INSIDE JEB

Twisted-wing parasites equipped for colour vision

Close-up of the eyes of a male *Xenos peckii*. Photo credit: Elke Buschbeck and Necati Kaval.

When *Xenos peckii* twisted-wing parasite males emerge as adults from within the body of the hapless wasp that served as their incubator, the race is on. With an adult lifetime spanning just a few hours, the male insects have to locate a female and mate before their time is up. And the challenge of locating a female mate – which is barely more than a fleshy bag of eggs with no eyes or limbs – is particularly problematic. Concealed within the body of her own host, only the female's head and mating channel protrude from the surface.

Despite their short lives and single-minded mission, the males are equipped with extraordinarily sophisticated hybrid eyes – composed of up to 50 micro-eyes, each equipped with a lens that projects a minute image onto a mini-retina of ∼100 photoreceptors. However, it was unclear whether these extraordinary creatures have colour vision. According to Elke Buschbeck, from the University of Cincinnati, USA, some evidence suggested that the nocturnal males may lack colour vision, but with the jury still out, Buschbeck and her colleagues Marisano James, Sri Nandamuri and Aaron Stahl embarked on a study to discover whether the insects' extraordinary eyes include the basic equipment for colour vision.

Having stumbled across a fertilized *X. peckii* female during the summer and nurtured the offspring in northern paper wasps until the adult males emerged, Buschbeck and her team had only 3 h to investigate the males' eyes before they perished. Cooling the insects to extend their life expectancy, Nandamuri and James then measured the electrical signals produced by the eyes in response to flashes of light ranging from ultraviolet to red wavelengths. Meanwhile, Aaron Stahl analysed the insect's gene expression pattern to identify which light-sensitive opsin proteins – which are essential for colour vision – are produced by the insects.

Impressively, the males' responses were strongest to green light (around 539 nm), while they responded more weakly to UV light (around 346 nm). And when the team analysed the results of Stahl's gene expression investigation, they identified one expressed gene that could produce a green-sensitive opsin, in addition to another that could produce a UV-sensitive opsin.

Although the team emphasises that these observations are not categorical proof that twisted-wing parasite (strepsipteran) males have colour vision, they say, 'the presence of distinct UV and green opsins presents the possibility that UV-green coloration could play a significant role in strepsipteran ecology, such as helping the male to find the female'. And they wonder whether our own limited colour vision means that we are missing one of the parasite's key tricks: could the females be advertising their presence in their cryptic hideaways by reflecting UV light – like bright homing beacons – to attract the males during their final desperate search? 'If so, this could help explain another aspect of the complex life cycle of these extraordinary insects', says Buschbeck.

10.1242/jeb.153841

James, M., Nandamuri, S. P., Stahl, A. and Buschbeck, E. K. (2016). The unusual eyes of *Xenos peckii* (Strepsiptera: Xenidae) have green- and UV-sensitive photoreceptors. *J. Exp. Biol.* **219**, 3866-3874.

Kathryn Knight

Making *Morpho* butterflies blue

Morpho rhetenor. Photo credit: Marco Giraldo.

For centuries, Renaissance artists pursued the most opulent pigments for their wealthy patrons, and lapis-lazuli-based ultramarine blue was the rarest and most prized of all. Although the lack of natural blue pigments has not hampered some species from decking themselves out in opulent azure tones, the exotic blue shades sported by animals ranging from kingfishers to *Morpho* butterflies share more in common with the iridescent colours of an oily film than the masterpieces of Vermeer.

Marco Giraldo, from the University of Antioquia, Colombia, explains that the colours visible in thin liquid films are produced when the thickness of the fluid layer is similar to the wavelength of the colour of light that is reflected. And this is exactly how the vivid blue colour of *Morpho* butterfly wings is produced: microscopically thin layers of chitin on the surface of the wing scales only reflect colours where the wavelength is similar to the separation of the chitin plates. Intrigued by the differences in shade across members of the *Morpho* genus, Giraldo and his colleagues, Shinya Yoshioka (Tokyo University of Science, Japan) and Doekele Stavenga (University of Groningen, the Netherlands), investigated how other components of the wing structure contribute to the butterflies' startling colours.

Assembling in Stavenga's laboratory and selecting 16 species from the 30 possible members of the *Morpho* genus, Giraldo and Chunzi Liu first photographed the

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Journal of Experimental Biology (2016) 219, 3823-3824

arrangement of scales on the wings of each species. In addition, they used scanning electron microscopy to learn more about the microscopic structure of the transparent 'cover' scales and the more deeply buried brown-pigmented 'ground' scales. Next, the team painstakingly measuring the light spectra scattered from the individual scales and tiny portions of the wings before precisely recording the spectrum of light reflected from intact wings.

'[We had] to deal with thousands of observations and try to see the big picture' says Giraldo, recalling the challenge of collating data including the size, shape, distributions and structures of the upper and lower scales. However, the team's big breakthrough came when they organised their observations according to the number of reflecting layer structures inside the scales and the amount that that the cover scales overlapped the ground scales beneath. 'We realised that it agreed with the phylogeny of the genus', says Giraldo. As the younger members of the genus became increasingly evolved, the cover scales became smaller until they were barely visible. So the transparent cover scales of the most ancient member of the *Morpho* genus, *M. marcus*, completely cover the pigmented ground scales beneath, while the cover scales of the youngest member of the genus, *M. aega*, were so tiny that they scarcely overlap the ground scales at all.

