

INSIDE JEB

Crushing snakes kill by blood constriction, not suffocation



A boa constrictor. Photo credit: Scott Boback.

Death by suffocation seems like an awfully protracted way to go and death by suffocation in the grip of a boa constrictor's coils is the stuff of nightmares. Yet Scott Boback from Dickinson College, USA, wasn't so sure that suffocation was all there was to the boa constrictor's technique. 'It looks like the [prey] animals are gasping for air', says Boback, but in 1994, Boback's colleague, Dave Hardy, had proposed an alternative. 'What Hardy saw was the speed at which the animals were dying... they were dying way too quickly for it to be suffocation. He suspected that it was circulatory or cardiac arrest because of the speed at which death was occurring', says Boback. But there were few data to support Hardy's suggestion and, although hard-core members of the herpetology community were aware of the possibility, the rest of us were left clinging to the old-wives' tale that boa constrictors kill by suffocation: until Boback put the crushers to the test.

'We have been studying constriction for a number of years,' says Boback, explaining that he had measured the pressure exerted by snakes crushing dead rats in earlier experiments. However, to find out what was really going on inside the snake's victims, he had to measure blood pressure in living anaesthetised rodents as they were squeezed. 'It was not something that we took lightly and we wanted to make sure that the animals [rats] did not experience pain or suffer', says Boback. Having anaesthetised a rat, Boback and his colleagues, Emmet Blankenship and Charles Zwemer –

backed up by undergraduate researchers, Katie McCann, Kevin Wood and Patrick McNeal – inserted ECG electrodes and blood pressure catheters into the rodent's body before offering the sedated animal to a hungry boa constrictor.

Fortunately for Boback, the snake struck, aiming a bite at the rat's head and coiling its body around the rodent as it began to squeeze. And, as the team watched the blood pressure and heart rate data stream onto the computer, they were amazed to see the rat's blood circulation shut down in a matter of seconds. 'I remember being in the room and the students were looking at the data in disbelief that it happened that fast. We could see the arterial pressure go down, the venous pressure go up and we could see this right when the snake was doing it [squeezing]', says Boback. And, as soon as the rat's circulation stopped and the oxygen supply was cut off, the team could also see the rat's heart beating more and more irregularly. Boback suspects that without blood flow to the brain, any animal caught in the snake's coils probably passes out in a matter of seconds, before other critical organs begin to fail.

Boback also suggests that the boas provide a glimpse into the evolution of crushing behaviour in snakes. He explains that ancient snake species that had not evolved constriction were probably restricted to capturing small meals that they could subdue easily. However, once the earliest boas had developed their quicker constriction technique for despatching victims, they were free to scale up the size of meals, sometimes tackling animals that are even larger than themselves. 'By understanding the mechanisms of how constriction kills, we gain a greater appreciation for the efficiency of this behaviour and the benefit it provided early snakes', says Boback.

10.1242/jeb.127779

Boback, S. M., McCann, K. J., Wood, K. A., McNeal, P. M., Blankenship, E. L. and Zwemer, C. F. (2014). Snake constriction rapidly induces circulatory arrest in rats. *J. Exp. Biol.* **218**, 2279-2288.

Kathryn Knight

One-way airflow fuels blowfly flight



Tethered blowfly ready for monitoring during flight. Photo credit: Lutz T. Wasserthal.

Sprinting at top speed with your lungs burning, it can be hard to imagine working any harder, but – in comparison – the exertions of flying insects are truly heroic. Lutz Wasserthal from the University of Erlangen-Nuremberg, Germany, explains that blowflies can increase their metabolism by 100-fold during flight and routinely maintain this mindboggling exertion for up to half an hour. 'It is of great interest to know how these insects manage the oxygen supply for these high metabolic demands', says Wasserthal. Diffusion of air through the tracheal system that delivers oxygen to every cell in the body was thought to be sufficient to meet the metabolic demands of small flies, but Wasserthal wasn't sure if it was adequate to supply the souped-up flight muscles of beefier blowflies. Some large insects are known to use the muscular contractions that drive their wings to help pump air through their bodies, but it wasn't clear if the minute body deformations associated with flight in blowflies were sufficient to pump air through their bodies. Puzzled, Wasserthal decided to investigate how air flows through blowfly bodies as they fly.

Gently gluing flies by their backs to a tether so that he could analyse every detail of their flight, Wasserthal attached minute polyethylene tubes to the spiracles (breathing holes) on the fly's surface to measure the spiracle air pressure as they flew. Fortunately, the flies were unfazed

by the restrictions of the tether and readily took to the wing. As Wasserthal recorded each wing beat, he could see the pressure at the spiracles at the front end of the insect's thorax decline in time with the wing's downbeat, pulling air into the fly's body. Then, as the fly raised its wings, the pressure at the spiracles in the fly's posterior thorax increased, drawing air through the body and expelling it out of the back end. Next, Wasserthal measured where CO₂ was emitted and found that it was clearly emerging from the spiracles at the rear. The airflow through the insect's body was in one direction, pulling air from the front through the oxygen-hungry flight muscles and expelling it out of the rear. And when Wasserthal measured the oxygen concentrations inside the insect's body, he was amazed to see that the oxygen was undiluted by mixing with exhausted air and close to external atmospheric levels. 'The unidirectional airflow guarantees fresh air and an inexhaustible oxygen content in the main trunks and air sacs for sustained flight: the flies never run short of oxygen', says Wasserthal.

Knowing that reversals of the heartbeat also contribute to drawing air through the resting fly's body – by redistributing haemolymph (blood), which then adjusts the volume of air sacs to suck air through the body – Wasserthal also measured the flying insect's heartbeat and was pleased to see that these heartbeat reversals happened more frequently when the insect was flying than when it was at rest. '[Heartbeat reversals] support forced removal of dissolved CO₂ by the haemolymph', says Wasserthal.

