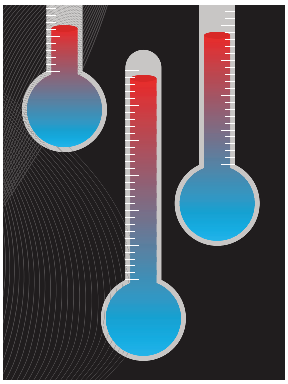
© 2016. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2016) 219, 2968-2970

OUTSIDE JEB

Some like it hotter than others

EXTREME PHYSIOLOGY



If you want to meet a truly tough fish, buy a ticket to Lake Magadi, Kenya. Here, the Magadi tilapia swim happily in the hot, alkaline waters of the lake, where oxygen levels soar and plummet daily and water chemistry pushes the boundaries of acid–base regulation. Few fish can survive such an extreme aquatic environment and this has attracted comparative physiologists for decades to the town of Magadi, where tilapia are easily studied in the nearby man-made lagoon. But not all Magadi tilapia are created equal, as discovered by Canadian scientist Chris Wood and a team of international colleagues on a recent expedition to Kenya. In fact, life is even more challenging in the fast-flowing hot springs that feed into Lake Magadi's southwestern shores. Remarkably, tilapia live here too.

Wood and crew trekked out to study this isolated population of Magadi tilapia, looking for the toughest tilapia yet. They noted some striking differences between the deep, static waters of the lagoon and the shallow, steamy waters of the hot springs. For example, in a given 24 h period, the lagoon tilapia endure an impressive swing in dissolved oxygen levels from ∼15% to 80% saturation, but their hot spring relatives eat breakfast in anoxia and lunch in super-saturated water! Also, during that same 24 h period, while the lagoon fish sweat it out in 33–36°C water, over in the hot springs, the tilapia's mercury peaks at a whopping 43°C and fluctuates by 11°C throughout the day. So a day in the life of a hot springs tilapia is no small feat, and Wood bet that these fish must have outstanding thermal tolerance and metabolic capacity.

Wood's study started heating up when he measured the upper critical temperatures of the lagoon and hot springs tilapia. When the researchers cranked the thermostat on the lagoon fish, they held out to a maximum temperature of 44.5°C – that's pretty toasty for a poikilotherm. But the hot springs fish toughed out temperatures to 45.6°C, the highest temperature ever recorded for any fish! Scarily, the hot springs fish died at a temperature that was only 2.6°C warmer than that in which they swim daily and that gap will quickly narrow if current climate change trends continue.

Next, Wood and his team began measuring the routine and maximum metabolic rates of fish from the two Lake Magadi habitats and again the hot springs tilapia set records. While routine metabolic rate in all Magadi tilapia is high, the fish Wood's team caught from the hot springs had metabolic rates that were quadruple the rate of the lagoon fish, putting them on a par with mammals of a comparable size. And, when they made the fish swim to exhaustion to measure their maximum metabolic rates, not only did the hot springs tilapia outperform the lagoon fish in the swim test, their maximum metabolic rate surpassed any previously recorded in a size-matched fish.

The Magadi tilapia remains a perfect fish for studying physiological adaptations to extreme environments and the hot springs population teeters on the edge of that extreme, making them true Olympians among aquatic athletes!

10.1242/jeb.130310

Wood, C. M., Brix, K. V., De Boeck, G., Bergman, H. L., Bianchini, A., Bianchini, L. F., Maina, J. N., Johannsson, O. E., Kavembe, G. D., Papah, M. B., Letura, K. M. and Ojoo, R. O. (2016). Mammalian metabolic rates in the hottest fish on earth. *Sci. Rep.* **6**, 26990.

Sarah Alderman
University of Guelph
alderman@uoguelph.ca

Leaf-footed bugs choose to lose legs

AUTOTOMY

For animals, the ability to escape from life-threatening situations is essential. Whether fleeing from a predator's grasp, or manoeuvring their way out of a fight, animals benefit from traits that allow them to escape more easily. One such trait found throughout the animal kingdom is autotomy: the ability to voluntarily shed an appendage, most commonly a leg or tail. This may seem like an extreme solution, but in instances where the choice is to lose a limb or lose your life, it's a no-brainer.

