OUTSIDE JEB

Zooplankton swim softly to stymie predators

It's true that zooplankton are drifters; tiny, often microscopic, organisms floating en masse through the seas, oceans and freshwaters of the world. But they don't just drift. Up close, they are really quite active. Just like many animals, zooplankton move to find food and mates, and do so using a wide range of propulsion methods to get them where they need to go. But as they go, microscopic zooplankton create tiny wakes, alerting predators to their location. Worse yet, to feed, zooplankton must filter or examine large volumes of water while they swim. More water, more wakes. Because zooplankton must move, and moving puts them at risk for predation, Thomas Kiørboe, of the Centre for Ocean Life at the Technical University of Denmark, and his team of international collaborators wanted to understand how these tiny creatures balanced the need to move with the need to stay alive. By comparing zooplankton that feed while they swim with those that are able to feed and swim (to relocate) independently, they sought to answer the question, do zooplankton minimize predation risk when given the opportunity? That is, is swimming independent of feeding as risky as swimming while feeding, in terms of the signals that zooplankton are sending to predators?

The authors examined the wakes (fluid disturbances) caused by swimming and feeding zooplankton across a range of size, morphology, ecology, species and swimming modes: from single-celled, rugby-ball-shaped dinoflagellates, which propel themselves with one tail and one side whip, to ~1-mm-sized copepods – crustaceans with four to five pairs of swimming legs on their underside, plus feeding appendages that generate a current. They used high speed cameras to film the zooplankton swimming through liquid filled with tracer particles to visualize the flow of the liquid around the organisms, and measured the peak and variability in swimming speed of the zooplankton, how far the flow field extended out from the zooplankton and how quickly the disturbances dissipated. They also noted how the organisms were swimming and whether zooplankton that swim to relocate and swim to feed use different movements for each task.

Kiørboe and his team discovered that the zooplankton that were only swimming did so in a way that disturbed the fluid around them significantly less than when they were feeding, and less than the zooplankton that always swim and feed. Swimming by itself resulted in fluid disturbances that dissipated more quickly than swimming and feeding, which meant that the wakes did not reach as far out from the zooplankton, potentially alerting fewer predators in the area.

The authors suggest that with zooplankton, similar to many animals, there are tradeoffs associated with the daily activities necessary for survival. Because feeding requires the movement of large quantities of water (relative to zooplankton size, of course) and food is an absolute necessity, the fluid disturbances caused by feeding are worth the risk: if they don't feed, they will die; if they do feed, they might die trying. Either way, zooplankton must feed, so the risks that come with feeding are offset by the benefits of feeding. However, swimming to relocate does not require the processing of large volumes of water, so zooplankton have evolved to minimize predation risks when swimming. And so these tiny drifters swim softly on, with their predators none the wiser.

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Casey Gilman
University of Massachusetts Amherst
cgilman@bio.umass.edu

A snail switch from feeding to fleeing

Anyone who has made the unfortunate decision to breathe while swallowing a liquid knows that some behaviours are incompatible with each other. The brain therefore has to ensure that, in case conflicting sensory information is received, the right behaviour is chosen: stop the breathing, swallow the liquid. This issue becomes acute when, for instance, an animal has the choice between eating a tasty morsel of food or fleeing a predator. How does the brain ensure that, if conflicting sensory information is received, the right behaviour is chosen? One mechanism, proposed by the pioneering ethologist Niko Tinbergen over 60 years ago, suggests that the brain has encoded a behavioural hierarchy, in which one behaviour can be blocked in favour of another, more important one. There is however little evidence to explain how the brain enacts this hierarchy.

In a study recently published in *Current Biology*, a team of researchers from the University of Sussex, UK, addressed this issue by looking at how *Lymnaea* pond snails choose between feeding and fleeing. The snail starts feeding when it detects sugar, but when the front of the animal is touched – mimicking an encounter with a predator – this behaviour is completely blocked. Instead, the snail withdraws, apparently to get away from the perceived predator. The experimenters decided to probe the mechanisms underlying this apparent behavioural hierarchy by applying a tried and tested technique within neuroscience to the snail: recording the electrical

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activity of identified cells within its simple nervous system.

