

OUTSIDE JEB

When natural armour does more than protect



A range of animals, from dinosaurs to armadillos, have a natural form of chain mail armour that is composed of bony plates in the skin called osteoderms. Individual osteoderms each act as miniature shields that are linked together through flexible connections, forming a resilient suit of armour that can reshape with the animal's movements. While natural armour plays an important role in defence against predators, recent work has demonstrated that it serves a range of other functions including thermoregulation. But, does having multiple functions compromise the strength of the armour?

Broeckhoven and colleagues from Stellenbosch University and the African Institute for Mathematical Sciences, in South Africa, sought to test whether increased strength in osteoderms came at the cost of decreased thermoregulatory capabilities by comparing the anatomy and mechanical properties of osteoderms in the armadillo lizard (Ouroborus *cataphractus*) and giant girdled lizard (Smaug giganteus). Although these lizards may have independently evolved heavy armour to avoid being eaten by mongooses, the armadillo lizard spends a lot of time out in the open in order to feed on termite nests and, therefore, is directly exposed to temperature fluctuations in the environment, whereas the giant girdled lizard inhabits burrows that shield it from the elements. Consequently, these species present an intriguing comparison because their different life history characteristics could influence

the selective pressures on their armour.

Sections of skin were removed from the backs of preserved specimens and imaged with a micro-CT scanner to visualize the internal and external anatomy of the tissues. The team then used a computer program to digitally dissect individual osteoderms from the micro-CT scans, calculate their thermal conductivities and determine the stresses and strains (deformations) resulting from a simulated mongoose attack. But how well do these computer simulations match biology? To address this question, they built a mechanical predator in the lab by attaching a canine tooth from a mongoose to a mechanical testing machine and then re-enacted an attack by having the 'predator' bite down onto the osteoderm until it broke.

Results from the computer simulations and laboratory experiments indicated that osteoderms were weaker in the armadillo lizard, fracturing at a force that was about 25% lower than that for the giant girdled lizard. In addition, the osteoderms in the armadillo lizard were better insulators as they had lower thermal conductivity and were therefore likely to be better able to maintain the animal's body temperature. Overall, the results seemed to indicate that osteoderms that were more thermally insulated were also weaker against attacks (and vice versa), suggesting a functional trade-off between thermoregulation and strength.

Yet, these lizards may get the best of both worlds by modifying their behaviour. Although the armadillo lizard has weaker osteoderms, it has another line of defence: it bites its tail and rolls up into a ball to avoid being eaten. Similarly, the giant girdled lizard compensates for the lower thermoregulatory capabilities of its osteoderms by hibernating and living in well-insulated burrows to avoid drastic temperature changes. Consequently, testing biomaterials in more ecologically relevant scenarios provides a promising avenue to understand the multi-functional roles of biomaterials and develop better bio-inspired armour.

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Broeckhoven, C., du Plessis, A. and Hui, C. (2017). Functional trade-off between strength and thermal capacity of dermal armor: insights from girdled lizards. J. Mech. Behav. Biomed. Mater. 74, 189-194. doi:10.1016/j.jmbbm.2017.06.007.

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Flying high, no training required



Whether it is for the Olympics, pearl diving or climbing Mount Everest, humans have to train intensively to prepare their bodies for extreme challenges. However, it is not entirely clear whether other members of the animal kingdom also go through bouts of training prior to extreme events. Barheaded geese (Anser indicus) have a reputation for performing one of the most extreme feats at altitude. Migrating across the Himalayas in as little as 7 h, the birds have to sustain one of the most metabolically costly forms of locomotion – flight – in high-altitude conditions, where oxygen is scarce. What is more, these birds fly straight from sea level to altitudes of more than 4500 m in a matter of hours, unlike humans, which need days to gradually habituate to highaltitude conditions. Working with the geese as part of a multinational collaborative project, Lucy Hawkes from the Centre for Ecology and Conservation at the University of Exeter, UK, and her colleagues set out to determine whether these birds 'train' for their annual highaltitude migration.

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.

Travelling to Terkhiin Tsagaan lake in Mongolia – where the bar-headed geese moult and are unable to fly, during a 2-3week period prior to migration - Hawkes and colleagues captured small groups of the geese by herding them with inflatable kayaks into shoreline nets. The team then surgically implanted data loggers in the abdomens of the birds to record their heart rate, acceleration and internal temperature and pressure. They then released the animals and recaptured them a year later, when the geese returned to the lake after their migration in order to remove the loggers and download the data.

To determine whether the birds trained for their migration, the authors looked at the activity that the animals undertook and the variation in their heart rate during the premigratory period. To estimate whether the geese exercised more prior to migration, the authors measured the acceleration produced by the animals as they moved around, which can clearly distinguish flapping from walking and resting. They found that the total amount of activity did not increase prior to migration, nor did the frequency of strenuous flapping on the ground – short, intense ground-based social displays which may also double as strength-training. If the geese were becoming physically fitter, the team also reckoned that their minimum, overnight heart rate would get lower, and their maximum heart rate during flight should get higher, but they found no evidence of either. Compiling the observations, Hawkes and her co-authors could not find evidence that bar-headed geese engage in any type of flight training activity prior to migration.

Hawkes and her colleagues also suggest that perhaps bar-headed geese use the rest periods during migration to allow their muscles to recover and rebuild, which may increase their fitness over the course of the migration and could explain the lack of training prior to their departure. In addition, the authors suggest that the cardiac and respiratory systems of the barheaded geese play an important role in ensuring their impressive performances at altitude, as they are adapted to take up as much oxygen as possible from the environment and quickly deliver it to the organs where it is needed. It appears that a combination of adaptations allows the bar-headed geese to fly high, no training required.

