

INSIDE JEB

Tarantula coordination disintegrates in heat



Texas brown tarantula (*Aphonopelma hentzi*). Photo credit: Anna Ahn.

Scuttling across the floor, a spider's movements have more in common with robots than you may at first realise. Instead of contracting muscles to extend a limb, spiders inflate their joints with haemolymph to straighten them - in much the same way that hydraulic fluid propels robot limbs. And temperature fluctuations may affect the movements of spiders and robots alike: fluid viscosity can increase dramatically as temperature falls, prompting undergraduate Nick Booster from Pitzer College, USA, to ask whether spider movements are affected by temperature change. 'I've always wanted to study spiders because they use hydraulics', says Anna Ahn from Harvey Mudd College, USA, so when Booster approached Ahn and Steve Adolph with his idea to study the effects of temperature on the arachnid's movements, they jumped at the chance. 'This is a fascinating question', Ahn chuckles, adding, 'We wanted to understand how temperature affects the haemolymph and whether impaired haemolymph movement might influence the spiders' ability to run'.

Choosing to test the athletic abilities of Texas brown tarantulas at temperatures that the animals encounter naturally (15, 24, 31 and 40°C), Booster and Harvey Mudd College undergraduate Frances Su painted white dots at four locations on the arachnids' forelegs and hindlegs before filming the animals as they scampered along a runway. Su recalls that the team had no problems getting the spiders to sprint when startled with a gentle puff of air, although collecting movies with a clear view of at least four strides was more troublesome. 'It was difficult when the spiders didn't run in the right direction', says Su; then Booster spent hours

painstakingly digitising the position of the spiders' limbs on the movies to accurately track their movements.

After months of patient analysis, it was clear that the spiders' hydraulic limbs were affected by temperature. Going full out at the lowest temperatures, the spiders could only manage a relatively sedate top speed of 20 cm s^{-1} . But, by the time they had warmed up to 40°C, they were rocketing along at a startling 53 cm s^{-1} . And, instead of increasing their stride length as they speeded up, the animals increased the frequency of each stride from a leisurely 4 strides s^{-1} at 17°C to an impressive 10 strides s^{-1} at the highest temperature. But, when the team analysed how the spiders coordinated the extension of their joints along the length of their legs, they found that the animals were becoming more uncoordinated at the highest temperatures: at the lowest temperatures, the spiders managed to extend the third and fifth joints at almost the same instant, but as the temperature increased, their control began to fall apart and the animals had more difficulties coordinating the two joints.

Initially, the team had suspected that the spiders may be hampered at lower temperatures by the increased viscosity of the haemolymph. Instead, the spiders' coordination was restricted at higher temperatures, because there may not be enough time for the haemolymph to flow through the leg and back to initiate the next stride at the spiders' blisteringly fast high temperature stride rate.

'Hydraulic extension may allow spiders to save space and mass in their limb, but it may come at the expense of control', says Ahn. And she adds that the inability of tarantulas to coordinate joint extension at high temperatures may partly explain why, instead of taking advantage of the heat of the day, her local tarantulas emerge at dusk when temperatures are cooler.

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Booster, N. A., Su, F. Y., Adolph, S. C. and Ahn, A.N. (2015). Effect of temperature on leg kinematics in sprinting tarantulas (*Aphonopelma hentzi*): high speed may limit hydraulic joint actuation. *J. Exp. Biol.* 218, 977-982.

Kathryn Knight

Hairy big-eyed bats are seed predators



Chiroderma villosum, hairy big-eyed bat, eating a fig. Photo credit: Marco Tschapka.

If you think feeding your picky toddler is tough, spare a thought for Insa Wagner. 'Chiroderma villosum [hairy big-eyed bats] insist on fresh figs', says Wagner from the University of Ulm, Germany, adding that windfalls and frozen fruits are unacceptable to the fussy eaters. Wagner initially became interested in the bats' diet when she noticed their fiddly eating habit – it took them nearly an hour to eat one fig. She also says, 'Most bats use fruit as chewing gum: they take a bite, chew it until all of the sugar is gone and then spit out the fibrous remains', adding that the animals often swallow intact seeds along with the juice or spit the seeds out untouched. However, in addition to processing the fruit pulp to extract the juice, the big-eved bats separated the seeds from the fruit flesh before pulverising them with their teeth and spitting the fragments away. Could the bats be chewing the goodness out of the seeds for nourishment? Wagner, her PhD supervisor Elisabeth Kalko, and Marco Tschapka, also from the University of Ulm, decided to find out.

