fish’s upper cardiorespiratory performance ‘ceilings’ as the Biotest perch and the acutely heated fish had similar maximum metabolic rate, cardiac output and heart rate. The Biotest perch did manage to keep their balance in slightly higher temperatures than the Baltic Sea perch, finally toppling over in water that was about 2.2°C warmer than that for the Baltic Sea group. However, this probably doesn’t give them an edge compared with their cool-water neighbors when it comes to surviving temperature extremes. As they live so close to their maximum temperature limit, the Biotest

perch had a significantly reduced warming tolerance, likely making them more susceptible to extreme heat waves than Baltic Sea perch despite years of acclimation to warmer waters.

Like the proverbial frog in boiling water, gradual temperature changes are easy to ignore, and some individuals may even adjust to a certain extent. But, Sandblom, Jutfelt and their colleagues have provided a curt reminder that complacency towards our changing climate comes with consequences. Just when the next heat wave will hit is anyone’s guess. The trouble is, most organisms can’t simply jump out of the water when it gets too hot.

10.1242/jeb.130252

Sandblom, E., Clark, T. D., Grans, A., Ekstrom, A., Brijis, J., Sundstrom, L. F., Odelstrom, A., Adill, A., Aho, T. and Jutfelt, F. (2016). Physiological constraints to climate warming in fish following principles of plastic floors and concrete ceilings. *Nat. Commun.* 7, 11447.

Sandra A. Binning  
University of Neuchâtel  
sandra.binning@unine.ch

## Active ear amplification allows crickets to stay tuned



When we hear crickets sing, we are given insight into a fierce competition for mates being fought around us. These singing insects are loudly proclaiming their quality to attract mates and to repel their rivals. Because cricket song carries such important information, it is vital that songs reach the right ears. For tree crickets (*Oecanthus nigricornis*), this might be tricky. This is firstly because lots of related species often sing in the same area and secondly because male song frequency rises with temperature. This means that for listeners, picking up the right song must be a bit like trying to tune

into a radio station that keeps changing frequency. Natasha Mhatre and colleagues wanted to know how tree crickets stay tuned to this fluctuating frequency as temperatures change.

Mhatre and colleagues first focused on tree cricket tympanal ears. These membranes on the legs of crickets are forced to oscillate in the narrow frequency band that corresponds to the species’ song by motor cells. This amplifies the frequencies to which these ears are tuned and enables crickets to better hear songs of their own species. Mhatre and colleagues measured the frequency of these oscillations at different temperatures. They found that ear oscillation frequency rose by 112 Hz for each 1°C increase in temperature, closely mirroring the rise in male song frequency across this temperature range. This means that as male song frequency shifts with temperature, so does the frequency that listeners actively amplify.

To see how this change in oscillation frequency affects what crickets hear, Mhatre and colleagues measured neural responses to sound (or neural tuning) at the prothoracic ganglion where auditory information is first processed. They found that neuronal responsiveness at low temperatures was greatest around the frequency at which males sing in low temperatures. At warmer temperatures, neural tuning was greatest around the frequency at which warmer males sing. In other words, neural tuning also shifted up with temperature.

So it seems that tree crickets actively tune into their own song across a range of frequencies. But what effect does this have in the wild? To find out, Mhatre and colleagues looked at the responses of cold and warm crickets to sounds corresponding to the frequencies that male crickets sing at in both warm and cold temperatures. The team found that a song produced at a high temperature would have to be 18.5 dB louder to be heard by a low-temperature ear. This means that by actively tuning in to the correct frequencies, crickets can hear singers that are over three times further away. This is one of the first demonstrations of the consequences of adaptive auditory processes. In addition, these results show us that by changing the frequency that they actively amplify, female tree crickets may be better able to

pick mates, while males can better defend their territories and decide when it is better not to pick a fight.

10.1242/jeb.130245

**Mhatre, N., Pollack, G. and Mason, A.** (2016). Stay tuned: active amplification tunes tree cricket ears to track temperature-dependent song frequency. *Biol. Lett.* **12**, 20160016.

**Ruth Archer**  
University of Exeter  
c.archer@exeter.ac.uk

## The pendulous, belly-flopping landing acrobatics of tree frogs



Frogs jump. They're darned good at it. Because of this, they've been one of the key groups used to study the oh-so-important first phase of jumping – take off. But what goes up must come down and if you're a tree-dwelling frog, that down can be 10 or more meters below if you miss your intended landing site. While a handful of studies have examined how frogs and toads land, these studies

have focused on landing on flat surfaces. Although this may be appropriate for land-lubbing jumpers, little is known about how the arboreal sort jump from branch to branch, let alone how they land.

Nienke Bijma and her collaborators at Kiel University in Germany wanted to find out not only how arboreal frogs land when they jump but also what role their toe pads play in helping the frogs stick to their landing location. They used high-speed video to record Amazon milk frogs (*Trachycephalus resinifictrix*), first as they hung from one front foot underneath a narrow horizontal rod, then as they landed after jumping from a flat landing surface 25 cm away.

The authors found that when the frogs were placed underneath a narrow rod and one front foot was placed on the rod, they were able to hold their body weight using only two toes – if they were the third and fourth toes. These findings supported earlier work on walking in tree frogs, which showed that the third and fourth toes are important for contact stabilization. And once the frogs had one foothold, they immediately placed another foot on the rod and attempted to pull themselves up: no one likes to be left hanging.

When it came to landing after a jump, the frogs used one of two strategies: the belly flop, or the reach-and-grab. When frogs landed with a belly flop, they impacted the rod perpendicular to their bodies and folded over it like a taco. Once the rod had abruptly halted their flight, the frogs

quickly grabbed the rod with their feet and held on. The authors suggest this method of landing is effective and accurate, but could potentially result in internal damage.

For the reach-and-grab strategy, if the frogs overshot the rod, they would reach with a back leg to grab it; when the frogs undershot, they would reach up with a front leg to grab the rod. These reaching-while-flying landing strategies caused the frogs to cartwheel around – sometimes landing on top of the rod – or sway back and forth underneath the rod, as they pulled themselves up towards it. For all landing strategies, the researchers observed the frogs lean towards the rod as they got closer, in order to make contact more easily, though this happened less frequently with the belly flop.

In contrast to the ground, which is unlikely to move when frogs and toads are mid-jump, branches of trees shift in the wind and under the weight of the animals themselves. So, while previous research has shown that each species of terrestrial frog and toad has relatively stereotyped landing strategies, the authors suggest it makes sense that arboreal frogs need to be more adaptable when it comes to dealing with what's at the other end of the jump.

10.1242/jeb.130260

**Bijma, N. N., Gorb, S. N. and Kleinteich, T.** (2016). Landing on branches in the frog *Trachycephalus resinifictrix* (Anura: Hylidae). *J. Comp. Physiol. A*, **202**, 267-276.

**Casey Gilman**  
University of Massachusetts Amherst  
cgilman@bio.umass.edu