10.1242/jeb.147678

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Speed limits for the animal kingdom



Ask anyone 'what is the fastest animal on earth?'. A guaranteed popular response will be 'a cheetah!'. But, if you ask 'why are cheetahs the fastest animals?', you might receive some quizzical looks and uncertain shoulder shrugs. Until recently, most scientists also felt this way. The largest animals should be able to move the fastest because they have more muscle to propel them to top speed, in theory. Why then are the largest animals - think elephants outpaced by mid-sized animals like cheetahs? This conundrum doesn't just hold for land-running animals but also for those that swim and fly: being mid-sized truly is the sweet spot for moving fast.

Myriam Hirt from the German Centre for Integrative Biodiversity Research and her colleagues from Friedrich Schiller University, Yale University, and Imperial College London, sought to solve the perplexing mystery behind animal speed. Hirt's team looked at whether the muscles that power movement may actually slow down the largest animals. The researchers focused on 'fast-twitch' muscle fibres, which animals use when pulling off their fastest performance. Though this type of muscle helps speedsters move quickly, fast-twitch fibres consume energy stores more quickly than they can be replaced, leading eventually to fatigue. The heavier an animal is, the longer it will take to reach its fastest speed, and the more

energy it will require to reach that speed. Hirt and colleagues predicted that the biggest animals never reach their true top speed because they burn up their fuel supplies before attaining their fastest pace.

Using the prediction that larger animals would tire out before hitting their potential top speed, the researchers modelled the maximum speeds that animals could attain based on their body mass and mode of locomotion (whether an animal travels on land, in water or in air). Hirt's new muscle-based model was incredibly precise and predicted animal top speeds with 90% accuracy in the 474 different species that the team tested. Impressively, the model was accurate for animals from 30 μ g (mite) to 108 400 kg (blue whale) in body size and for animals from vastly different habitats. On land, under water and in the air, Hirt and colleagues' model showed that mid-sized animals outpaced their larger counterparts. The researchers suggest that mid-sized animals have enough heft and power to move fast, but not so much that they are held back.

One exciting application for an allencompassing muscle model such as Hirt's is that researchers can use it to estimate speeds for long-extinct species. The researchers investigated whether their model could stand the test of time and predict top speeds for six different dinosaurs. The model showed that a nimble, mid-sized *Velociraptor* would have moved almost twice as fast as a massive *Tyrannosaurus* at their fastest paces, confirming the expectations of previous researchers, who thought *Tyrannosaurus* to be relatively slow.

The team's research also has exciting applications for currently living animals. Hirt's work could be a valuable starting point for investigating why some animals differ from their model's prediction by being either faster or slower than expected.

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Home invaders provoke neighbouring cichlids



Social alliances are rare. Only in a handful of species, such as fiddler crabs and chipping sparrows, do unrelated neighbours team-up when a member of the same species invades their territory. Near-by residents will aid their harassed compatriots and help to ward off the assailant, so long as the invader presents a threat to the neighbourhood. Posing a threat can really amount to being 'sexier' than the neighbour: having a larger claw or a prettier song. However, past studies focused solely on the point of view of the animals leaping to a neighbour's defence, and less often included how the resident under siege responded.

To capture both perspectives – that of the threatened animal and its allies – neuroscientist Chelsea Weitekamp and colleagues in Hans Hofmann's lab at the University of Texas, USA, compared how an intruder elicits different behavioural and biological responses depending on the social role of a cooperative territorial teleost fish, the African cichlid (*Astatotilapia burtoni*).

Initially, Weitekamp set up two fish tanks next to each other, each tank containing one male and two female cichlids, and allowed the neighbouring fish tank communities to acclimate to one another over the next 4 days. On the fifth day, Weitekamp placed an intruder fish into one of the tanks (the 'residents' tank), and noted how aggressively the residents and their neighbours responded to the interloper. Following harassment by the intruder, Weitekamp then measured how the encounter changed hormone levels in the blood and gene expression in the brain in both the resident and neighbouring males.

During the intrusion, the residents lashed out more often at the intruder than did their neighbours. And, although the resident and neighbouring males pumped similar amounts of the sex hormone testosterone and the stress hormone cortisol into their systems, only testosterone levels in neighbours, but not residents, predicted how aggressively a fish would respond.

Focusing on the effects of the intruder on the brains of the fish from the neighbouring tank, the team found that expression of the *egr-1* gene (which occurs when neurons are activated) in the amygdala region of the brain, which mediates social behaviour, increased as the fish became more aggressive. In addition, Weitekamp realised that as the concerned neighbours became increasingly aggressive, they expressed more genes that mediate social behaviours [such as the serotonin (*5-htr2c*) and dopamine (*d1r*) receptors] in the amygdala, in addition to producing more testosterone.

In contrast, Weitekamp found no evidence of any other changes in the brains or bodies of the resident fish, aside from soaring levels of testosterone as they lashed out. Further, resident fish's aggression didn't relate to any changes in gene expression or hormone levels.

These intriguing findings – that harassed residents become more aggressive during an intrusion while their neighbours enhance the social side of their characters – are beginning to shape our understanding of how social roles mediate divergent behavioural and biological responses to a territorial threat. In cichlids at least, a fellow territorial fish next door makes for the most vigilant and responsive neighbourhood watch.

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