INSIDE JEB

Reversing ants navigate successfully

Cataglyphis ant dragging a dead spider backwards. Photo credit: Matthias Wittlinger.

Scampering across the salt pans of Tunisia on their spindly legs, desert ants (*Cataglyphis fortis*) have a single-minded mission: locate food and get it back to the nest. Normally, individual raiders bear a tasty morsel in their mandibles and navigate home along the most direct return route, regardless of how tortuous the outbound journey was. However, their determination is often tested to the extreme when the robust animals stumble upon a particularly large piece of food – such as a dead spider or locust. Undaunted, the scavenger simply drags the feast backwards: 'They are really awesome', chuckles Matthias Wittlinger from the University of Ulm, Germany. However, how do the insects navigate while reversing? 'All the cues are from the other direction', says Wittlinger. Puzzled, Wittlinger and his colleagues Verena Wahl and Sarah Pfeffer travelled to their field site in the Tunisian desert to try to find out how the ants locate home while reversing with a heavy load.

Having tempted ants from their nest with a nearby pile of alluring biscuit crumbs, the scientists set the enthusiastic foragers a challenge. Abducting individuals as they arrived at the feeder, the trio transported the ants to a long metal channel lying parallel to the direction that they would turn to return home and presented them with a colossal biscuit crumb, weighing 10 times more than the ant itself: 'They say, "Wow, there is a large food item, let's get home"', chuckles Wittlinger. While filming the ants as they heaved the large lunch, the team quickly realised that they were onto something unexpected. Instead of weaving rhythmically from side to side as they would if they were using their normal tripod gait – always keeping three legs in contact with the ground as the other three swing forward – the ants' overall movement appeared less coordinated; they were not simply reversing their normal forward walking pattern. And when the ant reached the point at which they would expect to locate home in the metal channel, they performed a U-turn, indicating that they knew how far they had travelled, despite moving backwards. Their odometer was functioning regardless of their erratic walking style. Amazed, Wittlinger and Pfeffer began dissecting the fine details of the ants' reversing technique.

Pfeffer filmed the ants with a high-speed camera at 500 frames s^{-1} and saw that the reversing ants walked at about the same step rate as when they moved forward, about 10 strides s^{-1}. However, she says, 'Each leg was acting on its own', adding that they had completely done away with the conventional three-legged walk. She also noticed that they had increased their contact with the ground, 'They do it by faster swings and they often use leg combinations where more than three legs have ground contact to increase their static stability' she says.

Recalling the discovery, Wittlinger says, 'we have been trying for years to make them walk in a non-tripod way', in the hope of learning how they measure distances; now he had the perfect opportunity. 'There are a couple of hypotheses of how a stride integrator [odometer] would work', he says. 'One is that they would use an efferent copy of the motor signals [and sum the signals to calculate a distance], and the other one would be that they actually use each single stride and measure each stride amplitude, or the length of the stride or the swing'. Because the ants were able to determine precisely how far they had travelled, even though each leg was moving individually, Wittlinger says, 'The data suggest it is the second hypothesis'.

But Wittlinger and Pfeffer were still none the wiser about how the reversing ants managed to navigate when all of the visual and odour cues that they use to locate home were in the wrong position. 'We painted a white grid onto the desert floor and then we released the ant with a large food crumb [and] it walked towards the fictive nest site', says Wittlinger, who manually tracked the ant's progress with Pfeffer. However, the duo was surprised that the reversing ant periodically put down its cargo and began searching in a loop, before returning to the morsel and resuming its homeward journey. 'We think that this behaviour probably helps the ant to orientate. The early search loops are normally very short and often directed to the fictive nest site, and probably they scan the panorama searching for some cue', says Pfeffer.

So plucky *Cataglyphis* desert ants are able to navigate successfully while reversing, and now Wittlinger and Pfeffer are keen to learn more about how the animals use information gleaned during reconnaissance when they discard their precious cargo while reversing home.

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Kathryn Knight

Hot, thirsty bees motivate water collectors by begging

Madeleine Ostwald observing the hive. Photo credit: Tom Seeley.

Thirst is a sensation that we can all relate to; however, dealing with this basic physiological impulse takes on a whole new dimension when an entire bee colony craves water. 'We are interested in the social physiology of honey bee colonies, that is, how they work as physiological units', says Thomas Seeley, from Cornell University, USA, who was curious how the elderly bees that are tasked with gathering water know when the colony's collective thirst is

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running high. ‘Water collectors do not spend much, if any, time in the broodnest, and yet somehow they know when to start collecting water to control its temperature’, explains Seeley. Intrigued, the scientist and his colleagues Madeleine Ostwald and Michael Smith turned up the heat to make a bee colony thirsty.

Bees use three mechanisms to cool an overheated hive – nest evacuation, fanning with their wings and water evaporation – so Seeley and his colleagues raised the temperature in a glass-walled hive by positioning a lamp close to the broodnest to see how the bees responded. However, the water collectors did not spring into action immediately. It was only when the workers began desperately begging for water – by walking up to the face of another bee, contacting the bee’s antennae with her own and then extending her tongue between the mouthparts of the other bee – that the water collectors increased their water-bearing activity. By begging more, the thirsty nurse bees in the broodnest had prompted water collectors to embark on water-collection flights and the hive managed to stabilise its temperature at around 40°C.

