

Keeping track of the literature isn't easy, so Outside JEB is a monthly feature that reports the most exciting developments in experimental biology. Short articles that have been selected and written by a team of active research scientists highlight the papers that JEB readers can't afford to miss.

ADAPTATION



SEDUCTIVE SINGERS CHEW SOFTLY

It's impossible to be really good at everything; specialization has its costs and they're often paid for in the currency of tradeoffs. This is well understood in the world of biomechanics where bones built to be tough cannot also be stiff, muscles good at contracting at high frequencies cannot generate high forces and fast animals can't often run long distances. Although such biomechanical tradeoffs necessarily lead to certain limitations on organismal performance they need not always be thought of as constraints. This point is beautifully illustrated by recent work on Darwin's finches by Anthony Herrel of Harvard University and his colleagues Jeff Podos, Bieke Vanhooydonck and Andrew Hendry. They show that tradeoffs between the force and speed of jaw movements in these birds might actually facilitate, not constrain, species diversification.

The beaks of Darwin's finches have received their fair share of attention and are known to be essential for at least two tasks with intimate ties to fitness: feeding and song production. However, big, strong beaks that can be used to generate large forces – good for feeding on hard seeds – are likely to be cumbersome and might not be nimble enough for seriously seductive singing. Herrel and his co-workers set out to quantify this potential tradeoff in nine species of finches and then address its possible evolutionary implications.

Working with ~1000 banded birds of known size and beak morphology the research team encouraged every animal to bite a home-made force transducer multiple times, extracting the maximal bite force exerted by each bird. They also used high-speed video recordings of another 72 animals singing in the field to measure jaw movements during song production and relate them to beak size.

As predicted, large-beaked species move their jaws at slower speeds than species with small beaks: average maximal jaw closing velocities ranged between 0.11 m s^{-1} in the largest-beaked ground finch and $\sim 0.29 \text{ m s}^{-1}$ in the smallest-beaked warbler finch. In addition, birds with small, fast-moving beaks produced more complicated songs, but also significantly weaker bite forces, indicating a mechanical tradeoff in the jaws of these finches. At this point the authors aren't sure what accounts for this tradeoff but suggest that differences in the orientation of fibers relative to the axis of force production (i.e. pennation) in the jaw musculature likely plays a role. Highly pennate muscles are great at generating large forces but are limited in the distances (and hence velocities) they can contract over. Current studies quantifying jaw muscle architecture in these species are underway.

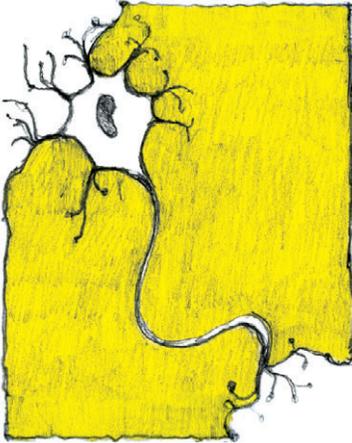
So, to summarize briefly, in Darwin's finches song quality hinges on beak velocity and gape, which depend on jaw muscles and beak size, which impact on bite force, which shapes diet. More simply, there appears to be a link between singing and eating; birds suited to cracking hard seeds will produce different types of song from less forceful feeders. Because mate selection is heavily influenced by singing, it is likely that specialization for distinct food types can severely limit the number of females attracted to a finch's song and lead to mating isolation, a major factor in speciation. The authors conclude that a biomechanical tradeoff between force and velocity may have played an important role in the diversification of Darwin's finches and could be a contributor to other songbird radiations as well.

10.1242/jeb.021667

Herrel, A., Podos, J., Vanhooydonck, B. and Hendry, A. P. (2009). Force-velocity trade-off in Darwin's finch jaw function: a biomechanical basis for ecological speciation. *Funct. Ecol.* **23**, 119-125.

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COMMUNICATION



CATERPILLARS MAKE NOISES LIKE ANTS

Ants primarily use chemical communication to identify themselves as members of the colony and to indicate their reproductive status. This system can be exploited by parasites, which imitate the chemicals produced by the ants and thereby gain access to the nest. In the case of the caterpillar of the *Maculinea rebeli* butterfly (the Mountain Alcon blue), the mimicry is so precise that *Myrmica schencki* ants that come across a caterpillar will pick it up and bring it back to the nest, as though it was an ant larva. However, Italian and British researchers, led by Francesca Barbero, noticed that once in the ant nest, the caterpillar was no longer treated simply as a larva. The ant queen acted as though the caterpillar was another, rival queen, while the workers behaved as though the intruder was a high-ranking ant. The scientists could find no chemical explanation for this phenomenon, so they looked for other ways the caterpillar might be imitating a queen.

Knowing that *Myrmica* ants use sound as an alarm signal, the team wondered whether acoustic signals might also account for the way the caterpillars were treated. First they tested whether the caterpillars were also capable of making sound and found that distressed *M. rebeli* caterpillars make a hissing noise, similar to the sound made by alarmed *Myrmica* workers. As ants make this hissing sound by rubbing together two parts of their bodies – one part carrying a ‘plectrum’ and the other a ‘file’ – the team suspect that the *M. rebeli* caterpillars may have similar structures.