Next the team investigated the optical mechanisms underpinning the colour of each species' wing colour and realised that thin reflecting structures in the upper surface of the ground scales of the ancient *M. marcus* butterflies worked in conjunction with the reflecting structures in the transparent cover scales to produced the vivid hue. However, the striking sky-blue tone of the *M. aega* wings is produced exclusively by deep stacks of reflecting structures in the ground scales, coupled with ridge structures on the surface of the scale that behave like colour-selecting diffraction gratings.

'We conclude that *Morpho* coloration is a subtle combination of overlapping pigmented and/or unpigmented scales, multilayer systems, optical thin films and sometimes undulated scale surfaces', says Giraldo and colleagues, who are keen to develop novel *Morpho*-inspired colour technologies that never fade to brighten our lives.

10.1242/jeb.153825

Giraldo, M. A., Liu, Y. C. and Stavenga, D. G. (2016). Coloration mechanisms and phylogeny of *Morpho* butterflies. *J. Exp. Biol.* **219**, 3936-3944.

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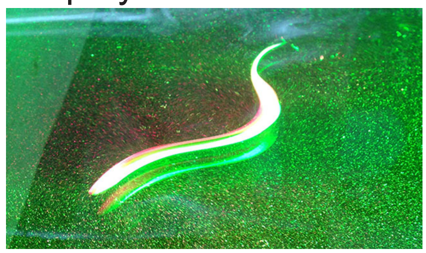
Bending sucks for lampreys



A lamprey swimming in a plane of laser light. Photo credit: Sean Colin.

Wriggling is a dependable swimming mode for a select band of aquatic species. From fish larvae and tadpoles to the gyrating motions of eels and lampreys, these sinuous swimmers appear to scythe through water effortlessly. 'We are interested in why [swimming] animals bend, as opposed to being rigid like engineered vehicles,' says Sean Colin, from Roger Williams University, USA. Yet, little was understood about how the writhing motions propel these animals forward until Colin and colleagues Jack Costello, Brad Gemmell and John Dabiri discovered that wiggling lampreys generate spinning regions of low-pressure water adjacent to their bodies that literally suck them forward. 'However, we still didn't know what hydrodynamic features led to these negative pressure zones and how they were generated', says Colin. It was only when chatting with Jennifer Morgan during a summer spent at the Marine Biological Laboratory (MBL), Woods Hole, USA, that he realised that sea lampreys may hold the key to answering these questions: the distasteful creatures are able to repair damage to their spinal cords. This could provide a way of temporarily disabling the rear end of lampreys to impair – but not prevent – swimming, so Colin decided to compare how healthy and temporarily semi-disabled lampreys move to find out how their flexible style generates suction thrust.

Working with Stephanie Fogerson, Morgan operated on several lampreys to sever the spinal cord halfway along the body to temporarily disable the rear portion of the body. However, Colin admits that working with the able-bodied and impaired lampreys could be enormously frustrating. Despite Gemmell's lamprey-wrangling talents, the fish rarely swam in a straight line through the sheet of laser light that was necessary to reveal the spinning vortex wakes produced by the fish. 'We recorded any sequences where the lampreys were swimming through the laser correctly', recalls Colin. Then, having discarded clips where the animals were accelerating instead of swimming steadily, Colin compared the swimming motion of the intact and partially disabled fish.

Tracing the body positions of both sets of lampreys, Colin could see that the writhing swimming movement travelled like a wave along the full length of the intact fish's body and became stronger, increasing in amplitude, as it moved toward the tail. However, the travelling wave failed to propagate beyond the point where the spinal cord had been severed in the partially disabled fish, so the tail simply waved passively from side to side.

Colin then calculated how fluid flowed around the fish's bodies and realised that the bending movement of the intact fish produces small spinning suction vortices that originate near the head and are then accelerated by the fish's weaving motion as they roll along the body toward the tail. In addition, the rippling movement ensured that the vortices were evenly spaced to generate maximum thrust. However, when he investigated the motion of the fluid flowing around the bodies of the partially disabled fish, the strength of the vortices failed to increase after passing the position where the spinal cord had been severed; 'the hydrodynamic features kind of fizzled out', says Colin.

Having identified the source of the novel propulsion mechanism, the team is keen to discover how commonly other species us suction thrust, which Colin says '[could] be useful for engineers in the development of novel and perhaps more efficient vehicles that can use flexible propulsors and rely on suction thrust'.

10.1242/jeb.153833

Gemmell, B. J., Fogerson, S. M., Costello, J. H., Morgan, J. R., Dabiri, J. O. and Colin, S. P. (2016). How the bending kinematics of swimming lampreys build negative pressure fields for suction thrust. *J. Exp. Biol.* **219**, 3884-3895.

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