Trends in
Ecology & Evolution

CellPress

Letter

Ant caste evo-devo: it's not all about size

Ehab Abouheif[1,*,@]

Ant colonies typically have a winged queen and a wingless worker caste. However, novel types of queens (e.g., wingless queens) and novel types of workers (e.g., soldiers) have repeatedly evolved across ants [1–3]. Of all the novel types of castes, biologists have most debated the origins of discrete soldier castes, which have been proposed to have originated as either: (i) variants of the worker caste [4], (ii) intermediates between the queen and worker caste [1,5], or (iii) variants of the queen caste [6]. Despite this plurality of models, current evidence supports a worker-derived origin of soldier castes [2,3]. According to this 'standard model', discrete queen, worker, and soldier castes are determined through a series of developmental thresholds, which are reprogramming events that produce nonlinear developmental responses to continuous environmental inputs. In ants, these thresholds are known to be mediated by juvenile hormone (JH) [3]. For example, in the ant genus *Pheidole*, queen and worker castes are determined by a JH-mediated threshold during the egg stage in response to temperature and photoperiod, whereas minor worker and soldier castes are determined by a JH-mediated threshold later during the larval stage in response to nutrition [7] (Figure 1A). These switch-like thresholds first decouple the queen developmental trajectory from those of minor workers and soldiers and, subsequently, decouple the soldier trajectory from that of minor workers [8] (Figure 1A). The developmental trajectory of each caste therefore behaves like a module that can be evolutionarily modified independently of others.

In their *Trends in Ecology and Evolution* article, Trible and Kronauer [9] propose a

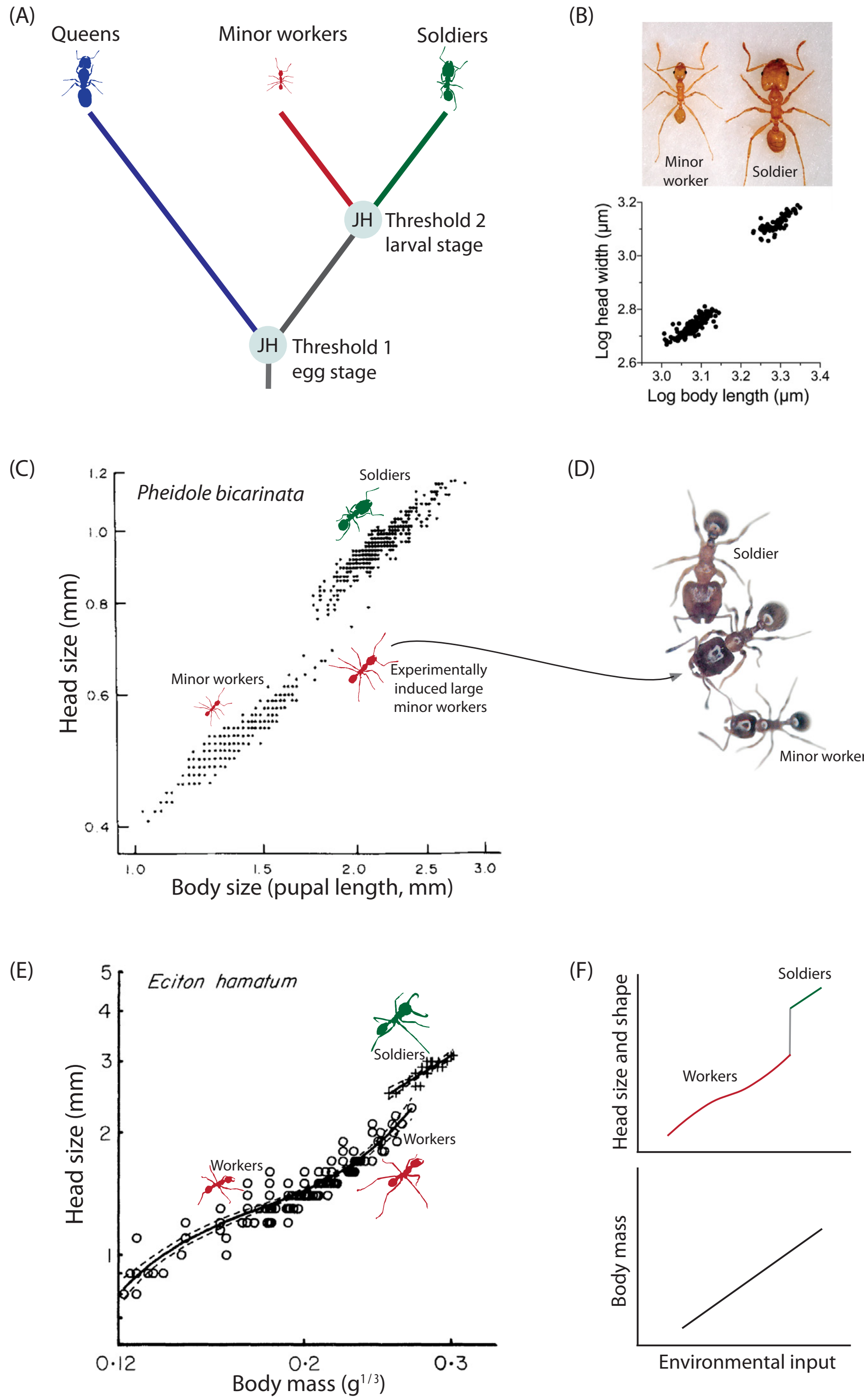

Figure 1. Thresholds, modularity, and trait-specific reaction norms underlie development and evolution of discrete soldier castes in ants. (A) Caste determination in *Pheidole* ants results in discrete queen (blue), minor worker (red), and soldier (green) castes. Two developmental thresholds (reprogramming events), which are mediated by juvenile hormone (JH), lead to decoupling of the developmental trajectories of