Next Barbero and her colleagues decided to find out how the worker and queen ants produce their respective sounds. The scientists used an electron microscope to compare the ‘plectrum’ and the ‘file’ on *M. schencki* workers and queens. These structures – each about half a millimetre long – were substantially different in the

two kinds of ant, and when a tiny microphone was introduced into the nest, the sounds made by the queens and the workers were quite distinct, and different from alarm ‘hissing’. The differences were entirely due to the shapes of the ‘plectrum’ and the ‘file’. When these sounds were played back to ants in the nest, the noises made by the queen prompted the workers to take up a guard behaviour, whereas the noises made by a worker did not, suggesting that the sounds enable the ants to identify the social status of the insect that produced them.

The next step was to see whether the caterpillars could imitate this sound. The team used the tiny microphones again, this time to record the noises made by *M. rebeli* caterpillars and pupae. The caterpillars and pupae made similar sounds which the scientists’ computers could distinguish from both queen and worker noises, but which were more similar to the sounds made by the queens. So the caterpillars could make sounds, but would they provoke the workers to behave defensively?

Playing back the *M. rebeli* noises to the worker ants, the noises made by the pupae had the same effect as the queen noises; the workers switched to their guarding behaviour. The caterpillars were able mimic key aspects of *M. rebeli* communication to successfully parasitize the ants’ nest.

It seems likely that this fascinating story is simply the tip of the iceberg. Many other *Myrmica* ant species are parasitized by other butterfly species. The authors suggest that acoustic communication may be widespread in these ants and that the caterpillars may be taking advantage of this. In a single study, Barbero and her colleagues made two important discoveries: they showed that ants use acoustic signals to communicate social status, and that a social parasite can imitate these signals in order to camouflage itself more effectively. In Darwin’s bicentenary year, this study of host–parasite relations is a tremendous example of the power of natural selection, and of the exquisite adaptations shown by parasites in their continuous combat with their hosts.

10.1242/jeb.021741

Barbero, F., Thomas, J. A., Bonelli, S., Balletto, E. and Schönrogge, K. (2009). Queen ants make distinctive sounds that are mimicked by a butterfly social parasite. *Science* 323, 782-785.

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CARBON CYCLE



FISH: THE GUTS OF THE CARBON CYCLE

Traditionally, oceanic calcification is credited to tiny marine plankton, mostly coccolithophores and foraminifera. These plankton combine seawater calcium with bicarbonate to form calcium carbonate, carbon dioxide and water, *via* the inorganic marine carbon cycle. When plankton die, calcium carbonate is released from their ‘skeletons’ into the ocean where some of it sinks to the ocean floor to form limestone sediments while some of it dissolves under the high pressures and low temperatures in the deep ocean to produce calcium and bicarbonate, which increases the water’s alkalinity. However, there is another source of calcium carbonate that has remained beneath the radar: bony fish guts!

Marine fish need to continually drink calcium-rich seawater in order to maintain the correct internal water and ion balance while bathed in their aquatic environment. Previous studies have shown that marine fish release bicarbonate into their intestines, which combines with calcium from the imbibed seawater to form calcium carbonate. This process allows fish to absorb water across the gut and also prevents them from developing kidney stones. The calcium carbonate precipitate (or ‘gut rocks’) is then released into the surrounding water. Rod Wilson from the University of Exeter and colleagues from Canada, England and the United States sought to determine how much marine fish gut rocks contribute to global levels of calcium carbonate.

The authors used two independent models to estimate the total amount of fish in the planet’s oceans. Taking into consideration the effect of both body size and temperature, they assessed global fish calcium carbonate production. The team estimates that a remarkable 3–15% of the calcium carbonate in the ocean comes from fish. Wilson and colleagues used a

conservative approach for their calculations and suggest that the contribution of fish may actually be up to 3 times higher. These findings show that fish make a substantial, but previously unrecognized, contribution to the marine inorganic carbon cycle.

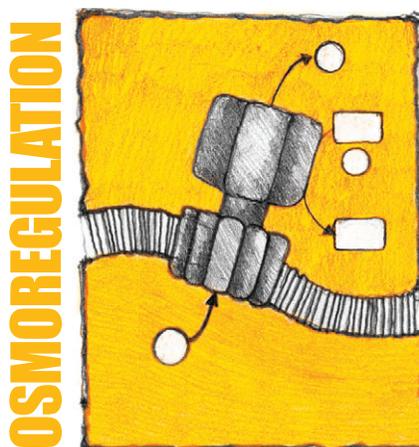
Next, the team sought to compare the influence of fish gut rocks on the environment with the effects of carbonates from more conventional sources. While calcium carbonate dissolves deep in the oceans to make the water more alkaline, studies have shown that carbonates also dissolve at much shallower depths and lower pressures than predicted to increase the total alkalinity of coastal waters; a phenomenon that has puzzled oceanographers for decades. Fish gut rocks have high levels of magnesium, which allows them to dissolve at shallower depths (<1000m) and lower pressures. Collating this information, Wilson and colleagues suggest that the dissolution of fish gut rocks at shallow depths could help to explain the perplexing observation.

