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# Natural history observations and kinematics of strobing in Australian strobe ants, *Opisthopsis haddoni* (Hymenoptera: Formicidae)

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**Abstract**

The strobe ants of Australia (*Opisthopsis* spp.) move with a rapid staccato gait, appearing as if they are under a strobe light. This extraordinary behavior has long caught the attention of natural historians, but the mechanics of strobing locomotion are as enigmatic as its function. We used high-speed video to track the movements of strobing *Opisthopsis haddoni* Emery, 1893 and *O. haddoni rufonigra* Forel, 1910 ants to develop plausible explanations for the phenomenon. We found that strobing involves periodic bursts of rapid acceleration and deceleration. The ants engage in walking with an alternating tripod gait, punctuated by pauses, with a strobing cycle frequency of 5 - 7 Hz. While stopped, ants distinctly tap their antennae on the ground and raise them again before resuming their gait. The peak speeds of strobe ants, at 50 - 60 body lengths per second, are impressive but are only sustained for an infinitesimally short period of time, and overall average speeds are slower due to the prolonged pauses between strobe cycles. We posit that strobing behavior may have evolved as a form of camouflage to move without easy detection or as a tradeoff to maximize high-speed locomotory behavior within the constraints imposed by the spatial and temporal demands for neurosensory processing.

**Key words:** Ants, locomotion, biomechanics, tracking, evolution.

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## Introduction

A year's worth of tropical rain falls over five months in the Top End of Australia's Northern Territory. The wet season had not yet exhausted itself, and during a brief respite from the torrents, the strobe ants burst from their nests fitfully. A glance at their stunning staccato motion, distinct from other more continuous movements of ants in the undergrowth, calls the attention of the observer. Before the rains chased the strobe ants underground, we took the opportunity to bring some of them into the laboratory, to understand how they strobe.

One century ago, William Morton Wheeler visited Australia and characterized the integrative biology of strobe ants, *Opisthopsis* spp. (Wheeler 1918). Since that time, to our knowledge, no aspect of these charismatic animals has attracted further investigation until the present. Without any prior characterization of the biomechanics or behavior of this kind of movement, we entered this project without a working hypothesis to explain the function of strobing. To develop hypotheses for why strobe ants strobe, we seek to understand how they strobe.

Strobing behavior, involving rapid movement punctuated by intermittent brief pauses, is a relatively uncommon mode of locomotion among the ants. Strobing is most conspicuous in all *Opisthopsis* species, endemic to Australasia. Two other lineages that overtly strobe are the pantropical subfamily Pseudomyrmicinae (*Pseudomyrmex* and *Tetraponera)* and the South American species *Gigantiops destructor* (Fabricius, 1804). These ants often perform brief pauses during forward movement without an apparent cause or function. These movements are sometimes referred to colloquially among ant biologists as wasplike.

When ants and other terrestrial hexapods walk, they generally use the standard alternating tripod gait (Hughes 1952, Full & Tu 1990, Zollikofer 1994b). When ants run quickly, they may briefly "trot" with brief intermittent aerial phases, and one extremely fast species, the Sahara silver ant (*Cataglyphis bombycina* (Roger, 1859)), sometimes runs with just four of its six legs (Zollikofer 1994a). The gait that produces the unusual strobing effect is undescribed. By quantifying the mechanics of strobing in *Opisthopsis*, we endeavor to describe an important aspect of their natural history, reveal relevant environmental and physiological constraints that can account for this behavior, and make inferences about the potential function of strobing.

## Methods

Field and laboratory work was conducted in Darwin, Australia, in the CSIRO Tropical Ecosystems Research Centre. Ants were identified using the TERC collection and verified by A.N. Andersen. Most of the work was conducted with

Fig. 1: Photograph of an *Opisthopsis haddoni* worker from the Northern Territory in Australia. Image by Alexander Wild and used with permission.

