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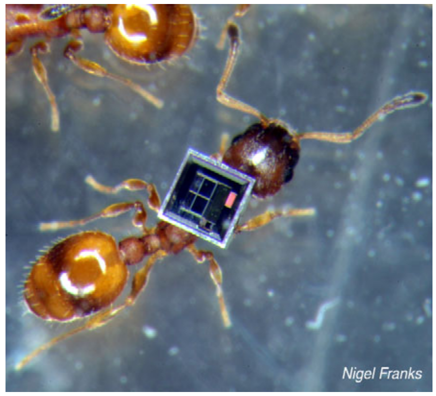
Inside JEB

WHY SLIM ANTS LISTEN TO THE COLLECTIVE STOMACH



Nigel Franks

A rumbly tummy is always a good sign that you need to get some food, but how do you know that you're hungry when you forage on behalf of a collective stomach? That is the problem faced by social insects. According to Elva Robinson from the University of York, UK, *Temnothorax albipennis* foragers are always the leanest occupants of the nest. However, 'It's not as simple as the lean ants know when they're hungry and that triggers foraging', explains Robinson, recalling that instead of consuming their honeydew load, slender foragers selflessly give it up to fatter nest mates. Robinson and her colleagues, Ofer Feinerman and Nigel Franks, wondered whether the skinnier ants forage because their mass has fallen below a critical threshold or whether the ants are motivated by their previous foraging experience and their slenderness is merely a side-effect of their frenetic lifestyle (p. 2653).

'But those things are generally almost impossible to untangle', says Robinson, adding, 'So that is where technology came in'. Realising that they could use minute radio frequency ID tags to selectively open the nest's exit, the team designed an experiment where they could produce tubby and slender foragers to find out which factor – thinness or experience – sent foragers searching for food.

Teaming up with Feinerman to build a computer-controlled door that was activated by the ants' ID tags, Robinson initially allowed all of the nest's occupants to roam freely around an experimental arena, which she equipped with a well-stocked feeder for 1 h a day. However, as soon as the first successful foragers returned, Robinson used a reader to scan their IDs and enter them onto a blacklist that banned them from embarking on further outings. Deprived of food, the nest then motivated the next cohort of foragers to depart, but they too were blacklisted upon their return.

Over a week, Robinson photographed the foragers to determine their fat levels and built up the blacklist so that at the end of that period the active forgers were fatter than the foragers had been on the first day. Then she wiped the blacklist clean to see which ants would be the first to leave: the leanest foragers with out-of-date experience that had suffered a week of setbacks, or the tubbiest foragers with the most recent experience.

The results were very clear. Robinson recalls that as soon as they could open the door again, the leanest ants were back out foraging. And, as she rebuilt the blacklist over the course of a second week, the foragers' girth increased as the slimmest forgers were systematically prevented from exiting the nest again.

So, an ant's leanness is the most important factor in deciding whether it goes out to forage. However, when Robinson took a closer look at the ants' activity patterns, she realised that experience also contributed to a lesser extent to the decision. 'For any given leanness, if the ant had got any foraging experience at all in the previous week it was more likely to come out than ones which didn't have any experience at all,' she recalls.

Considering the rationale of the ant's strategy Robinson says, 'There are good reasons why you would expect it to be important for lean ants to forage'. Explaining that lean ants are more mobile and less valuable than their corpulent nest mates she adds that the mechanism is self-regulating. Nests on the verge of starvation will have many foragers to satisfy their hunger, while foragers in well-fed nests will lose interest in foraging as they gain mass when forced to digest their honeydew cargo destined for the already full collective stomach.

10.1242/jeb.076679

Robinson, E. J. H., Feinerman, O. and Franks, N. R. (2012). Experience, corpulence and decision making in ant foraging. *J. Exp. Biol.* **215**, 2653-2659.

