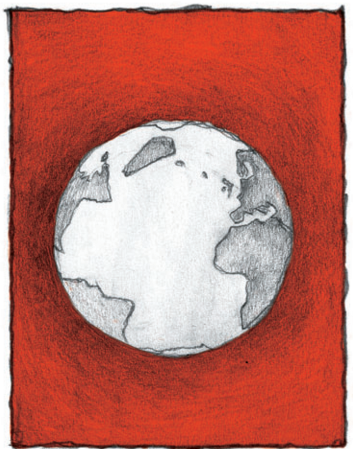
Keeping track of the literature isn't easy, so Outside JEB is a monthly feature that reports the most exciting developments in experimental biology. Short articles that have been selected and written by a team of active research scientists highlight the papers that JEB readers can't afford to miss.

Outside JEB

## DEVELOPMENTAL COSTS



### IS IT CHEAPER TO 'GROW UP' FAST?

It is well understood that a distinct relationship exists between temperature and most biological processes. This is especially evident in ectothermic (sometimes called cold-blooded) animals, whose body temperature closely tracks the temperature of their environment. Interesting trends have come from laboratory studies where temperature can be held constant and controlled tightly. For example, elevating the temperature of a lizard's nest can speed up embryonic development, but whether this is ecologically relevant is not known. In the wild, temperature can fluctuate drastically, which may require other mechanisms to be employed for staying warm or keeping cool and may increase or decrease the cost of certain biological processes. Based on past observations of eastern fence lizards whose nest temperatures were found to fluctuate by 20°C on a sunny day, Christopher Oufiero and Michael Angilletta from Indiana State University set out to model the effects of temperature fluctuations on the energetic cost of development in this lizard species.

They performed their research in the laboratory where they hormonally induced female lizards to synchronously lay eggs so that the all of the embryos were at the same stage as the duo tracked their development. Then Oufiero and Angilletta exposed the newly laid eggs to either a warm or a cool temperature cycling regime that was meant to mimic the lizards' natural habitat. As the eggs developed, the team measured each egg's oxygen consumption rate at various times to track their metabolic rate. Finally, the pair used mathematical models based on the metabolic rate measurements that determined the energetic cost of development for each embryo.

The team found that embryos that developed in warm conditions developed faster while maintaining high metabolic rates. Conversely, the embryos that developed in cool conditions developed slowly while maintaining low metabolic rates. However, upon hatching all of the lizards had developed to the same extent, regardless of their thermal history, and had expended the same amount of energy to get to that point. The team also found that the average metabolic rates for eastern fence lizards exposed to cycling thermal regimes were similar to those of embryos of a similar species held at a constant temperature.

Collectively, Oufiero and Angilletta's findings suggest that while temperature can clearly speed up or slow down the process, the same amount of energy input is required regardless. Understanding the effects of thermal cycling on the timing of development is ecologically relevant. Predictions can be made as to how human-related changes in environmental conditions may affect population growth or distribution of organisms. Additionally, Oufiero and Angilletta's findings provide a basis from which questions significant to evolutionary processes can now be addressed. Isolating the energetic cost of development to the embryo allows researchers to investigate the role of a parent or another outside source in the process. For example, in species where a parent creates and/or guards a nest, this additional invested energy can further speed up or slow down the hatching process. Ultimately, however, these lizards are not taking any short cuts. They are getting out of it exactly what they put in!

10.1242/jeb.036749

**Oufiero, C. E. and Angilletta, M. J., Jr** (2010). Energetics of lizard embryos at fluctuating temperatures. *Physiol. Biochem. Zool.* **83**, 869-876.

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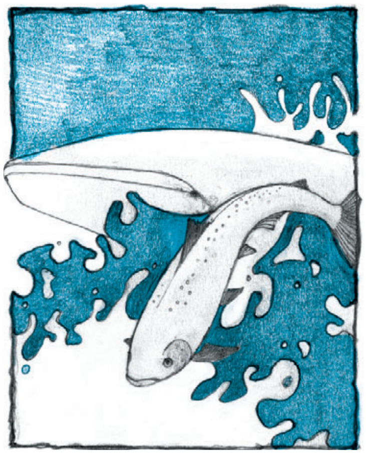
FOOD WEB STRUCTURE



## GOBY STABILIZES UPWELLING ECOSYSTEM

When the sardine fishery in the northern Benguela upwelling system, located off the southwest coast of Africa, collapsed because of over fishing in the 1960s the local ecosystem shifted dramatically to one dominated by jellyfish and the bearded goby. Surviving in the hypoxic and sulphide-rich environment – created by high-productivity and decay processes in the nutrient-rich upwelling – the bearded goby population has boomed despite becoming the primary prey species for seabirds, mammals and fish. Intrigued by the bearded goby's success, Anne Utne-Palm from the University of Bergen and colleagues from Norway, Namibia, USA, South Africa, Sweden and Saudi Arabia used a multidisciplinary approach to determine the role of bearded gobies in linking and transferring energy from the harsh conditions of the ocean floor to the food web in the water column.

