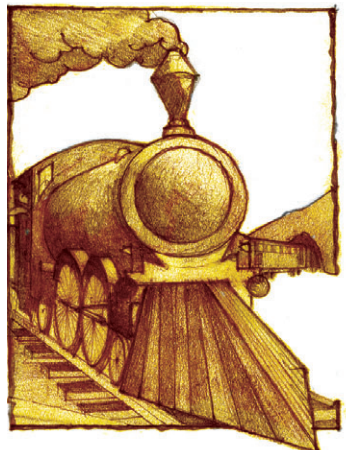
Keeping track of the literature isn't easy, so Outside JEB is a monthly feature that reports the most exciting developments in experimental biology. Short articles that have been selected and written by a team of active research scientists highlight the papers that JEB readers can't afford to miss.

Outside JEB

TRAPDOOR MOTION



BLADDERWORTS SUCK IT UP IN A HURRY

Hunters come in all shapes and sizes. In freshwater ponds, one particularly formidable hunter is actually an aquatic plant, the bladderwort. Bladderworts (in particular, *Utricularia* spp.) hunt small invertebrates. Along their branches, the plants have hollow pods (bladders) under negative pressure. Each pod is about 1 mm in diameter and has a trapdoor on a hair trigger. When a small critter brushes by, the door opens and sucks the prey into the pod (where it is eventually digested). It turns out that the biomechanics of how bladderworts do this is not well known. However, Amit Singh, Sunil Prabhakar and Sanjay Sane at the National Institute for Biological Sciences in Bangalore recently used high-speed videography to describe the mechanics of bladderwort trapdoor movements at sub-millisecond resolution and they published their work in *Biology Letters*.

First, the team set out to determine the pressure difference across bladder walls. To do this, they used a glass micropipette filled with water and a bubble as a pressure probe. After estimating the pressure within the bubble, they inserted the micropipette into individual bladders. The bubble then expanded towards the pod (pulled by the negative pressure); by measuring this expansion, they were able to estimate the internal pressures within individual bladders. As expected, internal pressures within pods were much lower than the pressure of the surrounding water. This differential disappeared immediately after trapdoor opening, then reset over the course of 20–30 min. Interestingly, trapdoor opening could not be triggered while the pressure differential was resetting. This suggests that each bladder possesses an internal sensing mechanism that keeps the door firmly shut until a pressure threshold is reached.

Next, Singh and colleagues filmed individual pods opening and closing with a very high-speed camera. The kinematics of trapdoor opening turned out to be incredibly fast. In response to mechanical stimulation, trapdoors opened within 300–700 μs, stayed open for 1–3 ms, then closed in 1–2 ms. These swings are an order of magnitude faster than previous estimates and are the fastest recorded movements in any carnivorous plant. By filming neutrally buoyant beads being sucked into bladders, the group was also able to measure the speed at which water moves through the trapdoors. The speeds involved were similar to theoretical estimates based solely on the pressure differentials across the bladder; in addition, the suction flows that developed were dominated by inertial forces. This helps explain why bladderworts are so effective at hunting; the speed of trapdoor movements and the large inertial forces easily outpace sensorimotor responses in prey animals. Small animals just have no chance to react.

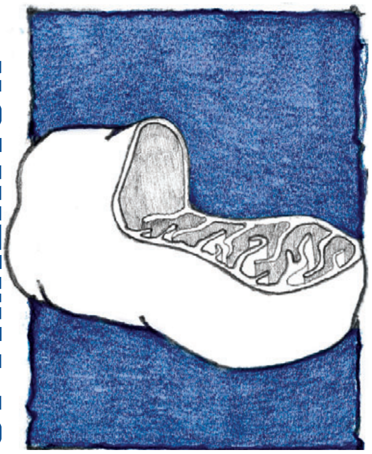
The work of Singh, Prabhakar and Sane is important because it shows that carnivorous plants are capable of moving much faster than previously thought. It is also significant because it is a descriptive study. This work represents a traditional way of doing biology that has fallen out of favour. Indeed, for many young biologists, 'purely descriptive' work is something to be avoided at all costs. But the work of Singh and colleagues bucks this trend and sends an important message. It shows that new discoveries can still be made by those who simply take the time to carefully describe what they see in nature.

10.1242/jeb.049841

Singh, A. K., Prabhakar, S. and Sane, S. P. (2011). The biomechanics of fast prey capture in aquatic bladderworts. *Biol. Lett.* doi: 10.1098/rsbl.2011.0057.