Kathryn Knight

TROUT CAN COPE ON SOME CARBS

Trout have voracious appetites, which the aquaculture industry satisfies with fishmeal and oil from marine fisheries. However, Biju Kamalam from the French National Institute for Agricultural Research explains that the fisheries that supply aquaculture are under increasing pressure, forcing aquaculturists to consider alternative protein and energy sources. 'The alternative is to replace fish meal with plant ingredients', says Kamalam, although plant ingredients are rich in carbohydrates that trout find difficult to use for fuel. However, while breeding two new trout lines with altered muscle fat content (one with a high muscle lipid content while the other had a low muscle lipid content), Françoise Medale and her colleagues found that the lines appeared to metabolise fuel differently from each other. The fish with high levels of muscle fat seemed to express the genes that code for proteins that metabolise carbohydrates at high levels. Could the high muscle fat trout handle a plant-based, carbohydrate-rich diet better than fish that are currently being farmed? Kamalam, Medale and Kamalam's thesis advisor, Stephane Panserat, decided to investigate the fish's metabolism (p. 2567).

Kamalam fed both the high muscle fat fish and the lean muscle fish either a fish meal supplemented with gelatinised starch diet or an unsupplimented diet for 10 weeks and then collected the livers, blood, muscles and adipose tissue from all of the fish for analysis. However, when the team compared the growth of the two fish lines they were disappointed to see that the lean fish grew better than the fat fish on both diets. 'We had thought that if the fat muscle fish was able to use the carbohydrate as an efficient energy substrate, the protein in the diet would be used for muscle growth and improve the growth of the fish', says Kamalam. However, both fish were capable of metabolising carbohydrate.

Next, the team compared the fish's blood glucose levels, suspecting that the fat fish would regulate their glucose levels better than the lean fish, only to find that the two lines of fish managed their glucose levels equally well. The fat fish also expressed more of the genes involved in fat production, suggesting that they converted excess glucose from their diet into fat in the liver before transporting it to other tissues. And when they analysed the gene expression pattern in the liver, they realised that the fat fish expressed more of the genes involved in producing the healthy omega-3 fatty acids, which are an essential component of the human diet. However, when they analysed the gene expression patterns in the fat fish's muscle and fat, neither tissue overexpressed genes involved in glucose metabolism, suggesting that they are not adapted to metabolise carbohydrate from their diet.

Finally, Kamalam analysed the activation by phosphorylation of two other proteins – one involved in nutrient sensing (mTOR) and the other involved in energy sensing (AMP kinase) – in the fish lines and found that the livers of the fat and lean fish are both able to use carbohydrate as an energy source. 'The preferred substrate of carnivorous trout will still be protein and lipids, but when we need to substitute the protein and lipid content of the diet with carbohydrates, they can adapt', says Kamalam. 'We think trout can't use much carbohydrate, but we provide evidence that they can use optimal levels of carbohydrate and use it for an energy substrate', he adds.

10.1242/jeb.075747

Biju Sam Kamalam J, Medale, F., Kaushik, S., Polakof, S., Skiba-Cassy, S. and Panserat, S. (2012). Regulation of metabolism by dietary carbohydrates in two lines of rainbow trout divergently selected for muscle fat content. *J. Exp. Biol.* **215**, 2567-2578.

Kathryn Knight

ANTS' SLOPE-SCALING COSTS

Watching frenetic leaf-cutter ants wielding chunks of leaf, nothing seems to get in their way; but even industrious leaf-cutter ants may opt to not take routes that incur sizeable metabolic costs. 'If you put an obstruction in front of an animal that increases the energetic costs, then it becomes a behaviour consideration as to which way the animal should go. Should it take the shortest route, which is straight over the hill but encounter steep gradients or should it go on longer routes and encounter shallower gradients?' queries Graham Askew from the University of Leeds, UK. Intrigued by the energetics of animal locomotion, Askew decided to identify the factors that influence the decisions taken by leaf-cutter ants while negotiating obstacles. Teaming up with graduate student Natalie Holt, Askew decided to measure the metabolic cost of climbing and descending slopes for leaf-cutter ants in order to begin to understand how the animals select routes (p. 2545).

