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INSIDE JEB

Pseudoscorpions tweak quartet footfalls when hanging, reversing and simply moving forward

A pseudoscorpion *Chelifer cancroides*.

Open a book in a dusty library and you might be in for a shock if a pseudoscorpion jumps out. Yet these mini arachnids pose no threat, even though they are equipped with the most fearsome pair of pincers. Instead, they subdue and dine on mites, booklice and larvae, and hitch rides on larger insects over long distances. For most shorter journeys, pseudoscorpions are equipped with four pairs of legs, yet no one knew how the tiny arthropods coordinate all eight limbs while moving forward, backward and even upside-down. 'They are capable of locomotion on many different surfaces and substrates', says Johanna Tross from Ulm University, Germany, so she, Sarah Pfeffer and Torben Stemme (both from University of Ulm) decided to scrutinise the manoeuvres of house pseudoscorpions (*Chelifer cancroides*).

'Torben Stemme caught the pseudoscorpions in an old hayloft in his parents' garden', says Tross, who kept the arachnids alive in the lab by feeding them leaf lice. Then, she and Pfeffer measured the insect's proportions, revealing that the impressive claws were approximately 25% longer (~3.9 mm) than the pseudoscorpions' body length (~3.1 mm). 'These oversized claws fascinated us', says Tross. And when she and Pfeffer filmed the animals scurrying around an enclosure, the pseudoscorpions preferred to hug the walls, walking at speeds of 14 m or ~4200 body lengths per hour – the equivalent of a brisk human walk. The dashing animals also appeared to take brief pauses as they scampered along – so brief they were barely perceptible (100–200 ms) – probably to allow them to take stock of their surroundings with their sensitive claws as their vision is so poor.

But what about the fine details of the pseudoscorpion's nimble footwork? This time, Pfeffer and Tross used Harald Wolf's Ulm University high-speed camera to film 65 arachnids as they walked forward and backward along an aluminium channel, as well as upside down on a piece of Perspex placed across the top of the channel. Impressively, the animals were 33% faster (~40 mm s^{-1}) when going backwards than when travelling forward (~30 mm s^{-1}), probably because the animals reverse when making a hasty exit, holding their claws wide ready to attack. And when the team analysed the creatures' footfall patterns, it was clear that they kept four feet in contact with the ground most of the time, alternating between one quartet of limbs – the first and third on one side and the second and fourth on the other – and the opposite quartet as they scampered along. In fact, the pseudoscorpions rarely deviated from this basic footfall pattern, no matter how fast they moved, in which direction and whether they were suspended from above, unlike humans and four-legged creatures, which switch gaits from running, walking and trotting to galloping as they shift up through the gears.

However, the amount of time the pseudoscorpions' feet remained in contact with the ground, and how well coordinated they were, varied depending on where and in which direction the animals were moving. The leg quartets were the most coordinated when walking forward, while the upside-down pseudoscorpions kept their feet in contact with the surface they were suspended from almost three times longer and took shorter strides. It was also apparent that the second pair of limbs is crucial for the creatures' stability, remaining in contact with the surface longest, especially when they are clinging upside-down.

So, pseudoscorpions stick with the same basic footfall pattern, regardless of how fast or in which direction or dimension they are moving in, but tweak how long they remain in contact for stability and stickability.

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Tross, J., Wolf, H., Stemme, T. and Pfeffer, S. E. (2022). Locomotion in the pseudoscorpion *Chelifer cancroides*: forward, backward and upside-down walking in an eight-legged arthropod. *J. Exp. Biol.* **225**, jeb243930. doi:10.1242/jeb.243930

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