The team then removed the nearby water supply for 2.5 h to find out how the hive coped, and this time the temperature soared dangerously to almost 44°C. ‘The water collectors continued visiting the empty water source, which they probed feverishly but unsuccessfully’, recalls Seeley. Ostwald and Smith also gauged the colony’s thirst by pipetting a 0.2 ml puddle of water onto the floor of the hive, which the bees gulped down in just 46 s – in contrast to the well-hydrated cool bees from earlier in the day, which took almost 5 min to drain the puddle. Despite increasing the air flow through the hive by recruiting more fanning bees and evacuating workers, the thirsty bees were unable to use evaporation to keep the hive cool. However, when the team returned the hive’s water supply 2.5 h later, the water collectors’ delivery rate skyrocketed, from 3.2 g 30 min^{-1} (when the hive was cool) to 22.8 g 30 min^{-1} as the colony satisfied its thirst; which is impressive when each bee can only carry 50 mg of water per excursion. Some even performed waggle dances to recruit additional water collectors.

Finally, the team set the bees another challenge when they warmed the hive briefly while providing unrestricted access to water before gathering bees later the same day to analyse their crop contents and the contents of brood cells. ‘We had to open the hive in the evening and then pluck bees, one-by-one, off the combs, and squeeze their abdomens so that they would regurgitate their crop contents to get data’, recalls Seeley, who narrowly avoided being stung in the eye by the disturbed insects. However, the team’s courage was rewarded when they discovered that the hive was stock-piling water in the brood comb. In addition, many of the bees had bulging abdomens full of water. ‘We called them the “water bottle bees”’, chuckles Seeley, who is now keen to find out whether water collector bees are also motivated by their own personal thirst.

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Surfing trout foiled by widespread obstacles

Rainbow trout (*Oncorhynchus mykiss*). Photo credit: Ken Hammond/USDA [public domain], via Wikimedia Commons.

Weaving their bodies from side to side while they take refuge behind an obstacle, most fish look as if they are working hard to stay put, whereas in fact they may just be surfing. James Liao, from the University of Florida, USA, explains that as water flows past an object, alternating vortices are shed from the structure, forming an oscillating jet of water that can sweep the fish’s body back and forth as they maintain a stationary position behind the object. Explaining that this specialised pattern of movements is known as the Kármán gait, Liao says, ‘they literally let the water currents swim their body instead of powering it with their muscle’, adding that Kármán gaiting fish drop their energy consumption by half as they joyride the obstacle’s wake. However, life in real rivers is rarely so simple, and he admits that interpreting the flow in such cluttered environments is extraordinarily challenging. So, instead of investigating how wake-surfing fish interact with the complex flows generated by tangled rocks and roots, Liao and his colleagues decided to analyse the wake generated by a pair of cylinders in a stream and find out how fish exploit this fluid motion to hold their position in more cluttered conditions.

Christina Walker and Liao selected trout that were just under 20 cm long and filmed them as they swam in water flowing at speeds from 20 to 120 cm s^{-1} behind a pair of 5 cm diameter D-shaped obstacles that were in line and separated by 1–11 cm. The trout adopted the characteristic Kármán gait weaving motion when the cylinders were closely spaced. However, as the separation between the cylinders increased, the fish performed the specialised motion less often.

Curious to find out why the fish were more reluctant to surf behind more widely spaced cylinders, William Stewart viewed the fluid motion behind the pair of objects and analysed the turbulence with Otar Akanyeti. Together, they saw that the obstacles produced a pattern of turbulence that was most similar to that of a single object when they were closely spaced; however, as the separation increased, the pattern of alternating spinning vortices that is essential if a fish is to remain in place became more degraded. And when Fang-bao Tian simulated the interaction between the vortices shed by the two cylinders, he and Stewart found that the turbulence generated by the upstream cylinder disrupted the spinning vortices produced by the cylinder at its rear as the separation increased, effectively destroying the clean flow pattern that was crucial for the fish to maintain its wake-surfing position.

‘Objects placed close together have stronger, more organised wakes that fish can identify and use… while widely spaced objects shed messy wakes that discourage Kármán gaiting’, says Liao, and he adds, ‘This study puts on the radar how important it is to consider how fish can exploit the wakes behind multiple objects to save in the cost of swimming’.

10.1242/jeb.145458

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Blue tit chicks from small nests develop endothermy faster

Huddled together in a nest for the first 3 weeks of their lives, tiny, defenceless blue tit chicks rely on their siblings and parents for warmth. The birds' minute muscles are too small to generate heat through shivering, although by the time the chicks are ready to fledge, they are mature enough to generate their own warmth. Fredrik Andreasson, Andreas Nord and Jan-Åke Nilsson, from Lund University, Sweden, explain that several factors, such as the nestlings' growth rate and development of plumage, affect when the youngsters develop the ability to maintain a stable body temperature. However, growing up in a large brood can reduce the amount of food available to a developing chick, despite reducing the urgency with which a chick must develop endothermy thanks to the insulation and warmth provided by family members, so Andreasson and his colleagues wondered how being reared in small and large families might affect the rate at which chicks develop the ability to regulate their own body temperature.

After reassigning blue tit chicks from the shores of Lake Krankesjön, Sweden, between broods to create large (15–16 chicks) and small (5–6 chicks) nests, the team then measured how the developing birds managed their body temperature when they placed individuals in a chilly cup for 5 min periods from the ages of 4–10 days. Even at the youngest age, the birds from the smaller nests coped better than the birds from the larger nests, which cooled 46% more (~0.6°C $g^{-0.67}$ min^{-1}) than the birds from the smaller nests (~0.4°C $g^{-0.67}$ min^{-1}). However, by day 10, chicks from both the large and small nests were all able to hold their temperature better and only cooled at ~0.1°C $g^{-0.67}$ min^{-1}. And when the team checked the temperature in the chick's nests, the larger broods were warmer (37.9°C) than the smaller broods (37.1°C). So nestlings from smaller broods developed endothermy faster than chicks from larger, warmer families, and the team says, 'We suggest that the development of endothermy in blue tit nestlings is not ontogenetically fixed, but instead may vary according to differences in developmental, nutritional and thermal conditions as determined by brood size'.

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