Stefan Pulver
University of Cambridge
sp553@cam.ac.uk

OPTIMIZATION



FORAGING NOT BASED ON LUCK FOR HORSESHOE BATS

If you spend more energy catching your next meal than it provides, you run the risk of creating an energy deficit, which will in turn negatively impact your growth and potentially your survival. This suggests that predators may adaptively choose prey that are more economically profitable. Klemen Koselj and colleagues, from the University of Tubingen and the Max Planck Institute for Ornithology in Germany, set out to determine whether prey selection in horseshoe bats is based on optimizing energy profitability. The team wanted to see whether the bats could learn which prey offered the greatest amount of energy, whether they could estimate how often they would encounter their prey, and whether they could integrate the two pieces of information and make prey selection decisions that would help to maximize their energy intake.

First, the team designed two different sized rotating propellers that simulated two different sized prey items and created echo patterns that the bats could distinguish using echolocation. The team then trained horseshoe bats to associate the large propeller with a large mealworm reward, and the small propeller with a small mealworm reward. Following training, the team ran each bat through a series of hunting trials where they were sequentially and repeatedly offered both large and small propellers. The order in which the propellers were presented was varied for each trial. The team also varied the frequency with which they were presented to mimic the effect of different prey densities and abundances. In theory, if the bats were making economical decisions about their meals, the more abundant the large prey the less often the bats should respond to smaller prey.

In fact, as the frequency of the larger prey increased (i.e. the more often the large propeller was presented to the bats), the bats preyed more predominantly on the larger prey and more often ignored smaller prey when it was presented. Conversely, as the frequency of the larger prey was decreased, the bats began to feed on both large and small prey items equally. This suggests that not only can bats distinguish prey items based on their energy content but also they can estimate their abundance based on how frequently they encounter the prey. These two pieces of information then contribute to the bats' prey choice, helping them to make adaptive decisions. This suggests that the prey selection biologists see in the field may be a result of bats choosing the most profitable prey.

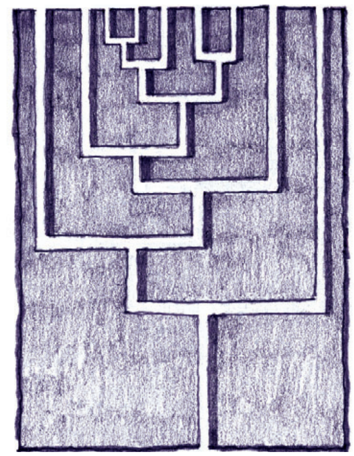
Koselj and colleagues have shown that bats can and do make economical decisions when hunting. Having a surplus in your energy budget allows for growth and reproduction, and choosing prey that gives you the biggest bang for your buck would certainly help you achieve that. Overall, this suggests that predators may be making complicated decisions about prey selection and that foraging may be based on more than happenstance.

10.1242/jeb.049833

Koselj, K., Schnitzler, H. U. and Siemers, B. M. (2011). Horseshoe bats make adaptive prey-selection decisions, informed by echo cues. *Proc. R. Soc. Lond. B.* doi:10.1098/rspb.2010.2793.

Carol Bucking
University of Ottawa
cbucking@uottawa.ca

COMMUNICATION



SQUIDS IN HEAT

Getting girls in the animal world is a serious business. Males need weapons such as antlers and canines to fight off competitors and secure mating rights. Because contests among males can be hazardous, it is essential that aggression be limited to occasions where the rewards of success outweigh these dangers. How then do males living in social groups know when it is appropriate to engage in this risky behaviour?

This is the question studied by an international group of scientists led by Roger Hanlon of the Marine Biological Laboratory at Woods Hole. Hanlon and his team noticed that when spawning males of the longfin squid *Loligo paeleii* came into contact with fertilized eggs they went berserk, squid style. Within moments of contact, males begin attacking one another with raised arms, beating their fins, initiating chases and grappling. The immediacy of the response implied the existence of a chemical signal, applied by females to the eggs, that triggered the males' outbursts.

Using an impressive range of purification methods, the authors isolated a single protein, a beta-microseminoprotein (loligo β-MSP), that females embed within eggs as they are being deposited in long strands – known as egg mops – glued to the near-shore ocean bottom. In nature, males approach egg mops using visual cues and then, after touching them with their chemosensitive legs, become agitated. Most impressively, the authors found that even in the lab where most natural cues (including females) were removed, exposure to recombinant loligo β-MSP smeared on the outside of an Ehrlenmeyer flask induced aggression.

But why does this happen? What is there to gain? The authors propose that loligo β-MSP is a reliable cue that males use to time their aggressive encounters to appropriate moments when females are present to notice. Males and females would both gain were this explanation true: males by outcompeting their rivals and therefore increasing access to females, and females by ensuring that they mate with the most robust males. A more one-sided alternative may also be plausible. By increasing aggressive encounters among males, females would be left alone to complete egg laying using stored sperm and males would be kept from eating eggs (they are eager cannibals as adults); males might also be encouraged to attack egg predators of other species. Here, females gain while males are pawns in their coercive game!