The team identified a cell, PeD12, which they found to be crucial in the behavioural switch: it is activated when the front of the animal is touched, and, importantly, when the team inactivated the cell, touching the front of the snail no longer elicited an escape response. Moreover, when PeD12 was activated by the researchers the feeding behaviour was blocked, and the withdrawal response initiated, independent of the touch stimulus. These findings suggest that PeD12 is both necessary and sufficient for the implementation of the behavioural hierarchy. How does PeD12 regulate these two behaviours? Another cell type, PIB, has been previously shown to inhibit the neurons responsible for feeding. Could PeD12 simply be switching on PIB?

In order to test this hypothesis, the team performed another set of electrical recordings. They found that, consistent with their hypothesis, there are direct connections between PeD12 and PIB, and that PIB is necessary and sufficient for PeD12 to switch off the feeding behaviour. Moreover, in a separate experiment, the team found that PeD12 is directly connected with the cells responsible for the withdrawal behaviour. This means that the choice between feeding and fleeing is governed by a remarkably simple circuit of neurons: upon the detection of a predator, PeD12 switches off feeding indirectly, through PIB, and switches on fleeing directly, through its connections with the fleeing (withdrawal) circuit.

The study provides direct evidence for the existence of a behavioural hierarchy encoded in the the *Lymnaea* brain, implemented by simple inhibition of the less dominant behaviour by an identified interneuron. Moreover, it makes a strong case that there is still plenty of mileage in applying age-old experimental techniques to simple model organisms in order to address central questions in neuroscience.

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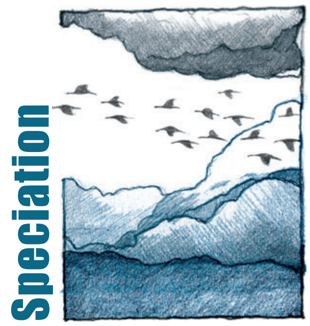
Pirger, Z., Crossley, M., László, Z., Naskar, S., Kemenes, G., O'Shea, M., Benjamin, P. R. and Kemenes, I. (2014). Interneuronal mechanism for Tinbergen's hierarchical model of behavioral choice. *Curr. Biol.* **24**, 2018-2024.

Maarten Zwart
HHMI Janelia Research Campus
zwartm@janelia.hhmi.org

New routes prove detrimental for young hybrids



For migratory songbirds, once your offspring fledge the nest and head south, the only influence you have as a parent on the migratory route your young will embark on is in the genetic input that you've provided. This is because young songbirds migrate alone and at night, without friends or relatives to guide the way. Having children is always hard work; parents might not always agree on how best to bring up their progeny, leaving offspring with conflicting guidance. But now imagine that your parents were from different sides of town and have provided you with vastly different genetic information about where you should be heading on your migratory journey, where do you end up then? A recent study by Kira Delmore and Darren Irwin, published in *Ecology Letters*, reveals how hybrid young display mixed-up migratory routes in response to this varied set of genetic directions, much to their own detriment.

The team, based at the University of British Colombia, Vancouver, Canada, fitted tiny geolocators to migratory Swainson's thrushes in western Canada. These devices acted like mini GPS loggers and recorded the annual migrations of these long-distance travellers, which breed in Canada and Alaska and regularly winter as far south as Venezuela and Argentina. However, the key to the team's study was that this population of thrushes is made up of two distinct groups. Even though the thrushes all look the same to the casual eye, they use remarkably separate migratory routes to get to and from their breeding grounds. They also interbreed freely, creating hybrid offspring that have a mixed genetic heritage from both migratory divides.

