INSIDE JEB

Falcons head off prey for interception

Falcon wearing a hood camera. Photo credit: Robert Musters.

Hurtling through the air, a falcon locks its sights onto a victim as they engage in mortal combat. Intrigued by how flocks of birds respond to aerial attack, Suzanne Amador Kane from Haverford College, USA, had realised that she couldn't interpret how flocks react to raptors until she understood the predator's hunting strategy. But when she investigated the literature, it was clear that little was known about how falcons pursue their prey. 'There were computational studies […] that simulated this behaviour', recalls Amador Kane, but no one had published any behavioural studies. Amador Kane was stumped until she and her team saw a BBC documentary and realised that she could mount minute cameras on birds of prey to get a falcon's eye view to understand their lethal strategy (p. 225).

Resorting to personal contacts and social networking, Amador Kane linked up with falconers around the globe who were happy to attach miniaturised spy cameras to backpacks and tiny helmets worn by their falcons to film encounters during flights. Then, when the movies rolled in, Amador Kane and her undergraduate student Marjon Zamani painstakingly located the prey's position on each frame by hand before reconstructing each pursuit from the falcon's perspective. Eventually, the duo simulated three possible strategies that the falcon could use to find out which agreed best with their observations.

In the first strategy, the falcon would simply fly directly after the prey, but this is almost always inefficient, wasting the predator's time and valuable energy when the victim takes evasive action. Calculating that the prey would always be found at the centre of each frame in the movie if the birds used this approach, it was clear that the falcons rarely followed the victim's path, ruling out the strategy.

Amador Kane and Zamani then tested the second strategy, which had been proposed by Vance Tucker over a decade earlier. 'Falcons have two regions of very acute vision: one directed almost in the forward direction and the other dramatically off to the side, 30–45 deg off', explains Amador Kane. Tucker had suggested that raptors would fly so that their prey was always at an angle of 40 deg to them, allowing the predator to keep the victim in the off-centre specialised visual region. However, if that were so, the falcon would fly in a spiral path towards the prey. The duo looked for evidence that the falcon viewed the prey at angles greater than 30 deg, but found that the birds did so only very rarely.

So the scientists tested the final strategy, where the falcon fixed the prey in its sights and manoeuvred to keep the prey's image motionless against the background in order to head-off the prey in the least amount of time. Amador Kane explains that there are two advantages to this strategy: first, the predators can view the prey head on with the central visual field, rather than off to one side; and second, the victim does not see the predator move until the final instant when the predator strikes. Analysing the video footage and simulations, Amador Kane and Zamani realised that this is exactly what falcons do.

So, falcons aim to head off their prey during pursuit, and it turns out that bats and even humans do this too. 'Think about chasing a toddler around in the playground: they keep zigging and zagging away from you… so you just have to head them off', says Amador Kane, laughing.

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Kane, S. A. and Zamani, M. (2014). Falcons pursue prey using visual motion cues: new perspectives from animal-borne cameras. *J. Exp. Biol.* **217**, 225-234.

Kathryn Knight

Fish lays Gray's paradox to rest

Puka, one of the two dolphins that participated in the study. Photo credit: Frank Fish.

When Mr E. F. Thompson stood on a ship cruising through the Indian Ocean in the 1930s and observed a dolphin speed past the vessel in 7 seconds, he had no idea that this single observation would lead Sir James Gray to formulate the enduring paradox that bears Gray's name to this day. Based on Thompson's anecdote, Gray estimated the power required to propel the boisterous mammal through the waves at 20 knots ($10.3\,\mathrm{m\,s^{-1}}$) and concluded that the animal did not have enough muscle to pull off the feat. Puzzled by the paradox, Gray suggested that dolphins must use a trick of fluid mechanics to sustain the remarkable performance.

And there the paradox stood until Frank Fish from West Chester University, USA, got his teeth into the problem 60 years later. 'I said, "Let's see how much power a dolphin can produce," so I used some hydrodynamics models that looked at the motion of the flukes and came up with the realisation that dolphins could produce very high amounts of power',

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recalls Fish. But these were only theoretical calculations. To really sound the paradox's death knell he would have to measure directly the force exerted by the animal on water and, although there is a method – known as digital particle image velocimetry (DPIV) – to visualise eddies in the water in order to measure the forces exerted by fish, it wasn't clear how the same approach could be used on dolphins: 'No one is going to let you put a 55 gallon drum of glass beads in with a dolphin and no one is going to let you shine a laser beam at a dolphin', says Fish.