However, Askew admits that measuring the minute amounts of carbon dioxide exhaled by the tiny insects was technically challenging. Designing a 30 cm long tube that could be inclined at a range of angles for the insects to run up and down, Askew and Holt used a recirculating air system to measure the miniscule quantities of carbon dioxide exhaled in the tube by the ants during their exertions. Allowing the ants to run at their own speed, the duo also rotated the tube when the insect reached the end so that it could continue running at the same angle until they had a reliable reading of its metabolic rate. Inclining the tube at 30 deg increments ranging from a vertical ascent to a horizontal run and finally a vertical descent, the duo filmed the ants' progress and recorded their metabolic rates.

Not surprisingly, the ants' speed fell dramatically as the angle increased, dropping from a speedy 2 $cm\,s^{-1}$ on the level to 0.7 $cm\,s^{-1}$ when scaling a precipice. Yet, when the duo analysed the insects' metabolic rates over the entire range of ascents and descents, they found that the insects all worked at the same metabolic rate. No matter which angle the ants were ascending or descending they produced carbon dioxide at a rate of 1.7 $ml\,g^{-1}\,h^{-1}$. 'They are putting in the same effort regardless of gradient', says Askew.

However, calculating the metabolic cost of moving a set distance along the tube, Askew and Holt realised that the insects that were ascending and descending the steepest slopes had the highest metabolic costs per unit distance. 'They are trying to maintain a constant metabolic rate. They do that by modulating speed and the consequence of that is that the cost per unit distance increases at the steepest gradients', says Askew.

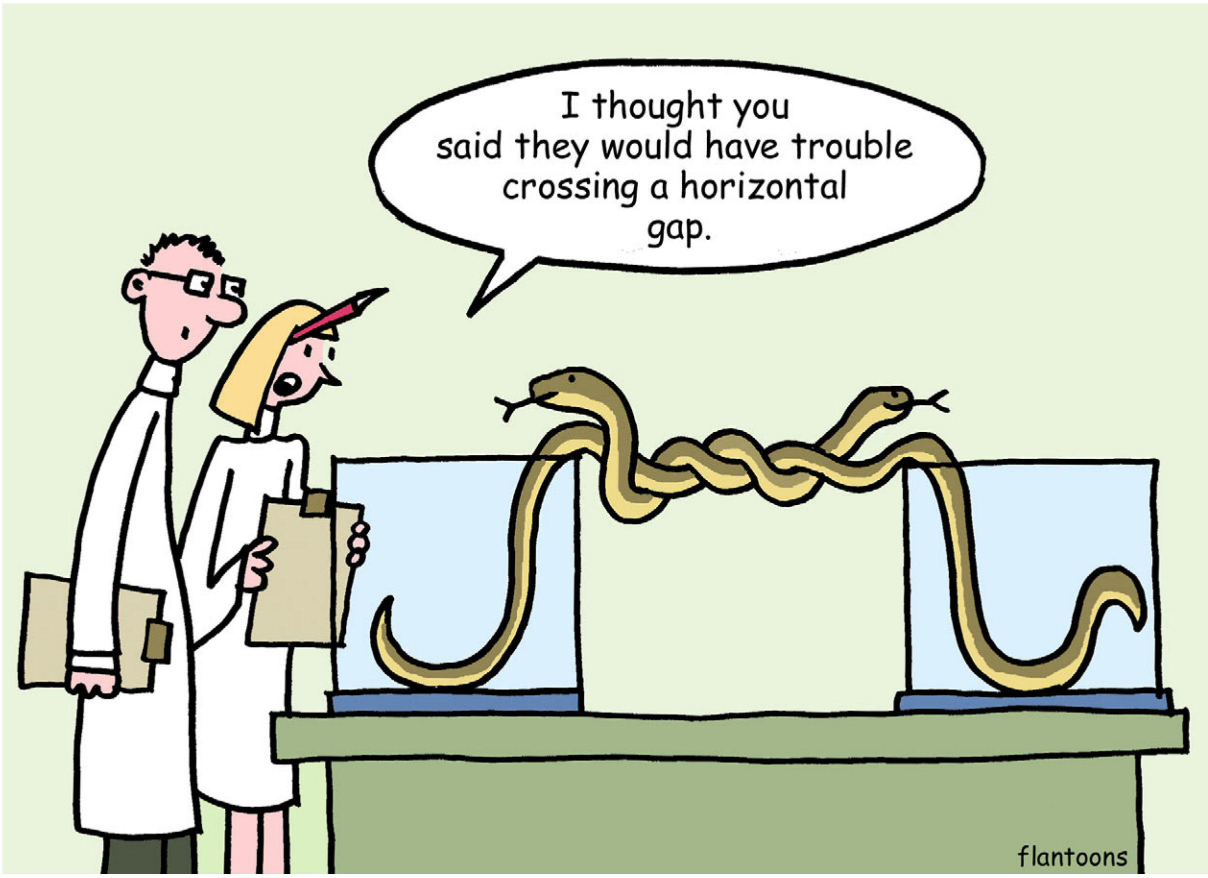
Finally, the duo calculated the vertical cost of locomotion over the range of ascents and descents. Explaining that insects have to trade off taking a shallower gradient – where the cost of locomotion is less but it takes longer to complete because it is farther – against a shorter route with a steeper gradient – which takes less time but at a higher cost of locomotion – Askew says, 'The vertical cost of locomotion tells you the optimal gradient at which the animals can gain height for the minimal energy expenditure'. Calculating the vertical cost of locomotion for ascent and descent, the duo found that the descending ants should select gradients between –45 and –51 deg, while climbing ants should select gradients ranging from 51 to 57 deg to minimise their time and energy expenditures. And Askew is keen to find which paths and gradients the ants select in practice and how their choices alter with time.