Amazingly, when these juvenile hybrids embarked alone on their migratory journey south, they didn't commit to the distinctive migratory paths that either of their parent populations take, but rather opted for a zigzag route, frequently flying down the middle of the two routes flown by each of the parents. Unfortunately for the hybrids, this middle of the road approach frequently leads them through sub-optimal migratory habitats such as deserts and high mountains. The team also suggests that taking these less than ideal migration routes is likely to impose a selection pressure that acts against the hybrid forms, ensuring that the two subpopulations remain purebred.

This study provides compelling support for how migration may play a role in speciation, while providing further evidence for the genetic control of migratory behaviour in songbirds. However, if your fitness is being reduced by pairing with an individual from a different migratory divide, it does beg the question; why not only mate with birds that follow the same migratory route as you? 'Data from hybrid zones has shown that when [population] densities are lower, more hybridisation [between subgroups] occurs', says lead author Delmore, 'suggesting they're just making the best of a bad situation, mating with someone rather than no one', she concludes.

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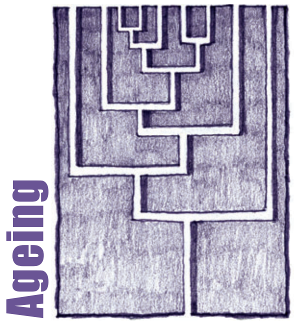
Delmore, K. E. and Irwin, D. E. (2014). Hybrid songbirds employ intermediate routes in a migratory divide. *Ecol. Lett.* **10**, 1211-1218.

Steve Portugal
Royal Holloway, University of London
Steve.Portugal@rhul.ac.uk

Deer with larger harems age faster

I don't know anyone who is happy about getting older. This is because ageing entails a deterioration of the organism which leads to decreased survival and reproductive performance. The process, however, varies between individuals, with some individuals experiencing more of the negative consequences of ageing than others. The disposable soma theory attempts to explain some of this variability by arguing that an animal that allocates more energy to reproduction early in life will have less energy to



allocate to cell and tissue repair during the same time period. In consequence, organisms that devote more energy to early life reproduction will exhibit increased senescence (loss of function due to ageing), which would translate into the deterioration of fitness-related traits later in life. Most of the studies that test the disposable soma theory have been performed in females, perhaps because of the general perception that energy investment in reproduction is higher in females than males. However, in many species, male competition for females and territories is fierce and, therefore, the disposable soma theory should also apply to these males. Red deer are one such animal; males actively compete for mates and a large amount of energy is allocated to the development of antlers. Do male deer with larger harems and bigger antlers during their youth therefore suffer the consequences later in life?

Jean-Francois Lemaître and colleagues from the Université de Lyon, France, the University of Edinburgh, UK, and the University of Cambridge, UK, analysed 40 years' worth of data from 155 male red deer. For each male, they looked at harem size and at the number of points of the deer's antlers throughout the years as indicators of energy allocation to reproduction during different life stages and, therefore, of ageing.

Although the number of points in the deer antlers did not decrease with age, harem size decreased between the ages of 10 and 16 years. Those males with larger harems during their youth also had larger harems later in life; however, the decrease in the number of females in their harem was faster than the decrease for males that had smaller harems in early life. In other words, by using harem size as an indicator of senescence, Lemaître and his team were able to show that the deer that allocated more energy to reproduction earlier in life aged faster.

This is the first study to show that a larger energetic investment in reproduction in early life stages is correlated with a more rapid deterioration of a fitness-related trait in males in a wild population. The authors suggest that a higher degree of tissue and cellular damage in these individuals due to the allocation of fewer resources to repair could lead to faster deterioration of the organism and therefore a more rapid decrease in reproductive performance. However, the faster degree of ageing in these deer might not negatively affect their overall reproductive output, because, even in later life, their harems are still larger than those of males who invest less in reproduction earlier in their lives.

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Viviana Cadena
The University of Melbourne
Viviana.cadena@unimelb.edu.au