That was until Fish met Timothy Wei, from the University of Nebraska, USA, at a conference. Wei had encountered the same technical problems when working with Olympic swimmers, but he had got round it by asking the Olympians to swim through a curtain of microscopic bubbles. Could the same approach work for dolphins? Fish contacted his long-time friend Terrie Williams and asked if he could test the method on her dolphins, Primo and Puka (p. 252).

Arriving at the University of California at Santa Cruz with a SCUBA tank of compressed air and a garden soaker hose to produce the curtain of bubbles, Fish teamed up with Wei, graduate student Paul Legac and Williams to put the dolphins through their paces. Filming the animals as they swam along the length of the bubble curtain, the team could clearly see the vortices set spinning by the dolphins' flukes demarcating the powerful jet of water propelled backwards as the animals surged forward. 'We were in this concrete underwater viewing area… it was cold and damp, but you would get really excited and forget about that as you saw the animal go past and you'd see the vortices come out so nicely', recalls Fish.

And when Legac and Wei calculated the amount of power produced by the animals as they cruised at a leisurely 3.4 $\mathrm{m\,s^{-1}}$, the animals were producing an impressive 549 W – approximately 1.4 times the power that a fit amateur cyclist can sustain flat out for an hour – rocketing to an eye-watering 5400 W when accelerating rapidly. There was no paradox; the dolphins did have enough muscle to power their impressive swimming performance because they are simply stronger than humans. And, having proved that the method works for dolphins, Fish is keen to test it out on even larger animals. 'If I can do it for a dolphin, can I do it for a whale? Can I do it for a manta ray?' he grins.

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Fish, F. E., Legac, P., Williams, T. M. and Wei, T. (2014). Measurement of hydrodynamic force generation by swimming dolphins using bubble DPIV. *J. Exp. Biol.* **217**, 252-260.

Kathryn Knight

Spiders pull in legs to attach

A female *Cupiennius salei* spider. Photo credit: Jonas Wolff.

Spider Man, insects and geckos all share the same effortless superpower: no matter how smooth a surface, they can hang on to it upside down. We have long been mesmerised by this remarkable ability and more recently engineers have been keen to replicate these animals' exotic attachment surfaces to produce artificial reusable adhesives that leave behind no residue. But there is one snag: 'A dead gecko doesn't stick anymore, so we think it [adhesion] is an active process, not a passive one like a suction cup', explains Jonas Wolff from the University of Kiel, Germany. According to Wolff, geckos and insects activate their adhesive surfaces by pulling their legs inwards to align the microscopic structures that attach them to smooth surfaces. Which made Ellen Wohlfart, Eduard Arzt and Stanislav Gorb wonder whether spiders use the same active process to secure themselves to walls. Intrigued by the possibility, the team tested how well the American wandering spider (*Cupiennius salei*) clings on to smooth surfaces after their adhesive pads have been inactivated (p. 222).

But spider wrangling is not without its risks. 'Normally they are peaceful, but if you try to grab them because they have escaped, they can bite you. The poison is not dangerous for humans, but it is not very nice', recalls Wolff. So, Wohlfart overcame the danger by briefly anaesthetising the bulky arachnids with a puff of carbon dioxide before attaching a human hair tether to it. Having allowed the spider to recover, Wohlfart gently lowered it onto a glass plate and then attached the tether to a force sensor, which was attached to a motor that gently pulled the spider in an attempt to tug it free in order to measure the adhesion force. Having measured the full attachment force, Wohlfart gently applied a dab of wax to the spider's front pair of feet to see how the loss of two sticky pads affected the animal's adhesion force. She then systematically disabled the second and third pairs of feet, eventually leaving the spider with only its hind feet to cling on with.

Repeating the experiments with another spider, only this time disabling the rear feet first, Wohlfart discovered that the spiders cling on with an impressive 97 mN of force when all eight legs were in action: three times more than the average weight of this species. But when Wohlfart measured the attachment force of the spider after its two rear-most legs had been disabled, the attachment force was reduced significantly to just 26.2 mN (27% of the original force), which is 42.7 mN less than expected if the spider was clinging on passively like a piece of sticky tape. And when both rear pairs of legs were out of action, the spider was left with just 9% of its original sticking power, certainly not enough to support its body weight.

The spiders were actively attaching themselves to smooth surfaces by pulling against the diagonally opposite leg to produce the shear force that aligns the sticky foot hairs that allow spiders to hang on. Wolff explains that by inactivating the hind-most pair, the spiders had effectively lost the attachment power of two pairs of legs. He also adds that the front two pairs of legs contribute less to adhesion than the rear, because spiders use their fore legs to manipulate prey, relying more on their hind legs for secure attachment.