This study shows that fish may play an unexpected role in the marine inorganic carbon cycle. Magnesium-rich gut rocks expelled from fish are a major contributor to oceanic carbonates and may help explain the elevated alkalinity of shallow seawater. Moreover, as the oceans become more acidified due to increased atmospheric carbon dioxide levels, the authors suggest that fish are likely to make an even larger contribution to the inorganic carbon cycle. Higher temperatures and elevated levels of carbon dioxide in fish blood will likely lead to them producing even more gut rocks, at a time when plankton are expected to begin producing less calcium carbonate. Though many questions remain, it seems that researchers are finally getting to the guts of the carbon cycle.

10.1242/jeb.023846

Wilson, R. W., Millero, F. J., Taylor, J. R., Walsh, P. J., Christensen, V., Jennings, S. and Grosell, M. (2009). Contribution of fish to the marine inorganic carbon cycle. *Science* **323**, 359-362.

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BRIDGING THE NEPHROCYTE GAP

The kidney is one of the main sites of blood volume regulation, osmoregulation and excretion in vertebrates. Its functional unit is the nephron, which can be found in countless copies in the kidney. Nephrons consist of a filtering element that is partially formed by podocyte cells, and a tubule, which reabsorbs everything that is needed by the body and secretes the remaining fluid as urine. Insect excretory systems serve similar functions but lack a nephron-like unit. Instead, insects are equipped with more independently functioning organs: Malpighian tubules for secretion and reabsorption and nephrocyte cells for filtering and disposing of substances that Malpighian tubules have difficulty dealing with. In a recent paper published in *Nature*, a team working with Helen Skaer at the University of Cambridge reports intriguing similarities between vertebrate podocytes and insect nephrocytes.

Knowing that both cell types are involved in filtration processes, Skaer and her multinational team addressed the question of whether the filtration units of podocytes and nephrocytes exhibit anatomical similarities. Undertaking a comprehensive ultra-structural study on *Drosophila* nephrocytes, the team found structures in the insect nephrocyte that are very similar to the vertebrate podocyte's 'slit-diaphragm' structure, which is part of the kidney's filtration mechanism. In the vertebrate kidney adjacent podocytes form delicate finger-like projections that interdigitate and enclose a tiny ball of blood vessels called the glomerulus. The fingers do not surround the glomerulus entirely but leave open narrow gaps (called filtration slits) that are bridged by the 'slit diaphragm', a structure composed of cell surface proteins. Looking at insect nephrocytes, which absorb potentially harmful substances, Skaer's team found infoldings in the plasma membranes

forming small cavities. Similar to the situation in podocytes, the cavities' entrances are narrow gaps that are bridged by cell surface proteins forming the nephrocyte diaphragm.

Working with *Drosophila* also allowed the scientists to look for molecular similarities between the vertebrate and insect diaphragm structures. As the genes encoding the major constituents of the vertebrate slit diaphragm were known, Skaer and her colleagues were able to examine the expression of corresponding genes in *Drosophila*. They found several of these 'orthologous' genes expressed in the insect's nephrocytes. In vertebrates two of the major components of the slit diaphragm are nephrin and NPH1, which interact across the filtration slit to bridge the gap. When the team took a closer look at these structures by immunoelectron microscopy, they found the *Drosophila* nephrin and NPH1 orthologues in close proximity at the nephrocyte diaphragm. Using yeast two hybrid analysis and co-immunoprecipitation they finally showed that the *Drosophila* orthologues of five known diaphragm components, including nephrin and NPH1, form a complex that closely resembles that of the vertebrate diaphragm. One of the major advantages of using *Drosophila* for this study is that it is possible to knock-out the expression of specific genes, offering Skaer and her colleagues the opportunity to knock-out expression of some of the diaphragm genes. Accordingly, when they generated flies lacking either the nephrin or the NPH1 orthologues, the nephrocyte's diaphragm was lost and its filtration function was significantly impaired, similar to what is observed when these proteins do not function properly in the vertebrate kidney.

In view of the striking functional, anatomical and molecular similarities between the slit-diaphragms of vertebrate podocytes and insect nephrocytes, it is tempting to speculate whether these cells derive from a common progenitor, although the answer to this is still pending. In any case, Skaer and her team have established a potent genetic model for investigating podocyte-related diseases.

10.1242/jeb.021709

Weavers, H., Prieto-Sánchez, S., Grawe, F., Garcia-López, A., Artero, R., Wilsch-Bräuninger, M., Ruiz-Gómez, M., Skaer, H. and Denholm, B. (2009). The insect nephrocyte is a podocyte-like cell with a filtration slit diaphragm. *Nature* **457**, 322-327.

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