INSIDE JEB

Suspended walking lemurs shift weight forward



Ruffed lemur (*Varecia variegata rubra*). Photo credit: David Haring.

Balancing on a skinny branch is tricky for most animals at the best of times. Although small lizards and snakes have few problems, larger primates may struggle to remain erect as they clamber on slender supports. But some primates seem to have got round the problem by simply slinging their bodies from all four limbs beneath branches. Michael Granatosky, Cameron Tripp and Daniel Schmitt from Duke University, USA, describe how this bizarre form of locomotion appears remarkably similar to walking on all fours and add that the unconventional orientation may have provided an essential evolutionary stepping stone for animals that eventually began swinging through the trees on two arms. However, Granatosky says, 'While many studies have explored the anatomy of suspensory species, no study has compared the movements of animals that walk below branches with all four legs versus those that swing with just the forelimbs'. Intrigued by the unconventional inverted motion, the trio set two species of lemurs - the ringtailed lemur that prefers to walk on the ground and the ruffed lemur that frequently suspends itself from all four limbs – the task of trotting along a pole and then slinging themselves beneath it to find out how the two forms of motion compare.

Rigging up a pole with sections attached to force plates to measure the forces exerted by the animals, Granatosky and Tripp then enticed the lemurs to proceed along the pole as they filmed the animals' movements. However, Granatosky admits that convincing the cunning animals to suspend themselves from the pole was easier said than done. 'At first we tried covering the runway with fruits, but most of the time the lemurs just knocked the food off and ate their meal on the ground', he recalls. Eventually, the team enticed the animals to hang beneath the pole by hanging some fruit below it. 'Once they learned that being upside-down means treats, it was smooth-sailing from there', he chuckles.

Having collected force measurements for 303 foot contacts as the lemurs advanced along, the duo dissected out the different force components to find how the two styles differed. And when the results were in, they were pleased that despite first appearances, the suspended form of walking was completely different from a conventional lemur stroll.

Describing how the animals elegantly picked their way along the pole while walking on the top surface, the team explains that the animals carried most of their weight on their hindlimbs, which also produced the forces that propelled them forward. However, the team was impressed to see this pattern reversed when the animals slung themselves underneath, with the lemurs using their arms to pull themselves forward in addition to taking most of the weight. They explain that this switch to forelimb weight bearing is unusual in primates, as most carry their weight on their hindlimbs to free their hands to manipulate food and other objects. However, they also point out that this load-bearing shift could have driven the evolution of specific adaptations to the limbs that would then allow them to begin swinging through the trees using their forelimbs alone.

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Granatosky, M. C., Tripp, C. H. and Schmitt, D. (2016). Gait kinetics of above- and below-branch quadrupedal locomotion in lemurid primates. *J. Exp. Biol.* **219**, 53-63.

Kathryn Knight

Juvenile hormone triggers forager switch in leafcutter ants

The Company of Biologists



Acromyrmex octospinosus leafcutter ant fungus chamber. Photo credit: Victoria Norman.

It takes all sorts of characters to build a city, and insect colonies are not that different from our own metropolises. Some residents perform caring roles while others provide defence or infrastructure, although few insects stay in a role for life. For example, honeybee workers perform a wide range of tasks - from cell cleaning and nursing when young to foraging in later life – and many of these transitions are controlled by juvenile hormone, which regulates growth. However, Victoria Norman and William Hughes, from the University of Sussex, UK, explain that little is known about the role of juvenile hormone in defining a place in society for other insect species. 'Direct experimental evidence for the influence of juvenile hormone outside of the honeybee model system is lacking', they say. So, the duo decided to find out how doses of juvenile hormone affect the behaviour of leaf-cutting worker ants.

Having gently applied six minute dabs of juvenile hormone to the back of young nurse ants over the course of a fortnight, Norman tested how the hormone affected each insect's behaviour by filming their activity and was impressed to see that they were significantly more active than ants that had received a dab of fake hormone. And when she tested their response to light, the hormone-treated ants were much happier spending time in the light, while the untreated ants preferred to shelter in the dark. Next, Norman checked the hormone-treated ants' reactions to an imposter by touching their antennae against the body of an ant from another species and found that the

hormone-treated ants were much more aggressive towards the trespasser than towards the untreated ants. And finally, when Norman introduced the hormonetreated ants into a mini nest full of workers tending fungus, the hormonetreated ants had no interest in sticking around to help with the cultivation, preferring to head out of the nest instead. The workers were behaving more like foragers, while the ants that had not received juvenile hormone treatment continued behaving like nest-bound workers. In short, juvenile hormone seemed to have caused the workers to transform from timid workers into fierce, more outgoing foragers.

