OUTSIDE JEB

# A round of applause for butterfly wings


Gently fluttering above a field of flowers on short, broad wings, butterflies are unlike any other animal aviator. With such large wings relative to their body size, these unusual fliers flap slowly, but inefficiently. So what can explain this unique body plan? Many different aerodynamic mechanisms have been previously suggested to play an important role in butterfly flight, but little data existed to assess their importance. Christoffer Johansson and Per Henningsson of Lund University, Sweden, set out to understand how these insects generate the forces of flight and shed light on the function of their iconic wings.

Johansson and Henningsson focused on the role of the wing upstroke in butterfly flight. Specifically, they looked for an important function at the end of the upstroke when the wings clap together, a phenomenon found in other flying insects that helps generate the lift that keeps them aloft. The team first filmed the butterflies at high speed, taking off in a wind tunnel, and used an aerosol mist to reveal the air movements generated by their wings. They found a clear difference between the downstroke of the wings, which created lift to support the body against gravity, and the upstroke, which created thrust to move the insects forward. These measurements also revealed that the wing clap, which generates lift in other insects, contributes primarily to thrust in butterflies; at the end of the upstroke, the surfaces of the wings meet above the insect, forcing a trapped volume of air out into a jet that propels the butterflies forward.

When analysing recordings of butterfly flapping, Johansson and Henningsson also observed that the wings formed a cup shape as they came together. The researchers hypothesized that the cup shape was important for improving the function and performance of the wing clap. Specifically, cupped wings could trap more air, while also forming a better seal at the edges, which together could result in a stronger, more efficient and more directed jet of air. To test this prediction, they constructed a mechanical clapper that mimicked butterfly flapping with either flexible or rigid wings. They found that the flexible wings, which were able to form a cupped shape, produced stronger and more efficient jets than the rigid wings, which slapped together.

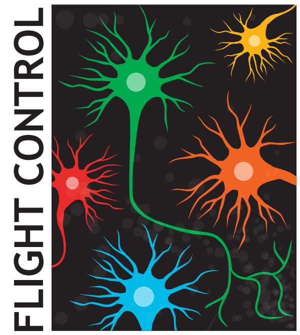
Using relatively large wings to flap slowly is not an efficient way of generating lift and creates a great deal of aerodynamic drag. Therefore, the ability of large flexible wings to generate thrust through such an effective clap may be key to balancing the apparent inefficiencies of butterfly flight. The strong jets generated by the wing clap may also contribute to the erratic nature of butterfly flight, which is useful to escape predators. This could explain the persistence of the butterflies' unusual body plan and flight style. Johansson and Henningsson have also identified the cupped wing clap as an alternative means of jet propulsion that may be exploited by other flying, or swimming, animals and robots. Clearly, butterflies and their exceptional wings are worthy of acclaim not just as graceful beauties but also as mechanical marvels.

doi:10.1242/jeb.235309

**Johansson, L. C. and Henningsson, P.** (2021). Butterflies fly using efficient propulsive clap mechanism owing to flexible wings. *J. R. Soc. Interface*. **18**, 20200854. doi:10.1098/rsif.2020.0854

**Jeffrey Olberding (000-0001-5426-9986)**
**University of California, Irvine**
**olberdij@uci.edu**

# Seeing the height at the end of the (wind) tunnel




Without street signs or GPS, animals develop specific and effective strategies for getting where they need to go. To efficiently navigate, honeybees fly lower when facing into the wind and higher when flying with the wind. To understand how some bees determine flight routes despite varying wind conditions, Emily Baird and colleagues at the Australian National University measured whether honeybees' sight governs their flight paths. They found that bees control their speed and distance from the ground by using different elements of their vision, and that the insects stay on track by making small swerves to the left and right in a wavy pattern.

