

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.

STARVATION EFFECTS



STARVING KNOTS MAINTAIN FOOD-PROCESSING CAPACITY

It's not fair. At the same time that we enjoyed ample Christmas dinners and complained about the consequent weight gain, many animals remained hungry as their prey vanished during the cold winter months. Even long-distance migrating shorebirds, such as red knots (*Calidris canutus islandica*), are affected by food deprivation if the food reserves in their winter homes become scarce, ultimately facing starvation in the worst case. In the final critical phase of starvation, when fat reserves are already depleted, animals eventually resort to breaking down protein stored in organ systems that are essential for survival. But do animals equally catabolise all organs during starvation or are certain organs protected from consumption as fuel for metabolism?

To answer this question, Maurine Dietz and Theunis Piersma from the University of Groningen in the Netherlands have ventured out into the field, patiently collecting and compiling body composition data from both healthy wintering knots and starved individuals over a 20 year period. Their samples consisted of birds in good health that had died accidentally during capture or after crashing into lighthouses. Secondly, they used starved knots that were found dead when their mudflat homes froze, rendering their mollusc diet inaccessible beneath the ice. Dissecting the birds, the team quantified a number of parameters relating to the animal's body condition, before drying the bird's organs and muscles to determine their fat and water content.

By comparing healthy over-wintering birds with starved ones, Dietz and Piersma found that the hungry birds were one-third lighter than the well-fed knots, and they had lighter pectoral and leg muscles, smaller gizzards and lighter intestines. Correspondingly, the intestines of starved

birds were about 5 cm shorter than in healthy wintering conspecifics. All of these changes in organ morphometry were attributed to prolonged fasting. Dietz and Piersma also found that the organ fat content of the two groups of knots differed greatly, with healthy knots having higher fat contents than winter-starved birds. When including these factors in their statistical analysis, the authors found their most interesting result. It turned out that only pectoral muscle and liver mass were lower in the starved knots compared with healthy wintering birds.

From this, Dietz and Piersma concluded that food-deprived knots 'burned' their pectoral muscles and liver tissue while starving, but maintained their gizzard and intestines, which are essential for digestion when the food supply returns. By doing so, knots apparently sacrificed flight capacity to preserve their food-processing capability. However, as knots walk while foraging, it is still adaptive to defend the essential digestive system components at the expense of flight capability, which can be restored during times of plenty. Finally, this interesting result again points to the tremendous plasticity of the gastrointestinal tract. Not only can it be elongated and shortened according to the bird's physical demands but also it is maintained at the expense of organs, such as skeletal muscle, that are less essential for survival.

10.1242/jeb.011536

Dietz, M. W. and Piersma, T. (2007). Red knots give up flight capacity and defend food processing capacity during winter starvation. *Funct. Ecol.* **21**, 899-904.

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CIRCADIAN CONTROLS



TIME FLIES

Many organisms have evolved an internal clock that regulates the daily control of complex behaviours, known as circadian rhythms. Circadian literally means 'about a day'. This intrinsic clock synchronizes behaviours, such as sleeping and waking, within a 24 h cycle. The molecular and cellular components of circadian rhythms have been studied extensively in the fruit fly, *Drosophila melanogaster*. Scientists have studied how *Drosophila* neural networks synchronize environmental cues with gene expression and behavioural responses and have identified specific genes and neurons involved in the coding of circadian patterns. Environmental cues that may impact circadian rhythms are those which themselves fluctuate predictably throughout the day; for example, light and temperature. A wealth of evidence indicates that light is a powerful regulator of circadian rhythms but the impact of temperature is less well characterized. The study by Ania Busza and colleagues from the University of Massachusetts Medical School in the 1st October edition of the Journal of Neuroscience investigates how circadian neurons interact to form a network that synchronizes *Drosophila* behaviour with temperature cues.

