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

COST OF TRANSPORT

NOT ALL MUSCLES WORK BEST AT THE SAME SPEED

Anyone that spends extended periods of time walking or running intuitively understands that for a given gait there is a particular speed that seems most suitable. Experts studying the energetics of human locomotion have shown that these so-called preferred speeds have something to do with the cost of transport (COT), or the energetic cost to move a given amount of body mass a given distance at those speeds. Namely, COT tends to be relatively low at preferred speeds compared with other possible speed choices. Given that the activity of skeletal muscles in the limbs and trunk accounts for most of the energetic cost of locomotion, it makes sense to ask whether large and important muscles involved in walking and running might also work most economically at speeds where COT is minimized. Indeed, as Dave Carrier of the University of Utah and colleagues Christoph Anders and Nadja Schilling of the University of Jena propose in a recent *PNAS* paper, if the COT was a major selective factor in the evolution of human locomotion, muscles of the limbs and trunk should be tuned to work most effectively at the same speed within each gait, minimizing COT at those speeds.

To test this idea, Carrier and colleagues used surface electromyography to measure electrical activity patterns in 13 leg and trunk muscles during locomotion in 17 men. For each muscle in each subject they summed the integrated electrical activity used to cover ~20–30 strides for a range of walking and running speeds, and came up with the cumulative muscle activity per distance traveled (CMAPD). These measurements of cumulative activity within a muscle across speeds were then used as a proxy for muscle metabolism.

The researchers found that most muscles exhibited a U-shaped curve relating CMAPD to speed within a gait, which is to say that for both walking and running, most muscles had an intermediate speed at which muscle metabolism was minimized. However, the actual speeds at which these minima occurred differed among muscles. For example, the vastus lateralis worked most economically during running at about $16\,km\,h^{-1}$ whereas the gluteus maximus did so at closer to $10\,km\,h^{-1}$. This difference is one of the most dramatic observed, but the point nevertheless is clear: not all muscles seem to work best at the same speed within a gait.

The authors use these results to argue that minimizing the COT was not the only important selective factor on limb and trunk muscles in human evolution. It is likely that these muscles evolved to perform a number of tasks well, presumably including things like climbing, throwing and acceleration. One of their more intriguing results was that the U-shaped curve relating CMAPD to speed during running was shallow for most muscles, implying that while there is an optimal speed for minimizing energetic costs, there is also a pretty broad range of speeds over which such costs don't change by much. Thus, while our muscles may not be specialized solely for economizing locomotion, they do a pretty good job of reining in the costs over a larger range of speeds than would be expected based on work on other animals, like horses. Such an ability to perform well across a range of speeds may well reflect selective pressure that acted on the physiological underpinnings of persistence hunting strategies in our ancestors.

10.1242/jeb.064121

Carrier, D. R., Anders, C. and Schilling, N. (2011). The musculoskeletal system of humans is not tuned to maximize the economy of locomotion. *Proc. Natl. Acad. Sci. USA* **108**, 18631-18636.

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COOPERATION

YELLOW SADDLE GOATFISH ARE TEAM PLAYERS

Spectacular discoveries within coral reefs continue to be made and in recent years the Red Sea has proven to be a treasure trove for neuroethologists in particular. For those interested in animal cognition and the evolution of cooperative behavior, a rich and diverse list of predatory species – found to utilize complex cooperative-hunting techniques – as been growing. In 1989, Christophe and Hedwige Boesch categorized four distinct levels of cooperative hunting in chimpanzees in their *American Journal of Physical Anthropology* paper. Previously, scientists theorized that each of these four hunting categories varied from species to species and reflected a spectrum of innate cognitive abilities. As such, the highest level of complexity, collaborative hunting, where hunters each coordinate and execute quite different but complementary actions on the prey, was thought to be absent in 'lower' vertebrates.

Therefore, it was quite remarkable when Carine Strubin, Marc Steinegger and Redouan Bshary from the University of Neuchatel, Switzerland, recently found that a tropical fish species, the yellow saddle goatfish (*Parupeneus cyclostomus*), appears to form relatively stable hunting parties and actually employs sophisticated and highly coordinated actions. In their paper published in *Ethology*, the team describes versatile, cooperative-hunting techniques used by goatfish that were previously only attributed to 'higher' vertebrate species.