To determine where gobies are located in the water column, the team performed acoustic surveys and trawl sampling. In addition, they conducted behavioural experiments to assess the fish's habitat preference and to test its aversion to jellyfish. They found that the gobies spend the day resting or hiding within the mud on the seabed and spend the night in the water column with the jellyfish that their predators avoid.

Next, the team performed physiological experiments to uncover how the gobies are able to tolerate the hypoxic and sulphide-rich environment in the sediments and found that the fish were able to maintain aerobic metabolism under extremely hypoxic conditions. They also found that hydrogen sulphide, which is a respiratory poison, suppressed the gobies' oxygen consumption at moderate and high levels. The team suggest that bearded gobies are able to tolerate the high sulphide conditions by being exceptionally anoxia tolerant. This is probably achieved by metabolic depression and having a high capacity to produce ATP in the absence of oxygen.

Finally, the team compared the stable isotope composition of goby muscle with that of jellyfish, krill and sediments, and examined the gobies' stomach contents to determine their diet. They found that although jellyfish made up a substantial portion of the gobies' diet, the fish also feed on organisms living on or within the hypoxic sediments during the day. The gobies ascend to the oxygen-rich water column at night when predators are scarce, to digest and probably feed on jellyfish.

This study shows that bearded gobies play a major role in the food web of the Benguela ecosystem. They transfer 'dead-end' resources such as jellyfish and organisms within the hypoxic and sulphide-rich mud back into the food chain for consumption by higher predators. The gobies also possess unique physiological and behavioural adaptations that allow them to flourish in inhospitable low oxygen and high sulphide environments where other species do not thrive. As climate change is expected to increase the frequency of sulphide eruptions and hypoxic water, bearded gobies will probably continue to be an important stabilizing force for the Benguela ecosystem.

10.1242/jeb.036798

**Utne-Palm, A. C., Salvanes, A. G. V., Currie, B., Kaartvedt, S., Nilsson, G. E., Braithwaite, V. A., Stecyk, J. A. W., Hundt, M., van der Bank, M., Flynn, B. et al.** (2010). Trophic structure and community stability in an overfished ecosystem. *Science* **329**, 333-336.

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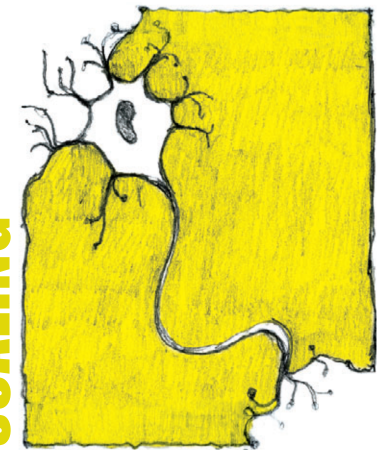
SCALING



## BIGGER ISN'T ALWAYS BETTER

Size matters in biology. Whether you want to think about bone shapes, heart rates or lifespans, an elephant and an elephant shrew are enormously different despite their similarity in name and mammalian heritage. Exploring size-related effects in biology is the study of scaling, and when it comes to the study of size in relation to the nervous system, the brain seems to almost always be front and center. However, how the central nervous system communicates with the rest of the body *via* the peripheral nervous system has now been framed in an interesting scaling context by Heather More and Max Donelan of Simon Fraser University working with colleagues from Canada, the UK and the USA.

Think of it like this: the time it takes for an animal to sense and respond to a stimulus depends, in part, on how long it takes electrical signals traveling along axons to move from place to place. Hence, axonal conduction velocity, which depends on axonal cross-sectional area, must be an important factor determining an animal's responsiveness. Of course, the signal conveying an irritation on the foot of an elephant (and the signal conveying the appropriate response) has a lot farther to travel than similar signals in an elephant shrew. If large animals are to be as responsive as small animals, then axonal conduction velocities and thus diameters would have to increase roughly in proportion to some linear measurement of body size like limb length.

To see whether this is what happens the researchers collected three independent data sets. The first involved using electrophysiological techniques to directly measure conduction velocities along major nerves innervating the medial gastrocnemius in six least shrews and one Asian elephant (see http://www.sfu.ca/locomotionlab/2010/06/29/nervespeedlimit/ for video of the elephants). To augment this data set the researchers also performed a literature review to identify maximum axonal conduction velocities among diverse terrestrial mammals spanning a broad size range. Finally, the team used nerve fixation techniques and scanning electron microscopy to measure axon sizes in the sciatic nerves of a least shrew and an African elephant.