Having shown that the minute deformations of the thorax produced by flight are sufficient to pump air through the blowfly's body, Wasserthal comments, 'The gas exchange is an interdependent performance of the flight apparatus and is thus very economic'.

10.1242/jeb.127761

Wasserthal, L. T. (2015). Flight-motor-driven respiratory airflow increases tracheal oxygen to nearly atmospheric level in blowflies (*Calliphora vicina*). *J. Exp. Biol.* **218**, 2201-2210.

Kathryn Knight

Bumblebees taste protein quality difference



Bumblebee collecting sweet exudate from sedge. Photo credit: Sara Leonhardt.

It's a sickening statistic: 50% of the UK's bee species have been lost since the 1950s and the number of honeybee hives in the US has plummeted from 6 million to 2.5 million. No matter where you are, bees and the agriculture that they support are at risk, so maintaining their health is of paramount importance. Sara Leonhardt from the University of Würzburg, Germany, explains that diet can significantly affect the insects' health – high protein diets can shorten the life expectancy of adult honeybees while benefiting larvae – so bees would clearly benefit from being able to assess the quality and nutrient content of their food. However, Leonhardt says, 'It remains unclear whether bees are actually able to perceive and assess the quality of pollen'. And even if they could, which senses might they use? Explaining that bumblebee foragers have to be able to assess the quality of the pollen and nectar that they deliver to the nest, because their nest mates do not provide feedback on the quality of the provisions, Leonhardt and Johannes Spaethe decided to ask bumblebees more about their ability to distinguish between the proteins in their diet.

Snugly sitting the bees in a tube with their heads protruding from the end, Fabian Ruedenauer was able to take advantage of the bees' tendency to stick out their tongues when they detect sugar to learn more about their preferences. Knowing that bumblebees can be trained to transfer their tongue extension behaviour to show when they recognise odours and flavours, Ruedenauer embarked on a painstaking set of experiments to test the insects' ability to

recognise proteins from different sources. Training the bees to recognise apple and almond pollen and the protein casein from milk, the team were pleased to see that the bees were capable of learning to recognise all three forms of protein. Then, Ruedenauer tested whether the bees could distinguish between the two pollens – which have different odours – by gently blowing a puff of pollen-flavoured air over the bee's head. Sure enough, the bumblebees could clearly distinguish between the two, sticking their tongues out whenever they encountered the pollen flavour that they had been trained to recall.

But could the bees distinguish between pollen mixtures of different concentrations and if so, which senses would the insects use? Mixing pollen and cellulose in different proportions and blowing the mixture's odour over the faces of restrained bees, Ruedenauer could see that the bees were indifferent to the strength of the mixture, responding equally happily to both the strong and weak mixtures. However, when Ruedenauer offered the bees the opportunity of tasting the mixture by dipping their antennae into the pollen/cellulose and casein/cellulose mixtures, the insects distinguished between the dilute and concentrated mixtures with ease. 'Bumblebees are able to learn the odour of pollen and casein using olfactory cues, but can only differentiate between concentrations of these substances when they can touch the food,' says Leonhardt.

Having shown that the insects are capable of differentiating food with different protein contents, Leonhardt and her colleagues are now testing whether bumblebees are able to translate this into foraging practice by selecting better quality food when offered a choice. They also want to discover whether the foragers' customers – the larvae that they supply – have an impact on the bees' sensitivity to the quality of their foraged food.

10.1242/jeb.127753

Ruedenauer, F. A., Spaethe, J. and Leonhardt, S. D. (2015). How to know which food is good for you: bumblebees use taste to discriminate between different concentrations of food differing in nutrient content. *J. Exp. Biol.* **218**, 2233-2240.

Kathryn Knight

Green anoles: Jacks of all escape trades



Evading a hungry predator is essential if your genes are to contribute to the game of life and speed is usually of the essence. However, it's not always that simple. Animals often drop their speed in favour of agility as they try to outmanoeuvre pursuers. And what happens if you take the pursuit into the trees, where prey have to negotiate branches of different girth? Wondering how green anole lizards adapt their flight in different contexts, Erik Sathe and Jerry Husak from the University of St Thomas, USA, began investigating how animals of different builds sprinted along branches of different widths, along the flat and through a maze of peg obstacles to find out which physical attributes prepared the lizards best for escape.

Sure enough, the sprinting animals were fastest on a flat surface and the

broadest pole (5 cm), reaching speeds of over 1.4 m s^{-1} , but they dropped to 0.8 m s^{-1} on the 2.5 cm pole and were reduced to a crawl (0.4 m s^{-1}) through the maze of pegs. Next, they investigated which physical characteristics gave the lizards an edge in each of the different settings and found that lizards with short toes and large forelimbs performed the fastest on the flat. Meanwhile, small forelimbs gave the lizards a speed advantage on the 5 cm pole. However, lizards weaving through the peg obstacle course performed faster when the muscle that pulls the forelimb back was large; and long toes and small limbs produced nimble animals that negotiated the peg obstacles best.

Overall, Sathe and Husak found that animals that performed well in one

context tended to perform poorly in others, suggesting that an animal's optimal performance is not fixed and may vary depending on the environment. They also suggest, 'Natural selection may act on an individual's ability to cope with substrate variation', adding that instead of optimising their performance in one setting, animals that live in complex environments may settle on the least worse compromise, making green anoles Jacks of all trades and masters of none in their complex tree homes.

10.1242/jeb.127746

Sathe E. A. and Husak, J. F. (2015). Sprint sensitivity and locomotor trade-offs in green anole (*Anolis carolinensis*) lizards. *J. Exp. Biol.* **218**, 2174-2179.

Kathryn Knight
kathryn@biologists.com