The team addressed this issue using the well-defined cyclic locomotor behaviour of *Drosophila*, which exhibits surges of activity in the morning and evening. The team performed the experiments in constant darkness to remove any circadian influence from light, monitoring the flies' activity levels as the temperature in the experimental chamber was slowly cycled between 20°C and 29°C. In this way, the authors could examine the cyclic pattern of locomotor activity in the presence of thermal cues alone. Using these techniques, together with genetic manipulations, the authors unveiled novel interactions between neurons in the circadian circuit. This circuit mediates the response to temperature cues

by raising the insect's activity levels in the morning and evening when temperatures are generally cooler.

In *Drosophila*, light/dark cycles stimulate two populations of neurons in the circadian circuit, which interact to generate the morning and evening peaks in activity. These are known as 'M cells' and 'E cells', controlling the morning and evening peaks, respectively. Using a genetic manipulation that allowed the investigators to selectively inhibit the activity of either M or E cells, they determined that these neuronal populations are also involved in the synchronization of behaviour with temperature cues. They found that M cells respond slowly to temperature changes compared with the more rapidly responsive E cells. The authors suggested that M cells set the pace of behavioural synchronization and help to prevent over-compensation to erratic temperature variations that occur naturally in response to the weather. E cells may help to fine tune the response of the M cells and it is the functional coupling between the E and M cells that allows for the proper timing of behavioural activity in response to temperature cycles. A final interesting point was the discovery of a distinct population of cells, termed temperature-sensitive cells, that contribute to an increase in evening activity and responded exclusively to thermal cues when both M and E cells were genetically inhibited.

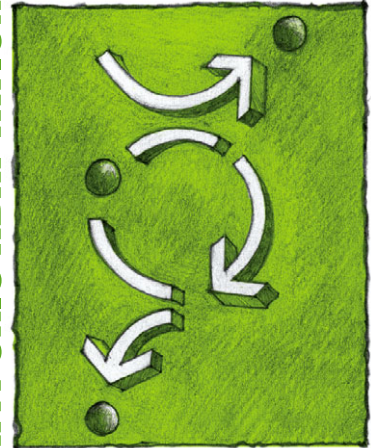
It seems that temperature, like light, utilizes specialized neuronal mechanisms to influence activity at different times during the day. So the next time you walk into a warm, dark lecture hall and feel the overwhelming urge to sleep, perhaps you can be forgiven.

10.1242/jeb.011577

Busza, A., Murad, A. and Emery, P. (2007). Interactions between circadian neurons control temperature synchronization of *Drosophila* behavior. *J. Neurosci.* 27, 10722-10733.

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HYPOXIC ADAPTATION



HIGH ALTITUDE IS NO PROBLEM FOR TIBETANS

Every breath we inhale brings oxygen into our bodies that our cells need to sustain metabolism. Normally we can supply enough oxygen to fuel metabolism, but at high altitude this can become a challenge. As barometric pressure declines with elevation, the air gets thinner and reduces the amount of oxygen we can load into our blood. Consequently, human populations indigenous to the high altitude plateaus of Tibet have evolved to cope with this problem. Tibetans breathe more than low altitude humans at elevation, which helps load oxygen into their blood. However, less is known about how the circulatory system works in Tibetan highlanders, so Serpil Erzurum and colleagues from the Cleveland Clinic, USA, wondered whether oxygen delivery throughout the body is higher in Tibetans. To investigate this, they compared how blood flow is controlled in highlanders from Panam Xiang, a rural district of Tibet that is 4200 m above sea level, with a sea level reference group of humans from the USA.

To get an idea of blood flow levels in the whole body, Erzurum and colleagues measured blood flow to the forearm of 88 Tibetans and 20 Americans, including both male and female subjects. They found that forearm blood flow at rest was twice as high in Tibetan highlanders as in low altitude humans. Furthermore, the Tibetans could increase their blood flow more than the sea level subjects during forearm exercise, better meeting the increased oxygen demands of muscle work. As a consequence of these higher flows, oxygen delivery to the forearm was always much greater in Tibetans. But what caused the higher blood flows in the highlanders?