*Opisthopsis haddoni* Emery, 1893, but *O. haddoni rufonigra* Forel, 1910 individuals were also included for comparative purposes (Fig. 1). Colonies of *O. haddoni* were observed in the field for ca. four hours in varying weather conditions and times of day. Live workers were collected near the laboratory, by placing glass vials over stationary workers outside the nest. Workers were rested for a minimum of five minutes before recording their movements.

Recordings of ant movements were conducted in an apparatus fashioned from a cardboard box, about 400 cm per side. The box was lined with white paper, open on the top and the front, and illuminated with four white LED flashlights, one per corner of the box. Ants were placed adjacent to the focal area near the bottom of the box, and movements were recorded with the high-speed function of an iPhone 6 Plus (Apple Inc., Cupertino, USA). The high-speed video recording feature of this consumer electronics device (including frame rates of 120 and 240 Hz) works surprisingly well in relatively low-light conditions and has been validated as a useful tool to track locomotory and projectile motion (Hechter 2013, Balsalobre-Fernández & al. 2015). Video files were recorded at 240 Hz in 1280 × 720 resolution, and with the camera 12 - 13 cm above the arena, the image of individual ants (~ 4 mm long) measured approximately 50 pixels in length. In two trials, the antennal funiculi from *Opisthopsis haddoni* workers were experimentally ablated, while leaving the scape intact, to evaluate the role of the antennae in the strobing process. Video clips in which individual ants were exhibiting strobing behavior were selected and analyzed to determine the kinematics of their movement. The positions of specific body elements (including thorax center, legs, and antennae) were tracked using ImageJ 1.46r (Rasband 1997) and ant trajectories were tracked as a moving point mass using Physlets Tracker 4.92 (Brown 2009). Lengths and camera perspective were calibrated using the dimensions of a microscope slide in the field of view.

The strobing movements of 13 *Opisthopsis haddoni* workers and three *O. haddoni rufonigra* workers were digitized, with a total of 330 strobe cycles analyzed for timing over 16,602 frames (Fig. 2). Analysis of variance was used to compare the timing of the mean duration of the stationary phases and the mean cycle time. The visualization and analysis of body movement patterns in ImageJ was conducted on a single representative individual using 2007 manually digitized coordinates.

In some trials, gaits of ants were recorded on soot-covered slides which bore the markings where ants contacted the surface with legs and antennae (Hangartner 1969). These marks on the slides were used to observe the tracks left by legs and antennae contacting the surface, to verify that legs and antennae touched the surface where they appeared to do so in the recordings.

## Results

The walking gaits of *Opisthopsis* can be classified into three distinct categories: slow, strobing, and flight. Strobing is the most frequent mode of movement for *O. haddoni*. If the ants are traveling from one place to another, then they may be expected to move with the characteristic strobing gait (see the video in Appendix S1, uploaded as digital supplementary material to this article, at the journal's web page).