While snorkelling along the shallow coast line of the Red Sea, Bshary's group reliably identified and tracked 17 adult individuals (based on coloration, size, and spot patterns on fins and body) for 3 months. Using digital photography, the team was able to distinguish individuals by the highly variable blue lines around the eyes and to analyse their behavior.

Observing the social behavior of the goatfish, Bshary's team found the hunting system to be dynamic and flexible; some individuals spent time in stable groups, while another individual exhibited a primarily solitary existence. In addition, the team found that the social groups were not necessarily exclusive or permanent. Some fish switched membership from group to group but the researchers noted that the individuals found within groups were consistently similar in size to one another. The researchers also witnessed the goatfish working as a team, each assuming a specific responsibility in the hunt, either as a chaser or as a blocker. Remarkably, each individual goatfish exhibited flexibility in their role, acting as a chaser and directly pursuing prey during one hunt, while acting as a blocker on other occasions – strategically encircling the prey as it hid among corals.

Prior to this study, such multifaceted and dynamic team-hunting behaviors had been primarily observed in mammals and birds. Clearly we are just beginning to appreciate that 'lower' vertebrates are to be included in understanding the evolutionary process of collaborative hunting.

10.1242/jeb.064071

Strubin, C., Steinegger, M. and Bshary, R. (2011). On group living and collaborative hunting in the yellow saddle goatfish (*Parupeneus cyclostomus*). *Ethology* **117**, 961-969.

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GLUCOSE TOLERANCE

BATS CAN HAVE THEIR CAKE AND EAT IT

Nectar-feeding bats (*Glossophaga soricina*) have a high sugar diet and consequently high blood sugar levels. Despite their sweet tooth, these bats do not suffer detrimental sugar-related health effects as would other mammals, including humans, and they are especially long lived – about five times longer than a similar sized rodent. Detlev Kelm, at the Leibniz Institute for Zoo and Wildlife Research, and a team of German researchers were curious as to how these bats regulate their blood sugar during rest and flight, wondering how they avoid the adverse effects of a high sugar diet. Their fascinating findings were published in a recent issue of *PNAS*.

The team first measured the bats' blood glucose levels at rest during a meal similar to that consumed in the wild. Interestingly, the bats' blood glucose levels after the meal far exceeded normal values for mammals of similar size and were among the highest ever recorded in mammals. The researchers speculate that the bats have evolved a physiological tolerance to glucose, avoiding the damaging effects of a high sugar diet and the shorter life span usually associated with it.

Next, the researchers set out to determine the role exercise has on regulating blood glucose by using three different exercise regimes after consuming either one big meal or several smaller meals. Overall, flying reduced the severity of blood glucose peaks seen in the resting bats. Moreover, the bats that spent more time flying after a meal had lower blood glucose peaks and their blood glucose returned to pre-feeding values faster. This suggests that bats use flight as a strategy to prevent blood glucose from rising to extremely high and potentially damaging levels.

In the wild, nectar-feeding bats spend up to 12 h a night feeding, flying about 60% of the time. As Kelm and his colleagues suggest, flying helps the bats not only to regulate blood glucose levels but also to devote more energy to searching for roosts or new food sources, perhaps providing a selective benefit to bats that spend more time flying between meals.

Lastly, the researchers wanted to know how high the bats' blood glucose concentrations were over a longer period of time (weeks) whilst being fed a diet similar to that found naturally. Blood glucose irreversibly reacts with haemoglobin in the blood to form glycated haemoglobin depending on the amount of glucose in the blood and on the lifetime of the red blood cells. Kelm took blood samples from bats and measured the amount of glycated haemoglobin. The nectar-feeding bats had normal levels of glycated haemoglobin in their blood in comparison to other mammals. Thus, the bats had low blood glucose levels over long periods of time and consequently were not chronically exposed to high blood sugar levels and their damaging effects.