'This is the first experimental evidence of the effect of juvenile hormone on division of labour in ant societies', say Norman and Hughes, and they add, 'This suggests that juvenile hormone may have a highly conserved role as a key endocrine mediator of division of labour within eusocial insect societies that has been key to their ecological and evolutionary success'.

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Norman, V. C. and Hughes, W. O. H. (2016). Behavioural effects of juvenile hormone and their influence on division of labour in leaf-cutting ant societies. *J. Exp. Biol.* **219**, 8-11.

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Striped catfish lose the plot in low CO₂ water

As the politicians keep on squabbling over the best ways to alleviate climate change, and CO₂ emissions continue rising, much of the gas ends up in our oceans and rivers. At first glance, it didn't seem as if this gradual acidification was going to pose a problem for the planet's fishy residents. Matthew Regan from the University of British Columbia, Canada, says, 'They are well prepared physiologically and



Striped catfish (*Pangasianodon hypophthalmus*). Photo credit: Sjannie Lefevre.

biochemically to tolerate even the most depressing of future CO₂ projections'. However, more recently it has become apparent that fish that have been exposed to future levels of CO2 experience behavioural problems: in addition to becoming hyperactive and bolder, they also suffer visual disturbance and anxiety, and are attracted to predators. The associated mild chemical imbalances in the fish's bodies affect their inhibitions. Following on from this discovery, Sjannie Lefevre and Göran Nilsson from the University of Oslo, Norway, wondered how fish that already reside in water with high CO₂ would cope if the situation was reversed and they were transferred into normal (low CO₂) water?

Teaching at a graduate course on airbreathing fish in 2014 organised by Mark Bayley at Can Tho University, Vietnam, Lefevre and Nilsson had the ideal opportunity to address the conundrum. The Mekong Delta is home to the striped catfish (*Pangasianodon hypophthalmus*), which thrives in high-CO₂ water. So, with a flourishing aquaculture industry on hand to supply the fish and a team of enthusiastic students available to run the experiments, they were in the perfect place to test the fish's reactions to low-CO₂ water.

Collecting fish provided by Do Thi Thanh Huong and Nguyen Thanh Phuong from a nearby farm, Regan and his fellow students Andy Turko, Joe Heras and Mads Kuhlmann Andersen transferred some of the animals into low-CO₂ water, while the rest remained in high-CO₂. Then, with the help of Colin Brauner and

Tobias Wang, they began testing the fish's reactions to a range of situations, from the arrival of an unfamiliar object (a brick) in their surroundings to how much time they spent schooling with their own kind, to find out how the water conditions had affected their behaviour.

Not surprisingly, striped catfish that resided in their habitual high-CO₂ conditions showed all of the usual reactions to unfamiliar situations, avoiding the frightening brick and remaining out of reach of a threatening predator. However, the fish that had been held in freshwater began behaving strangely. Not only were they unalarmed by the presence of the predator but also they were unfazed by the arrival of the brick. In addition, they were less attracted to a school of their own species and were much more active. However, when the team gave the low-CO₂ catfish a dose of a drug that counteracts the effects of the GABA neurotransmitter - the neurotransmitter that malfunctions and triggers bold behaviour when fish that normally reside in low CO_2 are exposed to high CO₂ – the emboldened catfish lost their courage and began behaving normally.

So, the GABA neurotransmitter had lost its inhibitory effects in the catfish that had been transferred to low-CO₂ water because of the subtle chemical changes in their brains caused by the alteration in their surrounding water. And Regan suggests that other species may be able to adapt their brains to the brave new world that striped catfish already survive in, provided they can keep pace with change.

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Regan, M. D., Turko, A. J., Heras, J., Andersen, M. K., Lefevre, S., Wang, T., Bayley, M., Brauner, C.J., Huong, D. T. T., Phuong, N. T. and Nilsson, G. E. (2016). Ambient CO₂, fish behaviour and altered GABAergic neurotransmission: exploring the mechanism of CO₂-induced behaviour by taking a hypercapnia dweller down to low CO₂ levels. *J. Exp. Biol.* 216, 109-118.