

## Eye structure correlates with distinct foraging-bout timing in primitive ants

Birgit Greiner<sup>1,\*</sup>, Ajay Narendra<sup>2</sup>, Samuel F. Reid<sup>2</sup>, Marie Dacke<sup>3</sup>, Willi A. Ribi<sup>4</sup> and Jochen Zeil<sup>2</sup>

Social insects have evolved remarkable physiological adaptations and behavioural strategies that enable them to access new temporal foraging niches (for example [1]). Here we report striking correlations between the timing of foraging bouts and the modification of eye structure in four species of ants belonging to the primitive genus *Myrmecia*. Most noteworthy, photoreceptor diameters progressively increase from 1.3  $\mu\text{m}$  in strictly day-active species, to 5.9  $\mu\text{m}$  in predominantly night-active species.

We studied four sympatric ant species of *Myrmecia*: a jack jumper, *M. croslandi*, and three species from the monophyletic *gulos*a species group, *M. tarsata*, *M. nigriceps* and *M. pyriformis* [2], and found that the forager traffic in each of these species occupies a distinct, barely overlapping time slot, varying from purely diurnal to slightly crepuscular to predominantly nocturnal (Figure 1A–D). Foragers of *M. croslandi* (Figure 1A) were exclusively day-active and left their nest in two distinct bouts, one hour after sunrise and at around 4 pm. Foragers returned throughout the day, all having arrived at the nest by 1–2 hours before sunset. Forager traffic of *M. tarsata* (Figure 1B) also exhibited two bouts of outgoing traffic, the first shortly after sunrise, starting half an hour earlier than *M. croslandi*, and the second around 5 pm. In contrast to *M. croslandi*, incoming forager traffic in *M. tarsata* occurred in two bouts, one in the morning and the second within half an hour

either side of sunset, with few foragers returning during the day. Outbound foraging activity of *M. nigriceps* (Figure 1C) occurred in one bout, starting about one hour before sunset, with incoming traffic peaking during twilight hours of the same day before the onset of astronomical twilight and around sunrise the next morning. A few foragers returned throughout the night. Outgoing forager traffic in *M. pyriformis* (Figure 1D) also occurred in one bout, but later than *M. nigriceps*, with maximum activity shortly after sunset. Most *M. pyriformis* foragers spent the night outside their nests, returning around daybreak, and did not forage during the rest of the day. The segregated pattern of foraging activity in these sympatric ants may have evolved to avoid competition.

*Myrmecia* rely primarily on visual cues for navigation and their mode of hunting involves rapid head and body movements that serve to fixate a prey animal in the frontal visual field before an attack is launched [3]. Ants have apposition compound eyes, an eye design that typically limits vision to conditions of high light intensities, because of the small facet lenses. It is known from nocturnal hymenopterans, however, that apposition eyes can be structurally adapted to operate at low light intensities [4–7]. These modifications involve large facet lenses, extremely wide photoreceptors and possibly also neural pooling of photoreceptor signals across ommatidia [7]. We therefore studied the functional anatomy of the compound eyes in these four species of *Myrmecia* ants

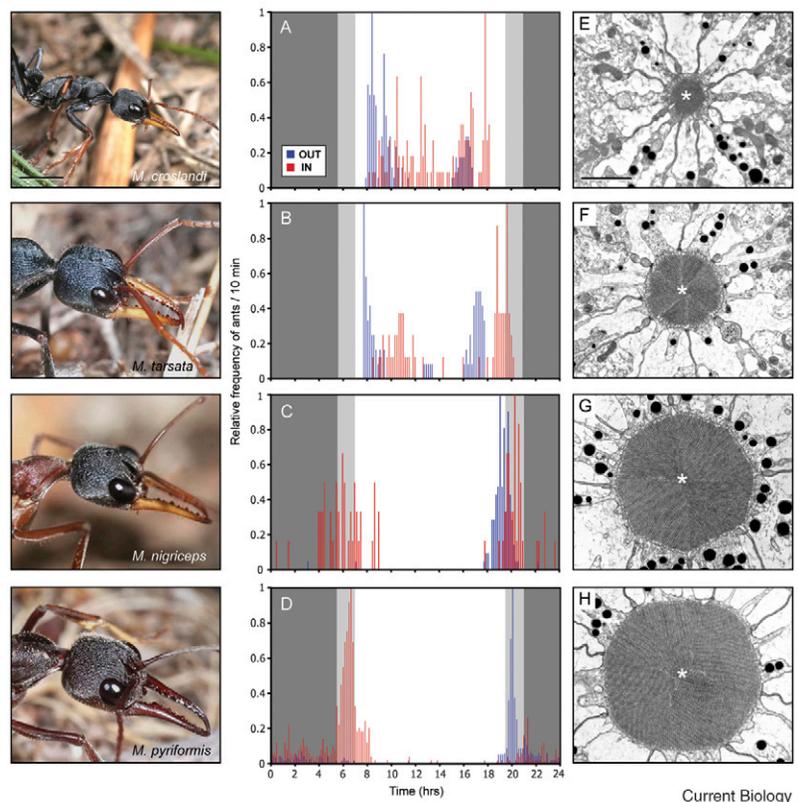


Figure 1. Foraging bout timing and photoreceptor diameters in four species of *Myrmecia* ants (left).