Signals between animals can convey unidirectional or bidirectional messages, with mutual or one-sided interests being served. In this case, it remains unclear whether loligo β-MSP is akin to a chemical come-hither or whether it is more similar to the robot bunny at the dog races. Fortunately, Hanlon and his team can put all this rampant speculation to the test. Is loligo β-MSP species specific or will it also rile sympatric squid? Does male aggression scale with the presence or absence of females? Finally, why does a highly visual predator require a chemical signal to tell it something that it can already see? The longfin squid still has some explaining to do, and this fascinating story is far from over.

10.1242/jeb.049817

Cummins, S. F., Boal, J. G., Buresch, K. C., Kuanpradit, C., Sobhon, P., Holm, J. B., Degnan, B. M., Nagle, G. T. and Hanlon, R. T. (2011). Extreme aggression in male squid induced by a β-MSP-like pheromone. *Curr. Biol.* **21**, 322-327.

Daniel E. Rozen
University of Manchester
daniel.rozen@manchester.ac.uk

HEAVY LOADS SLOW TRUCK DRIVERS AND ANTS

When carrying resources from a collecting point to the nest, one would assume that animals would attempt to carry as much as possible to maximize their foraging efforts. However, among social insects that is not always the best strategy. Foragers carrying large loads might overwhelm the individuals processing the resources in the nest, causing a bottleneck. Additionally, a heavy load slows the carrier down. That may not be a significant cost for a solitary forager, but it may reduce the gains for a colony as a whole. Carrying loads well below maximum carrying performance actually reduces the burden on the resource processors and speeds up the forager, allowing for more foraging trips per unit time. But there is yet another factor whereby lighter loads can increase colony efficiency. Walking foragers, such as ants, often forage along well-defined trails and, depending on the number of foragers, this can potentially cause traffic problems. In that context, when one ant is slowed down by a heavy load it also slows down those ants following behind, regardless of load size. This phenomenon, called the 'truck-driver' effect – where a heavily laden truck slows down normally faster cars – describes another situation where carrying too much negatively impacts whole colony foraging efficiency.

Alejandro Farji-Brener and colleagues, from CRUB-Universidad Nacional del Comahue e INIBIOMA-CONICET in Argentina, investigated and quantified the effects of heavily laden ants on foraging ant traffic in the leaf-cutting species *Atta cephalotes*. Working in Costa Rica, they first characterized ants and load sizes by collecting individual ants and their loads and determining leaf-cutting and ant dorsal surface areas. 'Highly laden' ants were 25% bigger and carried 100% larger loads than 'ordinary laden' ants. Then they performed two field manipulation experiments on foragers of several *A. cephalotes* colonies. In the first they identified highly laden ants and measured walking speeds for the highly laden ant, the ordinary laden ant following directly behind (treated ant) and another nearby ant as control. Then they removed the highly laden ant and mimicked the removal hand-motion over the control ant. After 5 s they then measured the treated and the control ant's speeds. In the second experiment they 'created' highly laden ants. Initially, the speeds of two ordinary laden non-consecutive ants were measured. Then the load mass of an ant directly ahead of one of the two measured ants was artificially increased by adding a 10 mg piece of aluminium foil to her leaf cutting. After 10 s the speeds of the treated ant (following the 'created' highly laden ant) and the control were measured again. They also investigated the relationship between numbers of highly laden ants and ant traffic flow.

Removal of highly laden ants increased ordinary laden ants' walking speeds from 1.9 to 2.9 $cm\,s^{-1}$. Similarly, the 'creation' of highly laden ants reduced their followers' speeds from 2.4 to 1.6 $cm\,s^{-1}$. These results clearly show how ant load can impact the overall colony foraging rate and, by extension, the intra-colony fitness. Furthermore, Farji-Brener's team also found a negative relationship between the number of highly laden ants and ant density (traffic) on foraging trails. Thus, at low traffic flow ants can cut and carry larger leaf fragments without the concern of slowing other ants, but when traffic flow increases they refrain from cutting larger fragments. It appears that individual ant foragers leaving the nest can estimate the outbound traffic flow and use this information to estimate the future flow of returning laden ants, thereby modulating the sizes of leaf cuttings made in order to avoid delays in overall colony foraging rates. This study shows remarkable flexibility in foraging behaviour and supports the idea that leaf-cutting ants make choices not only as individuals but also collectively.

10.1242/jeb.049825

Farji-Brener, A. G., Chinchilla, F. A., Rifkin, S., Sanchez Cuervo, A. M., Triana, E., Quiroga, V. and Giraldo, P. (2010). The 'truck-driver' effect in leaf-cutting ants: how individual load influences the walking speed of nest-mates. *Physiol. Entomol.* doi: 10.1111/j.1365-3032.2010.00771.x.

C. Jaco Klok
Arizona State University
cjklok@asu.edu