Autotomy is particularly common amongst invertebrates, with various insects, arachnids and crustaceans all reported to have the ability to self-amputate. Depending on the species, and often the animal's age, these lost legs may either grow back, or the individual may have to cope without it for the remainder of their life. However, considering that autotomy is such an extreme behaviour with potentially severe consequences, we still don't really know which species resort to autotomy, particularly within insects.

To try to bridge this gap, a team of researchers from the University of Florida focused their efforts on the Coreidae family of insects, better known as the leaf-footed bugs. Led by Zachary Emberts, they first looked at the frequency of leg loss within natural populations of nine species of this insect. By collecting adult leaf-footed bugs and noting if legs were lost, the team observed that depending on the species, between 7.9% and 21.5% of

Outside JEB is a monthly feature that reports the most exciting developments in experimental biology. 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.

individuals had legs missing. In addition, they looked at which legs were absent and saw that there appeared to be a larger proportion of hind legs missing. Interestingly, the hind legs of many of these species of leaf-footed bug are highly decorated, have enlarged femurs and are often used as weapons when fighting over mates.

Finding individuals with missing legs does not, however, prove that the species can autotomise, so to test this, the researchers attempted to induce autotomy in the lab by grasping a hind leg with forceps to simulate attack from a predator. Supporting the field results, all nine species successfully autotomised the leg. The authors noted that all of the breakages occurred at the same leg joint and were accompanied by a stereotypical 'raise-and-drop' movement of the abdomen. Intriguingly, in three species, they observed that only females autotomised the limb, despite the presence of male individuals with missing legs in the wild.

This work has helped to broaden our knowledge of the range of this extraordinary trait in insects, but has also raised some questions. In some species of leaf-footed bug, the hind leg is used as a decoy during attacks, distracting predators with its decoration, and here the ability to shed it quickly makes great sense. However, these insects also often use their hind limbs as weapons during sexual competition, so it is curious that they are prepared to shed them so readily, particularly as adults cannot regrow the limb once it has been lost. As sacrificing a leg in order to survive also reduces the animals' reproductive fitness, this appears to be one of nature's more extreme examples of cutting off your nose to spite your face.

10.1242/jeb.130302

Emberts, Z., St. Mary, C. M. and Miller, C. W. (2016). Coreidae (Insecta: Hemiptera) limb loss and autotomy. *Ann. Entomol. Soc. Am.* **109**, 678-683.

Michelle A. Reeve
Royal Veterinary College
mireeve@rvc.ac.uk

When symbionts overstay their welcome

Animals are increasingly understood to be complex cellular conglomerates. While some parts are derived from the genome of the host organism, the rest comprises microbial symbionts. In the best of cases, these pieces of the puzzle form tight partnerships that provide mutual benefits. However, because symbionts can also be a burden, it is sometimes useful for hosts to go it alone. But what if evicting symbionts makes things worse? In these cases, can hosts become addicted to their microbial passengers? In a fascinating new report in the Proceedings of the Royal Society, Series B, Julien Martinez and colleagues from the University of Cambridge, UK, describe just such an outcome.

Wolbachia bacteria are ubiquitous in insects and infect more than half of all species. While best known as manipulators of insect reproduction, these bacteria can also play defensive roles for their insect hosts. In *Drosophila*, they provide protection against the highly lethal fly virus *Drosophila* C virus (DCV). However, flies can also become resistant to DCV without *Wolbachia* via mutations in their genomes at a single gene called *pastrel*. If you can have one mode of resistance, why keep both? This is particularly true for *Wolbachia*, whose carriage can be highly costly to flies. And if you do carry *Wolbachia*, how does this affect the evolution of *pastrel*?

To address these questions the team established two groups of flies that were identical except for the presence or absence of *Wolbachia* symbionts. They then infected flies from these treatments with DCV. As expected, fewer flies with the bacterial symbiont died than those without it. Some flies without *Wolbachia*, however, survived, and this minority overwhelmingly carried mutations at the *pastrel* locus. By contrast, *pastrel* mutations in the *Wolbachia* flies remained at very low levels. This result indicated that, at least in the short term, bacterial symbionts suppressed the evolution of host resistance. But what about in the longer term?