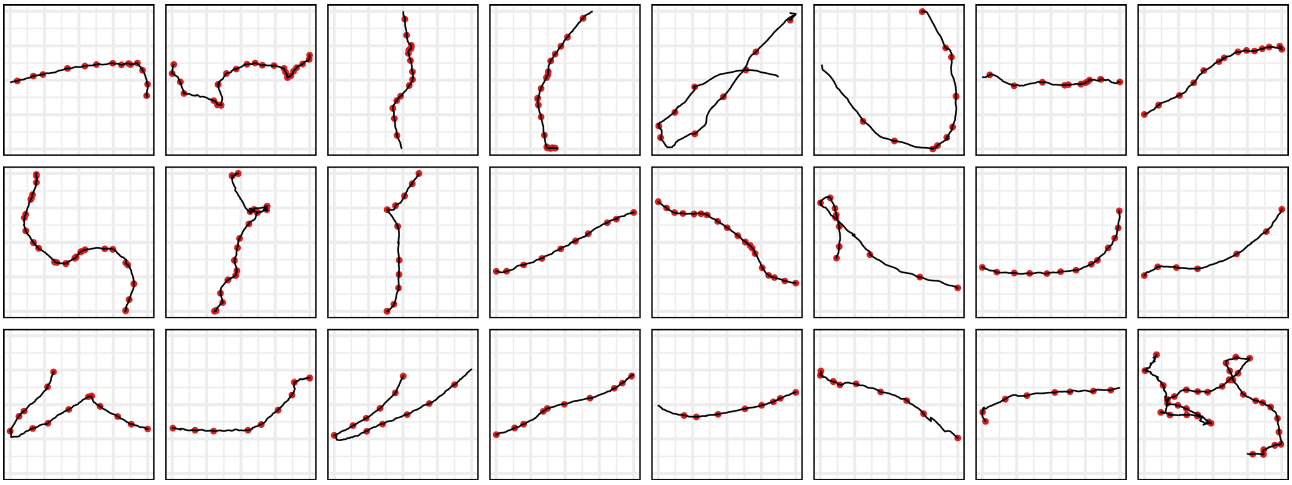

Fig. 2: Tracking the strobing behavior of *Opisthopsis*. Each of these panels illustrates the x - y trajectory of an individual strobing *Opisthopsis* ant. Red dots indicate positions of the paused stage of strobing cycles, as determined by using a drop in their velocity to below 1% of their maximum as a classification threshold. The duration of the displayed tracks spanned 0.53 - 5.6 s, and for clarity the tracks have been scaled to fit the available space, maintaining a fixed 1:1 coordinate system.

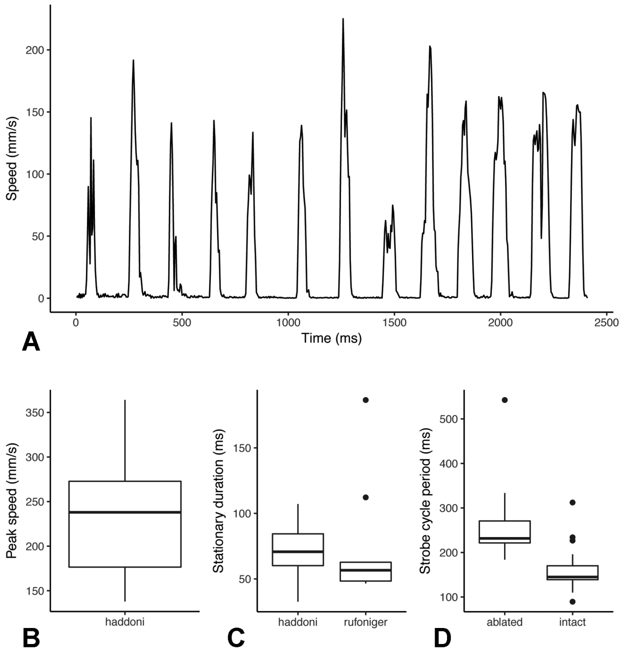

Fig. 3: Kinematics of *Opisthopsis* strobing. Panel (A) shows the speed time series data for a 2.4 s sequence of an individual *O. haddoni* strobing at approximately 5 Hz. The panels below summarize the characteristics of individual strobe cycles across multiple individuals, including their average peak speeds (B), the duration of the stationary period between movements (C), and the duration of the entire strobe cycle period (D).

However, when *O. haddoni* workers are moving slowly, such as loitering around a nest entrance or with an aggregation of workers at a rich food source, then they will not strobe, but walk more slowly with steps that are characteristic of other ants. Flight gait occurs when *O. haddoni* runs at a very high speed but without strobing. Flight typically happens when the vicinity of an ant is directly disturbed, for example, with a shoe, vial, or vertebrate predator. Flight gait lasts for only a few seconds before switching to a strobing gait. When ants are observed undisturbed in the field at a distance, flight gait is rarely observed.