What the authors found is surprising. The largest elephant axons were only approximately twice the diameter of the largest shrew axons. Similarly, measurements of axon conduction velocity revealed that nerve signals traveled a little less than twice as fast in elephants (mean=70 $m\,s^{-1}$) as in shrews (mean=42 $m\,s^{-1}$). These data fit well within the context of the data collected in the literature review, which led to an overall scaling relationship where conduction velocity is proportional to body mass$^{0.04}$, i.e. very little effect of size. Thinking through a concrete example, an elephant's limb is 100× as long as a shrew's, but its axonal conduction velocity is only twice as fast, indicating a 50-fold longer conduction delay for a signal moving through the elephant's peripheral nervous system.

In short, larger animals appear to be woefully less responsive than their smaller counterparts. Delayed response times in larger animals could mean that some of their reactions may take too long to be of much use. The authors propose the intriguing idea that large animals may need to rely more on predictive motor control strategies rather than feedback control as a result.

10.1242/jeb.036806

**More, H. L., Hutchinson, J. R., Collins, D. F., Weber, D. J., Aung, S. K. H. and Donelan, J. M.** (2010). Scaling of sensorimotor control in terrestrial mammals. *Proc. R. Soc. Lond. B* doi: 10.1098/rspb.2010.0898.

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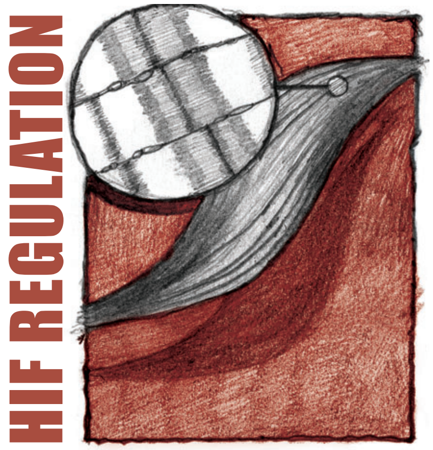


## OF HIF, MUSCLES AND NORMOXIA

Mammalian muscles present a wide range of contractile and metabolic properties resulting from the relative proportions of oxidative (type I) and glycolytic (type II) fibres making up a given muscle. Besides these innate properties, muscles are also highly plastic, responding to environmental change. In particular, oxygen availability has a strong influence on muscle metabolism. When oxygen concentration drops (hypoxia), proteins such as the hypoxia inducible factor-1 (HIF-1) are activated to orchestrate a switch to glycolytic (anaerobic) metabolism in an effort to spare oxygen. Over longer periods of hypoxia, HIF-1 also promotes increased vascularisation *via* angiogenic factors such as the vascular endothelial growth factor (VEGF) to improve oxygen delivery to the hypoxic tissue. The HIF-1 protein is composed of two components; HIF-1α is primarily regulated by oxygen availability, while the other subunit is constitutively expressed. When the oxygen concentration is normal, HIF-1α protein tends to be targeted for degradation, lowering HIF-1 activity. However, under hypoxic conditions HIF-1α is stabilized, allowing the HIF-1 dimer to act on several metabolic pathways to help the cell cope with low oxygen levels. Although the role of HIF-1 under hypoxia has been widely studied, relatively little is known about the function of this protein under normoxic conditions in resting muscle. Furthermore it is unclear whether this factor is differentially regulated in muscles with different metabolic phenotypes.

Remi Mounier, Bente Pedersen and Peter Plomgaard from the University of Copenhagen, Denmark, investigated these two questions by looking at different muscle fibre types in humans. Specifically, the team looked at gene and protein expression profiles in resting muscles, and hypothesized that primarily glycolytic muscles would present higher expression levels of HIF-1 and associated factors than oxidative muscles.

First, Mounier and colleagues selected three skeletal muscles, the oxidative soleus muscle (mostly type I fibres), the mixed vastus lateralis muscle (type I and type II fibres) and the glycolytic triceps brachii (mostly type II fibres) muscles. Using quantitative real-time PCR, the team established that HIF-1α mRNA expression was higher in glycolytic and mixed muscles than in the oxidative soleus muscle, as predicted by their hypothesis. In contrast, the mRNA expression of *VEGF*, a gene regulated by HIF-1, did not show any fibre type-specific pattern, confirming that HIF-1α mRNA levels do not necessarily reflect HIF-1 activity. So the team measured HIF-1α protein amounts in the muscles to see whether they correlated with the gene expression patterns. Contrary to their expectations, HIF-1α protein levels were threefold lower in glycolytic muscles than in mixed and oxidative muscles. In addition, VEGF protein levels were lowest in glycolytic muscles, intermediate in mixed muscles and highest in oxidative muscles.

The results of this study strongly suggest that different muscle types regulate the HIF pathway at different levels, and further investigation will be necessary to unveil the mechanisms responsible for this tissue-specific regulation. Furthermore, these results also confirm the presence of HIF-1 under normal oxygen conditions, and thus suggest that this factor may also play an important role in regulating skeletal muscle homeostasis even under normoxia.

10.1242/jeb.036772

**Mounier, R., Pedersen, B. K. and Plomgaard, P.** (2010). Muscle-specific expression of hypoxia-inducible factor in human skeletal muscle. *Exp. Physiol.* **95**, 899-907.

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