It is already known that nitric oxide, or NO, is a gaseous substance released by the endothelial cells lining blood vessels, and that it causes blood vessels to dilate,

increasing blood flow and oxygen delivery to tissues. However, NO is only active for a short time after release, because it is quickly converted to products such as nitrite, nitrate, and nitroso-protein compounds. The authors wondered whether the Tibetans' higher blood flow could result from higher NO levels, so they measured the amount of NO products in the blood of Tibetans and in the sea level reference group. As they suspected, the highlanders had more circulating NO products than sea level humans, explaining their higher blood flow.

The results of Erzurum and colleagues demonstrate how human physiology can evolve in different populations from diverse environments. They show for the first time that indigenous Tibetan highlanders not only breathe more than their low altitude counterparts, but also circulate oxygen around the body at a higher rate. Simply increasing the production of NO probably causes this difference, emphasizing how a little extra gas can go a long way!

10.1242/jeb.011551

Erzurum, S. C., Ghosh, S., Janocha, A. J., Xu, W., Bauer, S., Bryan, N. S., Tejero, J., Hemann, C., Hille, R., Stuehr, D. J., Feelisch, M. and Beall, C. M. (2007). Higher blood flow and circulating NO products offset high-altitude hypoxia among Tibetans. *Proc. Natl. Acad. Sci. USA* **104**, 17593-17598.

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IGUANAS EVESDROP ON MOCKINGBIRDS

Many animals use complicated behavioural defences, such as alarm calls, to warn their fellows of a predators' presence. However, some mammalian and avian species have learned to respond to the alarm calls of other species. The ability to recognize and respond to other species' alarm calls has only been described in species with vocal communication. In a recent issue of *Biology Letters*, Maren N. Vitousek and co-workers from Princeton University, USA, and University of Bath, UK, examined whether the silent Galapagos marine iguana (*Amblyrhynchus cristatus*) could recognize and respond to the Galapagos mockingbirds' alarm calls, and found that they do.

Vitousek and co-workers tested the iguanas' responses to mockingbird alarm calls by recording Galapagos mockingbirds' song and alarm calls in response to the Galapagos hawk (*Buteo galapagoensis*), which predated both species. Then they played the mockingbirds' song and alarm call sequences to clusters of juvenile and female-sized marine iguanas at three distinct sites on the island and recorded the reptiles' responses.

The team found that significantly more iguanas (45%) exhibited alert behaviour (where they raised their heads in response to the recorded alarm calls) in response to the mockingbirds' alarm calls than when the birds simply sang (28%). The team realized that marine iguanas are able to differentiate between, and respond accordingly to, the mockingbirds' alarm calls and songs. This is the first demonstration that a species that lacks vocal communication can associate the auditory alarm signals of another species with the threat of predation.

There was also a significant difference in the percentage of iguanas that exhibited

anti-predator behaviour during playbacks at the various sites. This could be due to differences in the volume of ambient noise at each of the sites, caused by different wind speed or the distance from the ocean. However, the authors suggest an alternative explanation for the different responses at each of the three sites. Vitousek explains that the hawks on Santa Fe Island have a highly predictable flight trajectory along the island's east coast. They appear first at the northern end of each site and then proceed south along the island's coastline until they capture prey. The study sites were positioned on this axis – and the team found that the iguanas were most responsive to both types of mockingbird recordings at northern sites where the predation rates are highest.

The team also explain that the energetic cost of escape behaviour can be substantial, so gleaning additional information about a predator's presence in response to the mockingbirds' call may enable the iguanas to respond more effectively. Energetics could also explain the iguanas' relative infrequency of running-and-walking escape responses. Instead, they make the most of the mockingbirds' signals by looking up to confirm the predator's location and the risk posed, consequently saving energy by not responding if the risk appears low.

