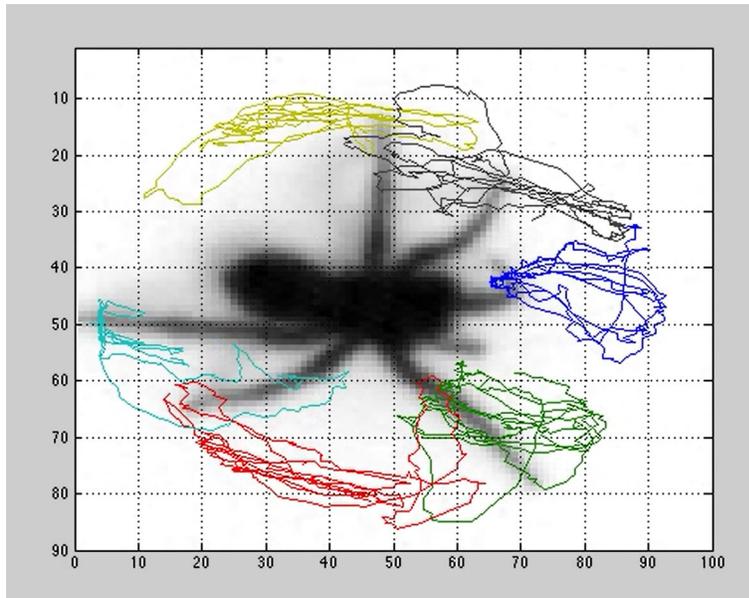


INSIDE JEB

Versatile wolf spiders limp or switch steps after limb loss



A wolf spider that is missing two limbs, with traces of the positions of each foot over the several strides. Photo credit: Andrew Spence.

While many bipeds and quadrupeds are capable of limping by on a reduced number of limbs, some creatures are actively prepared to shed one or two for the sake of survival. Crustaceans, arachnids, reptiles and a host of other creatures can eject (autotomise) limbs and other appendages when under attack. Having previously investigated the impact of tail loss on the mobility of lizards, Tonia Hsieh from Temple University, USA, was intrigued by the effect that misplacing entire limbs would have on invertebrates. Discussing the problem with Andrew Spence and Simon Wilshin, who were then at the Royal Veterinary College, UK, and Cornell University graduate student Paul Shamble, Hsieh wondered how spiders that have lost limbs adapt to life on fewer feet.

Most walkers tend to keep alternate feet in contact with the ground during a stride – arachnids usually balance on four alternate feet arranged in a quadrilateral, while six-legged beetles and cockroaches are stable on a tripod of limbs. Would the spiders that had been deprived of two

limbs attempt to maintain the same quartet footfall pattern and simply limp along on the reduced number of legs, or would they switch to walking like six-legged beetles?

Focusing on wolf spiders, which readily drop their limbs when gripped by a threat, Ryan Harris began scouring the veterinary college grounds in search of the voracious predators. ‘Capturing the spiders involved searching through the long grass with sample pots, while receiving confused looks from dog walkers’, he recalls. Back in the lab, Harris, Wilshin and Shamble filmed the spiders scampering around a Perspex arena, before carefully removing the left foreleg and right rearmost leg of each animal, leaving them with three legs on each side. ‘Simon suggested choosing the first and fifth limbs because this combination is on the same quartet of feet... This means that should the spiders keep moving their limbs in the same manner after losing two legs, they would be performing a very undesirable gait with only two legs in contact with the

ground for half the cycle’, explains Spence.

After filming the arachnids, Kyle Hovey painstakingly digitised over 80% of the movies, identifying more than 700 sequences that included at least three complete spider strides. The team eventually analysed 209 dashes and realised that the spiders preferred scuttling like six-legged beetles, completing 151 tripod style sprints. However, in 58 of the movies, the spiders had stubbornly stuck with their quartet footfall pattern, despite lacking two limbs. ‘The spiders were “limping”’, says Spence. The spiders maximised the time they were in the most stable position on four legs and took a quick step forward when balanced on two feet alone; Hsieh describes the movement as looking like ‘foooour–two–foooour–two–foooour’.

Even though spiders are usually ‘hard-wired’ to walk using limb quartets, they are capable of altering the order of their footfalls to make beetle-like tripod strides when necessary, and can even change the timing of their conventional quartet walk when they need to limp along on two limbs alone. The team was also impressed that the agility of the versatile arachnids appeared unaffected, as the amputees were as fast as they had been before the loss and could also maintain a straight course.

Having discovered how adaptable spiders are, the team is eager to design a robot that copes as well with limb failure as wolf spiders, and Hsieh is keen to find out how other spiders adapt to life on fewer legs. ‘I want to know: what is the algorithm that allows them to discover rapidly a novel, stable gait?’, she says.

10.1242/jeb.189936

Wilshin, S., Shamble, P. S., Hovey, K. J., Harris, R., Spence, A. J. and Hsieh, S. T. (2018). Limping following limb loss increases locomotor stability. *J. Exp. Biol.* **221**, jeb174268.

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