(A–D) 24 hour activity plots showing outgoing (blue) and incoming (red) forager traffic at the nests of the four *Myrmecia* species: (A) *M. croslandi*; (B) *M. tarsata*; (C) *M. nigriceps*; and (D) *M. pyriformis*. The duration of twilight is marked by light grey bar. (E–H) Ultra-thin cross sections of the distal photoreceptor (asterisk) in major workers of: (E) *M. croslandi*; (F) *M. tarsata*; (G) *M. nigriceps*; and (H) *M. pyriformis*. 1 mm scale for left column in top row and 2  $\mu\text{m}$  scale in E for E–H.

Table 1. Optical, eye size and body size parameters of four *Myrmecia* ant species.

	<i>M. croslandi</i> worker	<i>M. tarsata</i> major worker	<i>M. nigriceps</i> major worker	<i>M. pyriformis</i> major worker	<i>M. pyriformis</i> minor worker
Facet lens diameter ( $\mu\text{m}$ )	12–22; n = 1	18–26; n = 1	20–30; n = 1	20–30; n = 1	16–26; n = 1
Photoreceptor diameter ( $\mu\text{m}$ )	1.3 $\pm$ 0.1; n = 5	2.9 $\pm$ 0.1; n = 5	5.6 $\pm$ 0.1; n = 5	5.9 $\pm$ 0.1; n = 5	5.1 $\pm$ 0.1; n = 5
Optical sensitivity ( $\mu\text{m}^2\text{sr}$ )	0.06	0.5	1.1	1.6	1.0
No. of facets/eye	2363 $\pm$ 49; n = 5	2724 $\pm$ 67; n = 5	3210 $\pm$ 30; n = 3	3593 $\pm$ 66; n = 4	2320 $\pm$ 85; n = 5
Body length (mm)	12	27	27	30	14

to test whether temporal niche partitioning is associated with equivalent eye specialisations.

The eyes of major workers in each species are indeed specifically adapted to the light conditions at their respective times of foraging (Table 1, Figure 1E–H). The purely day active *M. croslandi* have the smallest facet lens and photoreceptor diameters (Figure 1E), followed by the diurnal/crepuscular *M. tarsata* (Figure 1F), while lenses and photoreceptor diameters are largest in the crepuscular/ nocturnal species *M. nigriceps* (Figure 1G) and *M. pyriformis* (Figure 1H). This translates into a 27-fold difference in optical sensitivity (for details see Supplemental experimental procedures) between day- and night-active species (Table 1). Interestingly, night-active wasps and bees have even wider photoreceptors and consequently higher optical sensitivities [8], suggesting that the slowly moving ants may be able to operate with lower optical sensitivity, possibly by having longer temporal integration times [9].

Because body length varies greatly in the ants we studied (Table 1; Figure 1 left), the differences in photoreceptor diameter could simply be due to differences in body size; but this is not the case. Comparing the compound eye of a minor worker of the crepuscular/nocturnal *M. pyriformis* with a body length of 14 mm to the day-active *M. croslandi* with a body length of 12 mm, we found photoreceptor diameters to be 4-times wider and facets to

be 1.2–1.3-times larger in the minor workers of *M. pyriformis* compared to the day-active *M. croslandi* (Table 1).

In conclusion, the large differences in photoreceptor and lens dimensions in these ants do not scale with body size but are clearly related to periods of foraging activity that occur in different ambient light conditions. Both superposition and apposition compound eyes have been modified in relation to ambient light conditions in a number of insect groups [10–12]. *Myrmecia* ants, however, represent an ideal model system to investigate the evolution of visual niche specialisation, including the metabolic and space constraints on eye design, as they exhibit such a tight correlation between the timing of foraging bouts and the structural adaptations of their apposition compound eyes. Moreover, in contrast to many flying insects, the walking, central place foraging ants may allow us to identify the range of visual tasks they are confronted with during their regular excursions.

#### Supplemental data

Supplemental data are available at <http://www.current-biology.com/cgi/content/full/17/20/R879/DC1>

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<sup>1</sup>Life Sciences Centre, Dalhousie University, Halifax, Nova Scotia, Canada B3H4J1. <sup>2</sup>Australian Research Council Centre of Excellence in Vision Science and Centre for Visual Sciences, Research School of Biological Sciences, The Australian National University, Canberra, ACT 2601, Australia. <sup>3</sup>Department of Cell and Organism Biology, Lund University, 22362 Lund, Sweden. <sup>4</sup>University of Human Sciences of the Principality of Liechtenstein, FL-9495 Triesen, Principality of Liechtenstein. \*E-mail: [birgit.greiner@dal.ca](mailto:birgit.greiner@dal.ca)