To measure the insects' flight routes, the team tracked their height and speed relative to the ground by analyzing videos of bees flying through a small wind tunnel, which enabled them to control the speed of the airstream the bees encountered (still air, slow 1 m $s^{-1}$ or fast 2 m $s^{-1}$), as well as the direction, so that the bees were flying into the wind or with it. To maximize the visual information available to the bees, the walls of the wind tunnel were lined with a pattern of intersecting perpendicular and parallel stripes made out of red tape on white paper. As the bees flew past the stripes, they swerved left and right, creating a wavy route that allowed the team to better see how they moved in relation to the stripes. Regardless of wind direction, they flew at similar speeds of

Outside JEB reports on the most exciting developments in experimental biology. The articles are written by a team of active research scientists highlighting the papers that JEB readers can't afford to miss.

Journal of Experimental Biology

0.5 m s$^{-1}$ but flew lower against the wind and higher when flying with the wind. By measuring what the bees could see based on where they were in the wind tunnel, the researchers determined that the bees maintained a constant view to each side regardless of wind direction, but their view of the ground changed at different heights, which would allow them to achieve different heights in different wind directions.

To test whether the bees were relying on the parallel or the perpendicular stripes to determine how high to fly, they used only one stripe orientation, or no stripes at all. When the bees' visual information was limited by only seeing perpendicular stripes, they maintained similar speeds and swerves to those with full vision but were no longer consistent in their ground height. In contrast, when they could only see stripes parallel to their path, they again flew lower against the wind and higher when flying with the wind. Without seeing perpendicular stripes, though, the bees sped through the wind tunnel at about 1.5 m s$^{-1}$ without swerving. To simulate low visibility conditions, the researchers tracked bees as they flew through the wind tunnel without any stripes at all – as though flying through dense fog. As with parallel stripes alone, the bees flew straight without swerving. However, without visual cues, their height was inconsistent and they instead modulated their speed to fly slower against the wind and faster with the wind.

Honeybees determine how high and how fast to fly according to what they see, and they judge what they see by weaving wavy flight paths in such a way that their own motion helps them to extract clues about their environment. Outside the wind tunnel, bees need to discover new paths based on ever-changing wind and visibility conditions. Instead of street signs, honeybees skilfully find routes using multiple strategies to determine where they are based on what they see.

doi:10.1242/jeb.235317

**Baird, E., Boeddeker, N. and Srinivasan, M. V.** (2021). The effect of optic flow cues on honeybee flight control in wind. *Pro. R. Soc. B.* **288**. doi:10.1098/rspb.2020.3051

**Ellen Lesser (0000-0001-7929-0503)**
**University of Washington**
**elesser@uw.edu**

## Morphological laws and functional claws


Claws are found in a huge range of vertebrates, ranging from reptiles and birds to mammals. These pointed structures at the tips of digits, usually covered by a sheath of keratin, come in a wide variety of shapes and sizes that can vary considerably between species and even between limbs or digits of an individual. Claws can be used in many ways, such as climbing, grasping prey or digging. The morphological form of a structure (or rather, the shape of a structure) is often used as a guide to help understand its biomechanical function, but the large diversity of claw shapes has made it difficult to understand the link between the shape of the claws and how they are used. While previous studies have attempted to link claw shape to where the animal lives in its habitat, the link between shape and function has proven trickier. Tracy Thomson and Ryosuke Motani, from University of California, Davis, USA, sought to clarify the links between claw shape and claw use by expanding the scope of measurements used to detail the shape and by categorizing the tasks for which animals use their claws in more detail.

After accessing the skeletons of 80 animals, a mix of mammals, birds and one reptile, the authors analysed 18 features of the claws that reflected their shape. Some of the features that they measured included the claw angles, how deep claws are at the base, the size of the areas where muscles attach to claws and how quickly a claw tapers down to a point. The authors searched the literature to put each claw into one of eight possible functional categories. For example, cursorial claws are used during running or jumping (e.g. cheetahs or ostriches), scansorial claws are used for climbing (e.g. squirrels), and amplectorial claws are used for grasping (e.g. birds of prey).