10.1242/jeb.076661

Holt, N. C. and Askew, G. N. (2012). Locomotion on a slope in leaf-cutter ants: metabolic energy use, behavioural adaptations and the implications for route selection on hilly terrain. *J. Exp. Biol.* **215**, 2545-2550.

Kathryn Knight

HOW BROWN SNAKES BRIDGE GAPS



For terrestrial animals, whose lives are firmly anchored on the ground, arboreal lifestyles seem precarious. But brown tree snakes thrive in this complex three-dimensional habitat, stretching and twisting across gaps in the tree canopy to hunt small birds and mammals. Yet, little is known about the stresses and strains exerted on the bodies of these snakes as they slither between branches. Intrigued, Greg Byrnes from Siena College, USA, and Bruce Jayne from the University of Cincinnati, decided to film brown tree snakes as they bridged gaps ranging from simple drops and vertical ascents, to wide horizontal head-on chasms and sidewise steps, to analyse the mechanical forces exerted on the reptiles' sinuous bodies (p. 2611).

The snakes were most successful at negotiating the head-on vertical climbs and drops, straddling gaps that were 65% wider than head-on horizontal gaps. And when they compared the snakes' ability to span sideways gaps – where they had to twist by 90 deg – with head-on gaps, the snakes were able to cross head-on gaps that were 13% larger than the equivalent sideways gap. Some snakes even negotiated gaps that were longer than their bodies, by manoeuvring their heads close to their destination perch before lunging to cover the last few centimetres.

Calculating the torques – turning forces – exerted on the snakes' bodies as they precariously extended their heads, the duo says, 'The orientation of the gap significantly affected all of the estimated torques'. Effectively, the snakes found sideways horizontal gaps harder to bridge than sideways steps – where they had to rise to reach the perch – while the sideways horizontal gap was the hardest of all to cross. The duo suggests that the snakes' ability to traverse gaps is restricted by their ability to keep their bodies rigid and the large torques that threaten to topple them when extending across the gaps.

Considering the snakes' agility in conservation terms, the duo explains that brown tree snakes were inadvertently introduced to the island of Guam after the Second World War. Since then, they have proliferated unchecked, decimating the island's indigenous bird and small mammal populations. Given that the Guam snakes can reach 3 m in length, Byrnes and Jayne warn that the snakes could be capable of spanning 1.5 m wide horizontal gaps and 2.2 m vertical gaps. They recommend that vegetation should be trimmed, producing chasms that are too wide for the animals to bridge if the island is to prevent their dispersal to other vulnerable locations.

10.1242/jeb.076646

Byrnes, G. and Jayne, B. C. (2012). The effects of three-dimensional gap orientation on bridging performance and behavior of brown tree snakes (*Boiga irregularis*). *J. Exp. Biol.* **215**, 2611-2620.

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