## Snap! Trap-jaw ants in Borneo also jump using their legs

Awide variety of animals jump – kangaroos, frogs, grasshoppers, and even humans – but one rarely sees this behavior in ants. Only three out of 326 ant genera (Bolton 2014) are known to jump using their legs: *Gigantiops* (Formicinae) in tropical South America, *Harpegnathos* (Ponerinae) in Southeast Asia, and *Myrmecia* (Myrmeciinae) in Australia, New Zealand, and New Caledonia. However, other ants have evolved the ability to jump by using their jaws.

These so-called trap-jaw ants snap their jaws – specialized elongate mandibles also used to catch prey – closed onto a hard surface to propel themselves backwards and escape threats (Wheeler 1922; Patek *et al.* 2006). This behavior has been best-studied in *Odontomachus* and *Anochetus* (Ponerinae), two closely related genera, but there are a few references (Mayr 1887; Biró 1897; Creighton 1937) from a third unrelated genus, *Strumigenys* (Myrmicinae). These tiny ants can jump as far as 47 cm, over 100 times their body length (Biró 1897). This curious behavior has not been mentioned in the literature since 1937 and may be rare, or else seen but not reported.

In 2011, I received a grant to study trap-jaw ants along elevational gradients in Borneo. I focused on a common species in Southeast Asia, *Odontomachus rixosus* (Figure 1). These ants are relatively large (1.3 cm) and live on the complex forest floor. As part of the project, I was mapping nests and collecting individuals. One of my first field sites in Borneo was at Niah National Park, located



Figure 1. Odontomachus rixosus worker.

in the heart of Sarawak. Upon discovering an O rixosus nest near the river banks in a recently flooded lowland rainforest, my local friend and field assistant Syria Lejau and I crouched down to collect some ants. But then we both froze - these ants were doing something I had never seen before. They were jumping. Forward. I subsequently observed this behavior many times at various locations throughout Sarawak; whenever I disturbed O rixosus nests, in addition to backwards-oriented mandible-jumps, ants would jump from leaf to leaf on the low vegetation and litter surrounding the nest entrance. These leg-powered jumps, spanning several inches, were forward-oriented (Figure 2a), and resembled the leaps of a jumping spider. Video recordings of this behavior are available on YouTube (www.youtube.com/watch?v=lOQgvlAakh4). I could not find any record of leg-powered jumps for this species in the literature.

In 2013, I returned to Borneo to document this newly discovered jumping behavior through a series of field and laboratory observations and experiments. Odontomachus' trap-jaw mechanism is a particularly well developed, hyper-fast motion, reaching speeds of over 60 m s<sup>-1</sup> (Spagna et al. 2008). The ants have two distinct backwards-oriented, mandible-triggered jumps: a "bouncer defense jump" (Carlin and Gladstein 1989) and an "escape jump" (Patek et al. 2006). For the bouncer defense jump, the ants approach a large intruding object and then snap their jaws against it, propelling themselves backwards away from it. For the escape jump, they try to avoid an intruder by shutting their mandibles against the substrate, which propels them vertically into the air. The trap-jaw mechanism almost certainly evolved for prey capture, but over time the ants started using it for jumping as well (Spagna et al. 2009). Trap-jaw-triggered, backwards-oriented jumps generally appear erratic; the ants do not seem to direct their trajectories toward a target but rather try to move away from a threat quickly. As a result, they land haphazardly, often on their backs (Figure 2b).

My research revealed that the previously undocumented leg-powered jumps in *O rixosus* always occurred as a result of disturbance, rather than general locomotion, and were directed at clear targets. I observed the behavior of workers after brushing leaf litter over nests with a wooden stick, and compared the results to undisturbed control nests; I never saw the ants jump unprovoked. In the field laboratory at Mulu National Park in Malaysian Borneo, I was able to induce leg-powered jumping only through targeted disturbance (ie touching the ant's legs). I also investigated whether ants relied on visual cues to orient their leg-powered jumps by presenting 12 ants from nine nests with a high-contrast and a low-contrast target. I disturbed the ants for 10 minutes and logged each jump. In total, I recorded 2825 jumps, 96% of which were forward-oriented leg-jumps, while the remainder were backwards-oriented. mandible-triggered jumps. On average, when performing leg-powered jumps the ants showed a slight preference to jump onto a dark rather than a white surface (ca 60%).