But working with the bats and their favourite figs proved challenging. Figs fruit asynchronously, so there are always some trees bearing ripe fruit in a forest: the challenge was finding them. 'I had a list of about one-hundred fig trees [*Ficus obtusifolia*] along the coastline of the Barro Colorado Monument that I had to check at least once a week for nearly ripe fruit', recalls Wagner, who foraged constantly for ripe figs to satisfy her bats.

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And collecting the fig-mad bats was also tricky. Wagner explains that hairy bigeyed bats are relatively scarce compared with the more common *Artibeus watsoni* (Thomas's fruit-eating bat). However, after patiently staking out ripe fruit trees and collecting individual animals, Wagner was ready to start investigating how they masticated each mouthful and how efficiently they extracted the seeds' nutrients.

Analysing how 12 bats chewed their fig meals, Wagner realised that the big-eyed bats spent three times as long chewing the seeds as they did the fruit pulp. And when she compared the number of seeds in the pellets of discarded pulp produced by C. villosum with the number of seeds in the fruit pulp pellets of A. watsoni, the C. villosum fruit pellets were almost seed free. She also found that the A. watsoni poo contained four times as many intact seeds as that of C. villosum. So, instead of distributing the seeds in their faeces, the big-eyed bats appeared to be consuming them, but were the bats deriving any benefit from the seeds?

Teaming up with Irene Tomaschewski and Jörg Ganzhorn from the University of Hamburg, Germany, Wagner analysed the nutrient content of the seed remains and discovered that the big-eyed bats were extracting almost all of the goodness from them (over 85% of the lipids, protein and sugars). And when Wagner tested the bats' fig preferences, she found that the bats always preferred F. obtusifolia figs, which have a higher seed content than the figs of other species. What is more, the bats were only interested in the seeds from strangler figs, which are covered in a slimy gel that the seed uses to attach itself to the trunk of a host tree to grow on.

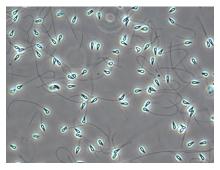
Chiroderma villosum acts more as a seed predator than a seed distributor', says Wagner, who also suspects that the gel coating on *F. obtusifolia* seeds helps the bats to separate the seeds from the fruit flesh, allowing them to extract more from their fig meals than other bats.

10.1242/jeb.122192

Wagner, I., Ganzhorn, J. U., Kalko, E. K. V. and Tschapka, M. (2015). Cheating on the mutualistic contract: nutritional gain through seed predation in the frugivorous bat *Chiroderma villosum* (Phyllostomidae). J. Exp. Biol. 218, 1016-1021.

Kathryn Knight

Optimistic future for sea urchins



Centrostephanus rodgersii sperm. Photo credit: Monique Binet.

When you cast your seed into the open, you'd better be sure that the conditions will be ideal to ensure the success of the next generation. And that approach seems to have served sea urchins perfectly well: that was until now. As global sea temperatures rise and the oceans begin to acidify, the tiny gametes that sea urchins entrust to the waves are under increasing risk. Monique Binet from CSISO. Australia, and an international team of collaborators say, 'Under near-future scenarios of ocean acidification, the swimming behaviour of marine invertebrate sperm is altered'. Sperm use a pH gradient (from low to high pH) to activate the energysupplying mitochondria that power the gametes when released into the ocean, so the team decided to test how future climate scenarios might affect the membrane potential of mitochondria that produce ATP, and how individual swimming performance is affected by acidification.

After collecting Centrostephanus *rodgersii* sea urchins from the rocky shoreline of Sydney's North Harbour and transporting them back to the lab at Macquarie, the team encouraged the sea urchins to release sperm ready to test the effects of environmental acidification. Next, they exposed the fresh sperm to seawater from one of three scenarios current ocean pH, -0.3 pH units below current ocean pH (the projected coastal water conditions in 2100) and -0.5 pH units below current ocean pH (the projected coastal water conditions in 2300) - before adding JC-1 stain to the sperm, which fluoresces green when the mitochondrial membrane potential is low, but produces orange/green fluorescence when the membrane

potential is high. Then, after allowing 15 min for the stain to penetrate the sperm, the team set the gametes a swimming test – they filmed the sperm in a drop of seawater under a microscope – to find out how well they performed and recorded the ratio of green to orange/green fluorescence in order to measure the membrane potential of the sperm mitochondria in all three environmental scenarios.