Analysis of the tracking data indicate that the strobing gait of *Opisthopsis haddoni* can be quantitatively characterized as a high frequency intermittent locomotory behavior that involves stationary pauses and bursts of movement (Figs. 2 - 3). Close inspection of the individual leg movements for a single ant's strobing behavior reveals a timing pattern relatively consistent with the alternating tripod insect walking gait (Fig. 4). The general movement pattern between stationary phases involves three steps per strobe, with most instances involving the following sequence: tripod-1, tripod-2, tripod-1, followed by a relatively long pause. Although there appear to be moments during which all six legs are moving (e.g., at times 170, 305, 440, and 455 in Fig. 4), these durations are relatively short and too close to the limit of our temporal resolution (4.2 ms) to make it possible to definitely classify strobing as a true aerial (e.g., jumping or skipping) gait.

The peak speed we recorded, in *Opisthopsis haddoni*, was 364 mm s$^{-1}$. Comparing individuals with intact antennae, the duration of the stationary phase in the strobe cycle was not different between species ($F_{1,12} = 0.01$, p = 0.92) and averaged 63.4 ms ± 21.2 standard deviations (SD). The period of the strobe cycle was significantly different between species ($F_{1,12} = 6.01$, p = 0.03), with the average cycle time of *O. haddoni rufonigra* (189.9 ms ± 40.9 SD) greater than that for *O. haddoni* (143.6 ms ± 26.0 SD). While *O. haddoni* is strobing, it is paused (not moving forward) for 43% of the time. In the trials with ants subjected to ablation of antennal funiculi, compared with *O. haddoni* with intact antennae, there was no difference in the duration of the stationary phase ($F_{1,11} = 1.18$, p = 0.30), but the period of the strobe cycle was longer ($F_{1,11} = 33.64$, p = 0.0001). The strobe cycles of ants with ablated antennae were 271.5 ms ± 47.9 SD long, nearly twice as long as those with intact antennae. Since the stationary durations were the same, the ablated antennae ants were running in longer continuous bouts. During the stationary phase of a

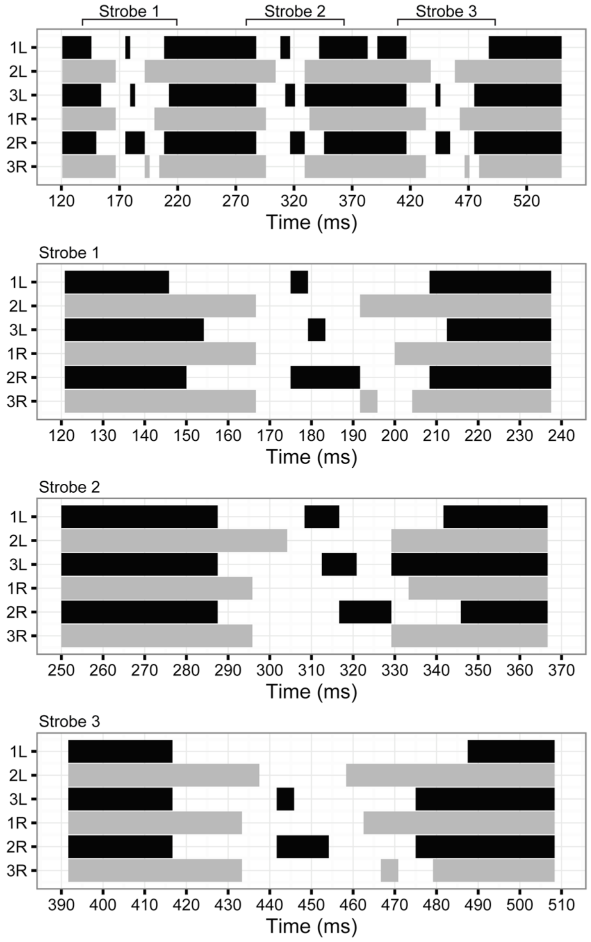

Fig. 4: Alternating tripod gait. By tracking the distal tips of each leg over a strobing sequence for a single ant, we were able to identify its gait pattern based on the classification of leg motion into two distinct tripod groups. Three strobe cycles are illustrated in top panel with a zoom for each depicted in the panels below. Solid shaded horizontal bars indicate periods of time during which a leg is stationary; gaps represent periods of time when a leg is moving. The coordination pattern is consistent with a tripod walking gait with two groups of three legs each. The first group (1L - 2R - 3L, in black) initiates the strobe and is followed by the second (1R - 2L - 3R, in grey).

strobe, the ablated antennae ants continued to wave their antennal scapes downward as if the antennal funiculi were still attached.