The evolution of two distinct jumping behaviors in O rixosus is surprising. Why has a second jumping behavior evolved in this species? Other ant species where leg-jumping has evolved share several characteristics: (1) they are diurnal, solitary hunters that catch live prev and forage in the complex leaf litter (Gigantiops and Myrmecia also forage in the

canopy; see Beugnon et al. 2001; Jayatilaka et al. 2014); (2) they possess relatively large eyes to track arthropod prey; and (3) they jump primarily to escape and to capture prey, although Gigantiops and Harpegnathos also use it for general locomotion (Urbani et al. 1994; Beugnon et al. 2001).

Odontomachus can use mandible-jumping as an escape mechanism when startled, but this gives them little or no control over the direction or distance of their trajectory. When they use leg-jumping instead, there may be an advantage to using a directed motion where individuals land on their feet and are therefore able to make swift headway in a specific direction. Mandible-jumping results in a chaotic landing and is not suitable for this purpose (Figure 2b). Leg-jumping may therefore have evolved as a more efficient escape mechanism to increase fitness or to better traverse the complex leaf litter environment.

In addition to using directed leg-powered jumping to flee from threats, O rixosus may also use it to capture prey. I did not observe O rixosus jumping during prey capture, but such observations would be problematic to document in the field, even if common, because of the difficulty of maintaining sight of individuals in the leaf litter. In addition, prey-capture-related jumps, if they occur, may be inconspicuous, as they are in Harpegnathos where the ants leap forward only short distances (usually about 2 cm) or progress by means of short forward "jerks" (Musthak Ali et al. 1992). So I cannot rule out the possibility that O rixosus' leg-jumping plays a role in prey capture. Successfully capturing live prey also requires strong visual abilities. All other leg-jumping ant species have extremely large eyes and while the eyes of Myrmecia are smaller than those of Gigantiops and Harpegnathos, the eves of Odontomachus are smaller still (WebFigure 1). The eyes of O rixosus are no larger than those of other non-jumping congenerics. In the case of Odontomachus, jumping to catch prey may be less important because of

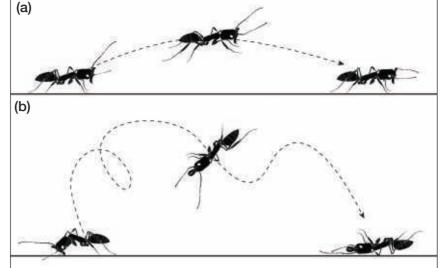


Figure 2. Jumping trajectory of O rixosus in (a) a leg-powered jump and (b) a mandible-powered jump.

their elaborate trap-jaw mechanism, including trigger hairs specifically designed to catch prey items at close range (Gronenberg 1995), which other leg-jumping species lack. However, vision must still play an important role in jumping; otherwise directed jumps like those from leaf to leaf would not be possible.

Finally, it is entirely possible that species other than O rixosus also use leg-propelled jumps. Indeed, several colleagues have since shared anecdotal observations of jumping ants in other genera (outside of the known "jumping ants"). Sometimes it is hard to distinguish between an intentional leg-triggered jump and the directed falls exhibited by many ants. Nonetheless, leg-jumping is probably underreported and may be present in more ant species. If it is, I predict that they will tend to be species living in structurally complex environments such as the forest canopy or a leaf-litter-covered forest floor and that they have excellent vison, like other jumping ants.

## Acknowledgements

This project received funding from the Lewis and Clark Fund for Exploration and Field Research (2011), The Explorers Club Exploration Fund (2013), the Southeast Climate Science Center, and NSF-CAREER (09533390). Acknowledgements are given to Mulu National Park staff, Sarawak Forestry, CA Penick, MW Moffett, AV Suarez, DR Tarpy, AL Traud, and RR Dunn.

## References

Please see WebReferences

D Magdalena Sorger Department of Applied Ecology and WM Keck Center for Behavioral Biology, North Carolina State University, Raleigh, NC (dm.sorger@gmail.com)