The authors then used several statistical analyses and found a method that can be used to reveal claw function based on their shape alone 96% of the time. They revealed that cursorial claws used for running and jumping tend to have a blunt sheath and rounded tip to help an animal to push off of the ground and provide friction. Scansorial claws should have greater curves to help the animals get a grip while climbing. These claws tend to have a thin and elongated cross-section with well-developed areas for muscle attachment for quick extension while ascending trees or bushes. Amplectorial claws found in predators such as kestrels and other birds that grasp onto prey typically have an enlarged muscle attachment site for powerful gripping. Those claws usually have a high level of curvature and a wide cross-section, which could help to steady struggling prey.

By taking care to choose accurate claw function categories and function-informed shape measurements, Thomson and Motani have shown common shape themes in claws that are used for specific functions. Their methods could help researchers to understand how extinct creatures that we only know from fossils used their claws, or to predict how animals that are difficult to observe may use their claws. This study is a promising look into the opportunities afforded by a better understanding of the bridge between the shape of a structure and its function.

doi:10.1242/jeb.235291

**Thomson, T. J. and Motani, R.** (2021). Functional morphology of vertebrate claws investigated using functionally based categories and multiple morphological metrics. *J. Morph.* **282**, 449-471. doi:10.1002/jmor.21317

**Amanda Palecek (0000-0002-9908-3103)**
**Clemson University**
**apalece@g.clemson.edu**

## The ultimate defense against piranhas


Picture the arch-nemesis of a fearsome piranha. What comes to mind? A giant, ferocious fish with teeth even more menacing than those of piranhas? A spiny, turtle-like fish that is as hard as a rock? Maybe something like an electric eel that could fight teeth with electricity? Whatever you're imagining, it's probably not the tiny, awkward, three-striped cory catfish, which can withstand bite after bite after bite from piranhas and then swim away. While cories do have some nifty armor, which consists of two rows of scutes – large, overlapping bony plates – on each side instead of typical fish scales, at only 2 cm long, cories are generally unassuming. A recent publication by a team led by Andrew Lowe of California State University, Fullerton, USA, reveals the secrets of the cories' surprisingly impressive defenses.

To determine the strength of cory scutes, Lowe and his colleagues used a fancy hole poker, called a materials tester, which consists of a needle that moves slowly into a material as it records the resisting forces. They found that the catfish's scutes are remarkably tough and can withstand more than 4 N of force before being punctured, although the mighty arapaima, which is also renowned for its thick scales, can withstand 150 N. To put things into perspective, these scrappy little catfish are more than 10,000 times smaller than giant arapaima, but it only takes about 40 times less force to puncture cory scutes than arapaima scales. Pound for pound, I would take cory armor over arapaima armor any day.

In addition to testing individual detached scutes, Lowe and colleagues tested a series of overlapping but detached scutes and intact scutes on the bodies of catfish to see whether the configuration of the bony structures matters. They found that attached scutes take more energy to break than detached scutes. This is because of the way that the scutes in each row overlap, while the tips of the scutes from the upper row interlock with the tips of the scutes from the row beneath in a herringbone pattern. This overlapping pattern allows the force from the tip of a piranha's tooth to be spread out over a larger area. The overlapping and interlocking pattern of the scutes make them act as a single tough piece of armor, distributing the pressure from a piranha's sharp teeth, while remaining flexible and jointed to allow for easy swimming.

By poking scutes from both sides, Lowe and his team also found that the internal surface of the scutes is stiffer than the outside surface. This allows the scutes to function like a bike helmet, with a stiff layer to protect against scrapes and cuts and a softer layer to provide padding that reduces internal injuries. Furthermore, Lowe found connective tissue mixed in with these layers, making them less likely to catastrophically break even if they are punctured.