Although the nectar-feeding bats' secret to a long life was not entirely revealed, Kelm and his colleagues used elegantly designed experiments to figure out how the nectar-feeding bats use flight to take advantage of a high sugar diet and avoid its harmful effects. So perhaps we can all eat our cake, as long as we run a marathon right after.

10.1242/jeb.064139

Kelm, D. V., Simon, R., Kuhlow, D., Voigt, C. C. and Ristow, M. (2011). High activity enables life on a high-sugar diet: blood glucose regulation in nectar-feeding bats. *Proc. R. Soc. B* **278**, 3490-3496.

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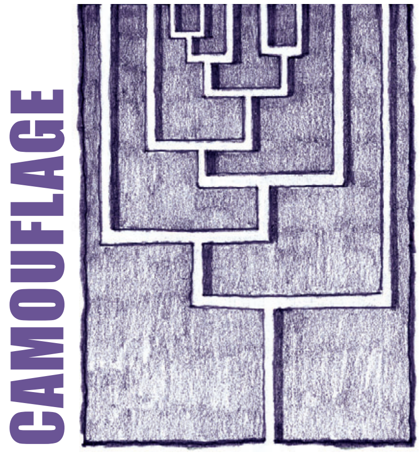

CAMOUFLAGE COMBO FROM THE DEEP

There are probably few places that conjure up images of desolation more than the depths of the earth's oceans. In these aquatic wastes there is little or no daylight, food is lacking and mates are in short supply.

Even so, going about your business undetected by predators in these places is harder than you might think. At levels where daylight can penetrate, an animal's silhouette can be detected under the downwelling light, and in the darker depths some predators have developed photophores that they use as searchlights.

Animals have therefore adopted different camouflage strategies in order to deal with this. Transparency vastly reduces an animal's visibility under ambient light, whereas red or black pigmentation helps reduce the reflection of the directed light emitted by photophores.

However, in the lower mesopelagic zone, found between 600 and 1000 m below the surface, animals are faced with a dilemma. This is where the optimal camouflage strategies overlap, as some daylight reaches these depths, but searchlight-carrying predators can also be found here. An animal can't both be transparent and have pigmentation at the same time, so what possible solution is there for these animals? Sarah Zylinski and Sönke Johnsen, publishing in *Current Biology*, have uncovered a mechanism that solves this dilemma.

They had noticed that the appearance of a small octopus, *Japetella heathi*, and a medium-sized squid, *Onychoteuthis banksii*, varies from transparent to pigmented. Could this be in response to different light conditions? To test this, they first studied what appearance these animals had under ambient light conditions to simulate downwelling daylight.

They found that both animals were transparent under these conditions, making them ideally camouflaged for the upper levels of the mesopelagic zone.

Next, they exposed transparent animals to a beam of light with a wavelength similar to that produced by photophores, to simulate exposure to a predator searchlight.

They found that these animals changed their appearance to the pigmented form within a second of exposure to the beam, and they eventually took evasive action, as if to protect themselves from predators. This suggests that these animals change their appearance in response to a threat from searchlight-bearing predators.

But does the pigmentation actually help them to remain undetected? To test this, the authors measured the reflectance from live *Japetella* skin, in either the transparent or pigmented form.

They saw that the reflectance of the pigmented skin was twofold lower than that of the transparent skin when illuminated with light of a wavelength similar to that emitted by mesopelagic predators. This reduces the animal's visibility when illuminated by predator searchlights and suggests that switching camouflage mechanisms gives the animals a real advantage.

The authors' findings show that some animals have developed the ability to switch between two different camouflage strategies, allowing them to quickly respond to different predator threats as well as changing optical conditions. Although the mechanism that regulates this switch is currently unknown, it will be interesting to see how widespread these adaptations are and what additional strategies could be deployed to avoid predator detection in dynamic environments.

10.1242/jeb.064063

Zylinski, S. and Johnsen, S. (2011). Mesopelagic cephalopods switch between transparency and pigmentation to optimize camouflage in the deep. *Curr. Biol.* **21,** 1937-1941.

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