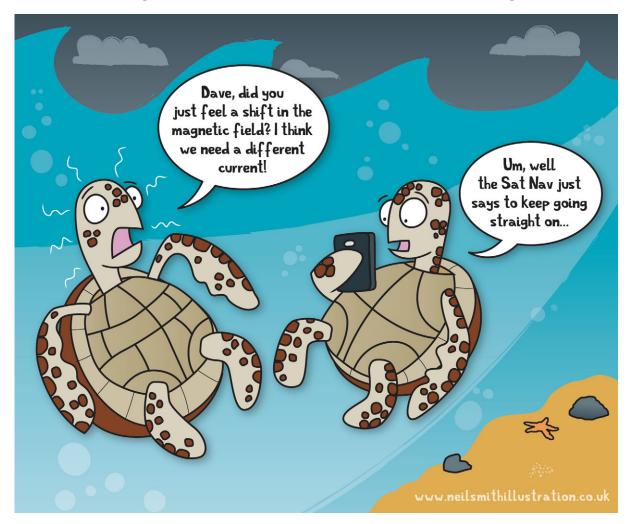
Not surprisingly, the sperm mitochondria became increasingly unhappy as the pH dropped, with the membrane potential falling up to 42% at -0.3 pH units, and plunging by as much as 55% in the 2300 pH scenario. However, the -0.3 pH unit reduction did not appear to impact the sperm swimming speed adversely sperm swam even faster than under present day conditions - but the performance of the -0.5 pH unit sperm suffered as their swim speed plummeted. Although the sperm were not equally affected by the adverse conditions; there were large variations in swimming speed in both of the future climate conditions.

So, even though the sperms' mitochondria were impaired, and Binet and her colleagues point out that the sperm are currently near their pH tolerance tipping point, the team is optimistic about the future of C. rodgersii sea urchins. Explaining that lower mitochondrial activity will allow the sperm to eke out their meagre energy reserves for longer and extend their longevity, the team says, 'Increased sperm longevity increases fertilisation success when sperm-egg encounter rates remain high over prolonged periods'. And they also suggest that the broad range of sperm responses may provide the sea urchins with an opportunity to side-step their apparently bleak future. The team says, 'Substantial interindividual variation in responses of sperm swimming to ocean acidification may increase the scope for selection of resilient phenotypes, which, if heritable, could provide a basis for adaptation to future ocean acidification'.

10.1242/jeb.122200

Schlegel, P., Binet, M. T., Havenhand, J. N., Doyle, C. J. and Williamson, J. E. (2015). Ocean acidification impacts on sperm mitochondrial membrane potential bring sperm swimming behaviour near its tipping point. J. Exp. Biol. 218, 1084-1090.

Kathryn Knight



Magnetic sense essential for correct turtle turning

It's one of the greatest ocean odysseys: when tiny loggerhead turtles strike out from their birth beaches on the coast of North America into the Atlantic, their migration will take them all the way to Europe and back before they return home. Nathan Putman and colleagues from the University of North Carolina, Chapel Hill, USA and the Centre de Recherche Halieutique Méditerranéenne et Tropicale, France, explain that the tiny voyagers use a range of senses to guide them on their way, including detecting and responding to the local magnetic field. However, untangling the relative contributions of different sensory mechanisms at individual locations along the way is tricky. So, Putman and his colleagues decided to take a hybrid approach: integrating lab-based experimental observations of hatchling loggerhead sea turtle responses to the magnetic fields at specific locations along their route with simulations that investigated

the consequences of ignoring the magnetic field at the locations where the hatchlings' responses to the magnetic field were strongest.

Testing which directions the tiny reptiles swam in when they experienced the magnetic fields that exist near Portugal, the Straits of Gibraltar, the Canary Islands, Suriname and Barbados, the team found that the hatchlings in the Portuguese magnetic field swam in a southerly direction, while those experiencing the magnetic field near Barbados swam northwards. And when they simulated the turtles' route as they moved passively in the strong ocean currents, going with the flow in regions where the turtles did not respond to the magnetic field did not pose problems: the currents simply carried them in their preferred direction. However, the youngsters appeared to encounter problems near Portugal and Barbados,

lingering longer than was safe in the cold northern waters near Portugal and failing to enter the Antilles Current – that would bear them home – in the waters off Barbados. Next, the team set the simulated turtles swimming strongly in the directions that they selected when exposed to the magnetic fields near Portugal and Barbados, and this time the youngsters stayed on track.

The team says, 'Our findings suggest that the magnetic navigation behaviour of sea turtles is intimately tied to their oceanic ecology and is shaped by a complex interplay between ocean circulation and geomagnetic dynamics'.

10.1242/jeb.122226

Putman, N. F., Verley, P., Endres, C. S. and Lohmann, K. J. (2015). Magnetic navigation behavior and the oceanic ecology of young loggerhead sea turtles. J. Exp. Biol. 218, 1044-1050.

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