When people think of effective armor, they usually think of the biggest, heaviest, thickest outer protection, like that of medieval knights. However, different types of armor defend in different ways against different types of weapons, which is why modern soldiers wear Kevlar vests instead of plate armor to defend against bullets. Cory catfish armor may not be the bulkiest of defenses, but it works extremely well against piranha teeth by redistributing puncture forces to a greater area, in much the same way as chainmail protected knights from sword slashes.

doi:10.1242/jeb.235325

**Lowe, A., Summers, A. P., Walter, R. P., Walker, S. and Paig-Tran, E. M.** (2021). Scale performance and composition in a small Amazonian armored catfish, *Corydoras trilineatus*. *Acta Biomaterialia* **121**, 359-370. doi:10.1016/j.actbio.2020.11.045

**Noah Bressman (0000-0002-2916-3562)**
**Chapman University**
**NoahBressman@gmail.com**

## Born to be fit? GPS-tracking reveals links between early-life behaviour and survival


The key principle of natural selection is that only the fittest survive long enough to reproduce. Individual quality or acquired experience from very early in life are believed to predict an animal's ability to cope with the dangers of wildlife. Although research has suggested that more active animals are often fitter, few studies had put the theory to the test by directly comparing the activity of juvenile animals and their subsequent survival in the wild. White storks engage in long-distance migratory flights to breed in Europe and overwinter in Africa. As youngsters face high mortality during their first migration journey, Shay Rotics at the Hebrew University of Jerusalem, Israel, together with an international team of experts realised that these birds were an excellent case study to test whether an active lifestyle in early life predicts subsequent survival.

Across four consecutive years (2011–2014), Rotics and colleagues headed out to farmlands across Saxony-Anhalt in Germany looking for nests of white storks. Sometimes, the researchers monitored the birds with the help of drones to estimate the age at which they would fledge in preparation for their first migratory flight. About 2 weeks before the youngsters fledged, the scientists deployed advanced solar-charged GPS trackers on a total of 93 birds. In addition, 83 of the GPS trackers were also equipped with accelerometers to capture the fine detail of the birds' activities. The data captured by the GPS trackers covered the time the birds were still in their nests (known as the pre-fledging period) as well as the ~15 day period after they had taken to the wing (known as post-fledging period), when they gradually became fully independent and ready to start their long-distance journey.

By analysing the early-life activity patterns recorded on the GPS body-acceleration trackers, Rotics and colleagues found that the youngsters' daily activity levels increased as they were growing older. Importantly, the birds that were more active during the pre-fledging period were also most active during the post-fledging period. Even more interestingly, the birds that had a more active lifestyle during either the pre-fledging or post-fledging period had better chances of surviving their first year of life and of successfully completing their first migration. This effect was particularly pronounced in the birds that increased their daily activity faster during the post-fledging period. The researchers suggest that an active lifestyle might reflect that the youngsters are stronger, perhaps have a bolder personality, or are better skilled, which might in turn explain why these birds had better chances of survival later in life.

The team also discovered that the birds that were 'too hasty' or took too long to depart on their migration had lower chances of surviving than those birds that showed intermediate post-fledging durations – it seems that the case of the 'happy medium' is best for departing stork chicks. The researchers argued that the 'hasty birds' possibly did not acquire sufficient experience to prepare successfully for migration. In contrast, the birds that took too long to depart were also slower to increase their daily activity as they grew, possibly reflecting a delay in their development that left them unfit to face the risk of migration.

This study highlights that tracking is a powerful tool for capturing variation in the lifestyle of wild animals. These results clearly show that the differences that set successful youngsters apart from those that won't make the migration grade can manifest in early-life activity levels, serving to predict the fate of individuals as they depart on their first life-defining adventure.

doi:10.1242/jeb.235283

**Rotics, S., Turjeman, S., Kaatz, M., Zurell, D., Wikelski, M., Sapir, N., Fiedler, W., Eggers, U., Resheff, Y. S., Jeltsch, F. and Nathan, R.** (2021). Early-life behaviour predicts first-year survival in a long-distance avian migrant. *Proc. R. Soc. B.* **288**. doi.org/10.1098/rspb.2020.2670

**Valeria Marasco (0000-0002-2981-7909)**
**University of Veterinary Medicine Vienna**
**valeria.marasco@vetmeduni.ac.at**