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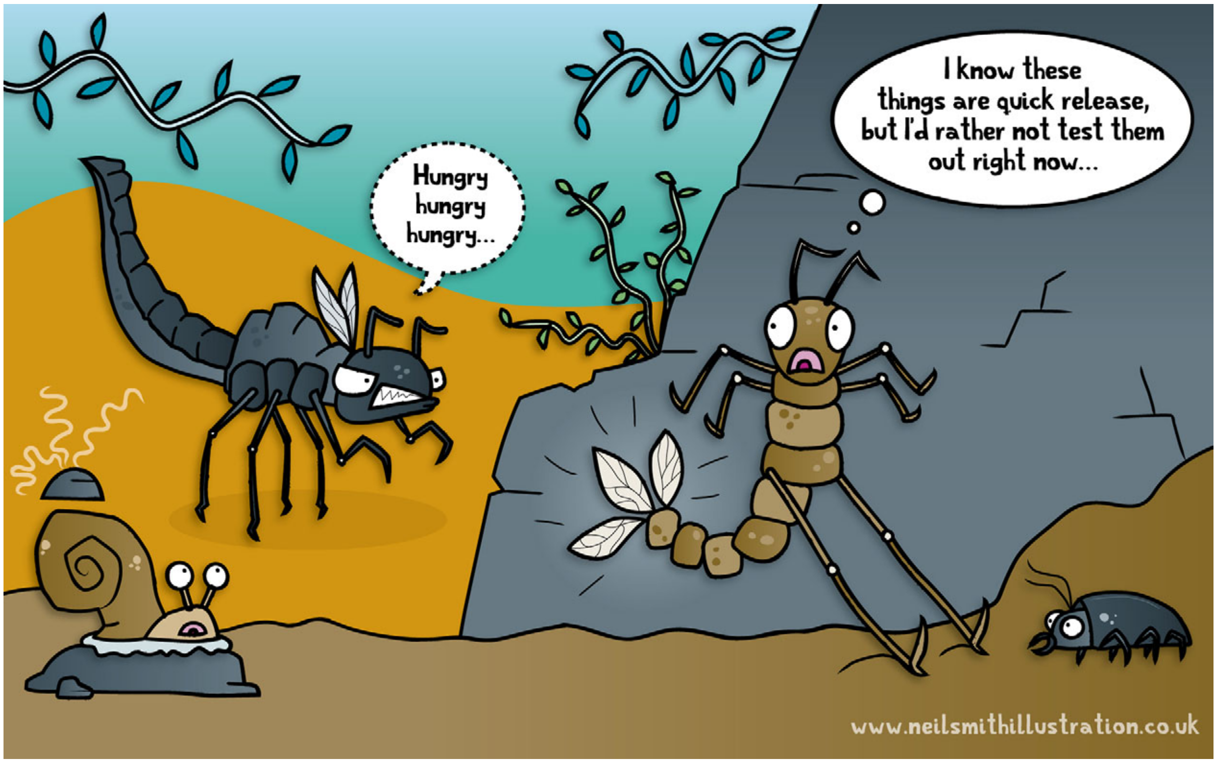
Wohlfart, E., Wolff, J. O., Arzt, E. and Gorb, S. N. (2014). The whole is more than the sum of all its parts: collective effect of spider attachment organs. *J. Exp. Biol.* **217**, 222-224.

Kathryn Knight

Damselfly larvae select quick release lamellae for survival



Adult damselflies are a spectacular vision of summer, streaking through the air above pond surfaces. Yet survival through their earlier aquatic life stages is extremely precarious. Equipped with leaf-like lamellae hinged at the end of the abdomen for propulsion, the structures provide the perfect appendages for passing predators to grab onto. But the larval insects have a self-preservation mechanism that helps them to escape hungry predators: they self amputate – autotomize – trapped lamellae. Jennifer Gleason, Douglas Fudge and Beren Robinson from the University of Guelph, Canada, explain that the ability of a larva to shed its lamellae with ease improves its chances of survival, which might lead larvae that inhabit heavily predated waters to develop relatively fragile lamellar joints to increase their chances of survival (p. 185). To test the theory, the Canadians measured the force required to break damselfly larvae lamellar joints, as well as the size and cuticle thickness of the joint. They discovered that the joints of damselfly larvae from fishless ponds – where carnivorous dragonfly larvae flourish – were much more fragile than the joints of larvae from ponds where there were few dragonfly larvae. 'This suggests that autotomy may evolve in larval damselflies under selection from small grasping predators like larval dragonflies by favouring smaller joint size or reduced cuticle area of lamellae joints', says the team.

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Gleason, J. E., Fudge, D. S. and Robinson, B. W. (2014). Eco-mechanics of lamellar autotomy in larval damselflies. *J. Exp. Biol.* **217**, 185-191.

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