The antennae of the workers are touched to the surface during the stationary phase of the strobe cycle, and the distance between the antennae is unchanged, and greater when the ant is surging forward. Individual plots of velocity time series show there is individual variation among trials with different individuals, though the generalized alternating pattern of acceleration and full-stop is consistent for each individual during the observation of strobing gait in a trial.

## Discussion

The strobing gait of *Opisthopsis* is among their most distinctive features. As described above, the uniqueness of this behavior can be characterized by its discontinuous and high frequency (~ 6 Hz) bursts of speed. Although the average walking speed of a strobing ant (~ 36 mm $s^{-1}$) is not remarkable, the peak speeds during the active phase of strobing (~ 225 mm $s^{-1}$ or 50 - 60 body lengths per second) are on par with running *Cataglyphis* and rank below some of the fastest documented insect runners, such as cockroaches and tiger beetles. They are sustained however, only momentarily for small fractions of a second (Fig. 3). One additional distinguishing feature of *Opisthopsis* are their extraordinarily large eyes (Fig. 1). While there are no clear functional hypotheses why some ant lineages have evolved relatively large eyes, at least a few of these genera (e.g., *Pseudomyrmex* and *Gigantiops*) have also been observed moving with a degree of intermittent walking akin to that of *Opisthopsis*. Large eyes might facilitate predator avoidance or prey detection, but the ant lineages with large eyes are not exceptionally unique in predation risk or foraging habits. The rapid bursts of acceleration and deceleration, as in other examples of intermittent locomotion, may be energetically costly, may play a role in predator-prey dynamics, and / or may be associated with svisual or chemosensory information processing (Kramer & McLaughlin 2001).

When tiger beetles, *Cicindela repanda*, are in pursuit of prey, their default mode of pursuit involves fast movements punctuated by brief pauses. While they are capable of continuous pursuit of a moving target, this discontinuous motion is hypothesized to be necessary for the beetle to discriminate the image of the moving target against the image of the background which itself is changing due to the beetle's own high linear and angular velocity. Tiger beetles move so quickly that they lose the ability to have clear vision, and briefly stop to regain a visual image of prey while in pursuit (Gilbert 1997). When tiger beetles lack the ability to visually navigate the landscape, they use antennae to compensate for the lack of information (Zurek & Gilbert 2014). The mean duration of runs between pauses in tiger beetles was 164 ± 25 ms (Gilbert 1997), which is similar to the duration of the individual strobing runs of *Opisthopsis haddoni*.

An alternative and non-exclusive hypothesis for the discontinuous predatory behavior of the tiger beetles is that they themselves are often the object of predation by animals (e.g., lizards) that pursue moving targets but not stationary ones (Gilbert 1997). One of us (TPM) has observed multiple predation events by a jumping spider that mimics *Opisthopsis haddoni*, presumably *Myrmarachne rubra*, which closely associates with the nests of *O. haddoni* (see Ceccarelli 2010). If *Opisthopsis* is subject to high rates of predation by specialized jumping spiders, it is conceivable that strobing has evolved to detect this predator using a combination of visual and olfactory signals. However, since the natural history of *Opisthopsis* is heretofore undescribed, we are not able to put this hypothesis into context.