Martinez and his colleagues next reared both groups of DCV-infected flies through nine generations. Although viral resistance increased in both fly groups, the effects on *pastrel* mutations were dramatically different. While *pastrel* mutations rapidly increased in frequency in the flies lacking *Wolbachia*, becoming fixed in these populations, the ascent of mutations in the gene was markedly slower in flies harbouring the symbiont. More strikingly, the group estimated that while DCV imposed very strong natural selection to increase the frequency of *pastrel* mutations in the no-symbiont group, this was almost entirely absent in flies carrying *Wolbachia*. In short, *Wolbachia* carriage arrested the evolution of genomic mutations for DCV resistance.

So why is *Wolbachia* an addiction? Simply, because flies carrying costly bacterial symbionts suspend fighting DCV on their own. Thus, when DCV is common, *Wolbachia*-mediated protection might become the only form of protection available, despite the fact that *pastrel* mutations could do just as well at much lower cost. At present, the authors are not sure if this result extends to other defensive symbionts. It is also unclear whether this type of addiction occurs with symbionts playing non-defensive roles in other animals or plants. More generally, is this the selfish route by which transient symbionts become permanent? If so, it would suggest that the alliance between animals and microbes is not always a simple one and that even highly mutualistic interactions between

Journal of Experimental Biology (2016) 219, 2968-2970

microbial symbionts and hosts may have coercive origins.

10.1242/jeb.130286

Martinez, J., Cogni, R., Cao, C., Smith, S., Illingworth, C. J. R. and Jiggins, F. M. (2016). Addicted? Reduced host resistance in populations with defensive symbionts. *Proc. R. Soc. B* **283**, 20160778.

Daniel E. Rozen
University of Leiden
d.e.rozen@biology.leidenuniv.nl

Diving beetles that handle heat better have bigger backyard

Whether it's birdwatching or catching Pokémon, everybody knows that different species have different geographical ranges. Some species like Canada geese, have far-flung populations spread across an entire continent, while others like the Christmas Island frigatebird are found only on a single tiny island in the middle of the ocean. While explanations for why some species have broader ranges than others vary, for diving beetles it might come down to their ability to perform under stress.

Diving beetles in the genus *Deronectes* are found throughout Europe; some species are found over areas covering thousands of kilometres, while others only cover an area with a 100 km radius. Rebekah Cioffi and her colleagues at Plymouth University, UK, along with Andrés Millán from the University of Murcia, Spain, thought each species' distribution might be linked to their physiological plasticity in response to thermal stress. Since the climate of regions distributed towards the poles tends to be more variable than those in more equatorial regions and the species with the most widespread ranges tend to occur in more polar areas, the researchers thought that perhaps only those species that are able to rapidly adjust how their bodies function can become geographically widespread.

To test this idea, the researchers set out on a trans-European mission to collect five closely related species of *Deronectes* beetles, then brought them back to the lab to test their performance under heat stress. They warmed up the beetles to 15, 20, 25, 30 or 35°C, then held them at that temperature for 24 h before placing them in the deep freeze until they could later measure the beetles' metabolic stores, such as carbohydrates (glycogen and glucose) and fats. The researchers also measured the beetles' ability to mount an immune response and defined their plasticity as the difference between the highest and lowest values for each measurement.

Cioffa and colleagues found that the value that best explained the breadth of distribution of a diving beetle species included both the degree of plasticity (how much the measure of lipids, glycogen and glucose changed after changing temperatures) as well as how strongly the insect's immune system responded to pathogens. In particular, diving beetles that had more northerly and widely distributed ranges also seemed to have a greater ability to burn fat under thermal stress, which makes sense because fats are a more dense form of energy storage than carbohydrates and the fat body in insects is also involved in the production of important immune molecules such as antimicrobial peptides.

While the ability to survive harsher conditions closer to the poles is still important for an insect species to spread across vast geographical ranges, the researchers suggest that for diving beetles at least, having physiological systems that can bend with changing temperatures can be another important trait that allows them to spread far and wide.

10.1242/jeb.130294

Cioffi, R., Moody, A. J., Millán, A., Billington, R. A. and Bilton, D. T. (2016). Physiological niche and geographical range in European diving beetles (Coleoptera: Dytiscidae). *Biol. Lett.* **12**, 20160130.

Katie Marshall
University of British Columbia
kmarshall@zoology.ubc.ca