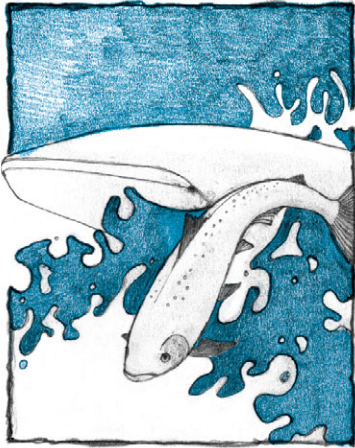
This is the first time that a non-vocalizing species has been shown to recognize another species' calls in order to acquire information about a common predator's movements. However, how the marine iguanas recognize the mockingbirds' alarm calls isn't clear. The team suggest that it may involve associative learning of the complex auditory signals, and further research is required to establish whether this ability is learned, or whether naive iguanas are capable of recognizing and responding to the mockingbirds' alarm calls. The team are also keen to know whether all marine iguanas are capable of eavesdropping, or whether it is a specific trait of the residents of Santa Fe Island.

10.1242/jeb.011544

Vitousek, M. N., Adelman, J. S., Gregory, N. C. and St Clair, J. J. H. (2007). Heterospecific alarm call recognition in a non-vocal reptile. *Biol. Lett.* **3**, 632-634.

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MORPHOLOGY



SHIFTING SHAPE IMPROVES ESCAPE

A wide variety of invertebrate animals are known for their capacity to develop different forms depending on the presence or absence of predators. Among vertebrates, crucian carp exemplify such ‘predator-induced phenotypic plasticity’ and exhibit fairly streamlined, torpedo-like body morphology in predator-free environments, in contrast to a substantially more deep-bodied shape when living in waters containing a piscivorous predator such as pike. Previous research has already highlighted the potential benefits of this shape difference in relation to vulnerability to gape-limited predators – pike probably have a hard time getting their jaws around the deeper-bodied morph. However, Paolo Domenici, an expert in fish escape behavior from the CNR-IAMC (National Research Council – Marine and Coastal Environment

Institute) in Oristano Italy, along with colleagues Håkan Turesson, Jakob Brodersen and Christer Brönmark from Lund University in Sweden, hypothesized that the shape change might also influence the carp’s ability to get away from a predator.

Interspecific studies of fish escape behavior have shown that body shape indeed has a significant impact on performance variables such as acceleration and turning rate during an escape maneuver. Thus, Domenici and colleagues decided to exploit the body form differences between crucian carp morphs to test the relationship between body form and locomotor function within a single species, where fewer potentially confounding factors come into play. Both deep- and shallow-bodied fish were collected from local ponds (with and without predators, respectively) in Lund, Sweden and acclimated to laboratory conditions over several weeks. Animals of each morph were then placed into the testing arena, where a high-speed digital video camera was used to record their startle response following the impact of a small, plastic cylinder dropped onto the water surface from a height of 1.1 m. Each animal’s center of mass (marked prior to the trial) and snout-tip positions were digitized to quantify various performance variables such as velocity, acceleration, rate of rotation and the cumulative distance traveled.

Deep-bodied fish taken from ponds with predators perform significantly better during escape behaviors than fish from predator-free waters. Specifically, they move further,

faster and exhibit a higher turning rate than their shallow-bodied conspecifics, exhibiting improvements of approximately 15–20%. In addition, carp from predator-filled ponds also possess a significantly higher fraction of muscle mass relative to body mass, which, along with their increased depth, may help to explain their higher levels of performance. Although apparently good for escape, the increase in body depth does come with tradeoffs, particularly in the context of the energetic costs of steady cruising, which are higher in deeper-bodied animals. Nonetheless, this work provides indirect evidence that in crucian carp, shape changes that occur as animals develop in the presence of predators probably improve their likelihood of survival. The authors believe their results may also have more general implications, namely that the evolution of deep bodies in other fish species may reflect past selection on escape performance. Continued work that characterizes escape and/or survival rates during actual interactions between predators and the different carp morphs will be an essential step toward solidifying the importance of phenotypic plasticity and increased body depth for improving escape capacity and ultimately fitness in these animals.

10.1242/jeb.011569

Domenici, P., Turesson, H., Brodersen, J. and Brönmark, C. (2008). Predator-induced morphology enhances escape locomotion in crucian carp. *Proc. R. Soc. B* **275**,195-201.

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