If *Opisthopsis* spp. are particularly susceptible to a predator that leaves a trace signal on the surface, the stereotyped antennation behavior during strobing events might be the primary function of strobing. In every strobe cycle we observed, the ants discretely came to a full stop, lowered their antennae to the surface, lifted their antennae, and after having antennae in an elevated position, commenced forward movement. The antennation may, or may not, be the primary function of the strobing movement, but it is integral to strobing. Strobing, and the concomitant antennation, occurs both on foraging paths as well as in novel environments. As nearly all ants that follow pheromone trails do not strobe we doubt this can account for strobing. Without antennae, we found that the duration of the stops was unchanged, but the duration of forward movement doubled. This suggests that while sensory feedback may be involved, it is not strictly necessary for the action of a potential strobing central pattern regulator. Intriguingly, similar constraints associated with sensory information processing have also been proposed to explain the strobing behavior exhibited by phorid flies which walk in remarkably similar 5 - 8 Hz stop and go bursts (Miller 1979).

In his account of trying to collect running *Opisthopsis*, W. M. Wheeler reported (1918) that they are "very difficult to catch, as they look backward as well as sidewise and forward and dodge about with such adroit zigzag movements that it is almost impossible to seize them with the tweezers or fingers. I finally resorted with greater success to slapping them with the hand, but this is apt to crush them or to make them fall from perpendicular surfaces."

Although in our analysis there were no apparent systematic changes in walking direction between strobe cycles and we did not find evidence for strobing being associated with a particularly "zigzag" movement (Fig. 2), we concur with Wheeler that field sampling of foraging *Opisthopsis* is more difficult than nearly any other kind of ant. Once *Opisthopsis* are disturbed, they often switch from a strobing gait to the faster flight gait, but only for one or two seconds before returning to a strobing gait. While our current study only considered strobing by individual ants, future fieldwork examining the kinematics of strobing in collective groups will be particularly informative for learning how this behavior varies within dynamic social, chemical, and visuospatial contexts.

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## References

Balsalobre-Fernández, C., Glaister, M. & Lockey, R.A. 2015: The validity and reliability of an iPhone app for measuring vertical jump performance. – Journal of Sports Sciences 33: 1574-1579.

Brown, D. 2009: Tracker video analysis and modeling tool. – <http://physlets.org/tracker/>, retrieved on 25 January 2015.

Ceccarelli, F.S. 2010: New species of ant-mimicking jumping spiders of the genus *Myrmarachne* MacLeay, 1839 (Araneae:

Salticidae) from north Queensland, Australia. – Australian Journal of Entomology 49: 245-255.

Full, R.J. & Tu, M.S. 1990: Mechanics of six-legged runners. – The Journal of Experimental Biology 148: 129-146.

Gilbert, C. 1997: Visual control of cursorial prey pursuit by tiger beetles (Cicindelidae). – Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology 181: 217-230.

Hangartner, W. 1969: Structure and variability of the individual odor trail in *Solenopsis geminata* Fabr. (Hymenoptera: Formicidae). – Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology 62: 111-120.

Hechter, R.P. 2013: Hockey, iPads, and projectile motion in a physics classroom. – The Physics Teacher 51: 346-347.

Hughes, G.M. 1952: The co-ordination of insect movements. I. The walking movements of insects. – The Journal of Experimental Biology 29: 267-285.

Kramer, D.L. & McLaughlin, R.L. 2001: The behavioral ecology of intermittent locomotion. – American Zoologist 41: 137-153.

Miller, P.L. 1979: A possible sensory function for the stop-go patterns of running in phorid flies. – Physiological Entomology 4: 361-370.

Rasband, W.S. 1997: ImageJ. – U.S. National Institutes of Health, Bethesda, MD, USA; <http://imagej.nih.gov>, retrieved on 25 January 2015.

Wheeler, W.M. 1918: The ants of the genus *Opisthopsis* Emery. – Bulletin of the Museum of Comparative Zoology 62: 341-368.

Zollikofer, C. 1994a: Stepping patterns in ants – influence of body morphology. – The Journal of Experimental Biology 192: 107-118.

Zollikofer, C. 1994b: Stepping patterns in ants – influence of speed and curvature. – The Journal of Experimental Biology 192: 95-106.

Zurek, D.B. & Gilbert, C. 2014: Static antennae act as locomotory guides that compensate for visual motion blur in a diurnal, keen-eyed predator. – Proceedings of the Royal Society B-Biological Sciences 281: art. 20133072.