(Figure legend continued at the bottom of the next page.)

falsifiable alternative to this standard model, called the 'hourglass model'. According to this model, discrete soldier castes originate through queen–worker intermediates that are induced as a function of body mass or size. It assumes that body mass or size causes variation in caste-specific traits, such as head size, eye size, or ovariole number, along what they call 'caste reaction norms'. In the phenotypic plasticity literature, a reaction norm is defined by how a phenotype varies in response to environmental inputs (e.g., nutrition) [8]. By contrast, the hourglass model defines a caste reaction norm by how a caste-specific trait varies in response to changes in body mass or size, which is essentially an allometric curve. All caste reaction norms are assumed to be broadly sigmoidal in shape, which would reduce the frequency but not prevent the appearance of individuals that are intermediate in mass or size. Consequently, these intermediate-sized individuals would develop phenotypes that are intermediate between those of queens and workers. How then are discrete queen, worker, and soldier castes produced? According to the hourglass model, they are produced by discrete environmental inputs, such as low or high quality of nutrition, which results in small or large body sizes. This in turn causes the expression of worker traits in small individuals and queen traits in large individuals. If the colony experiences intermediate environmental inputs, then soldiers that are intermediate between queens and workers would be produced. The hourglass model therefore predicts that discrete queen, worker, and soldier castes would develop and evolve along a one-dimensional body mass or size axis in the absence of caste-specific developmental thresholds.

While I agree with Trible and Kronauer [9] that body mass or size is an important variable in ant caste development and evolution, to suggest that it is the only causative factor is unsupported by current evidence. Here I argue that the hourglass model is falsified by the fact that body mass (or size) and caste-specific traits are capable of being decoupled during ant caste development and evolution. In most *Pheidole* species, minor workers and soldiers differ discretely in both head and body size, forming two separate allometric lines [2,7] (Figure 1B). However, by manipulating JH and caste ratio in *Pheidole bicarinata*, Wheeler and Nijhout [7] generated individuals that overlap in body size with soldiers, yet they are minor workers with a minor worker head-to-body allometry (Figure 1C,D). This demonstrates that head size and shape can be experimentally decoupled from body size in ants. Furthermore, this discontinuous head-to-body allometry experimentally generated in *P. bicarinata* has evolved in the army ant *Eciton hamatum* [10] (Figure 1E). The most parsimonious explanation for this type of discontinuous allometry, where workers and soldiers overlap in size, is a steep and sigmoidal reaction norm (a developmental threshold) for head size and shape, but a continuous reaction norm for body mass or size (Figure 1F). Finally, head size and shape have also been evolutionarily decoupled from body size in colonies of *Cephalotes augustus* and a species of *Carebara*, where soldiers are the same size or even smaller than workers [6]. Together, these observations show that each trait within a caste, including body mass or size, is modular and has its own independent reaction norm.

the queen (blue line), minor worker (red line), and soldier (green line). (B) Most species of *Pheidole*, like in *Pheidole hyatti* shown here, have minor workers and soldiers that differ discretely in head size and body size (top) and form two separate allometric lines (bottom) (reproduced from [2]). (C) Discontinuous head-to-body allometry in *Pheidole bicarinata*, in which experimentally induced large minor workers (red) overlap in size with soldiers (green) (reproduced from [7]). (D) Image from Diana Wheeler showing a soldier (top), minor worker (bottom), and an experimentally induced large minor worker (middle), which represents an actual data point corresponding to a large minor worker in the graph in (C). (E) Discontinuous head-to-body allometry in the army ant *Eciton hamatum* (reproduced from [10]). The allometric line of the workers (red) overlaps with that of the soldiers (green), indicating that there are workers that overlap in size with soldiers. (F) The discontinuous allometry in *E. hamatum* in (E) is most parsimoniously explained by two separate reaction norms (top and bottom): a steep sigmoidal reaction norm for head size (top), where the steepest part of the curve (gray) corresponds to a developmental threshold, however, body mass or size is most parsimoniously explained as a continuous reaction norm (bottom).

Although I have focused on discrete soldier castes, thresholds generally decouple the developmental trajectories and evolution of all castes. For example, in several *Mystrium* species, which only have a worker caste and a novel wingless queen caste, all queens are smaller than workers [11]. In *Brachyponera luteipes*, queens are winged and overlap in size with workers, yet workers have larger heads and no ovaries [12]. Collectively, all of these observations falsify the core assumptions of the hourglass model, which assumes that caste-specific expression of traits is caused by body size and that developmental thresholds are absent.

[1]McGill University, Department of Biology, 1205 avenue Dr. Penfield, Montreal, Quebec, H3A 1B1, Canada

*Correspondence:
ehab.abouheif@mcgill.ca (E. Abouheif).
@Twitter: @ehab_abouheif (E. Abouheif).
https://doi.org/10.1016/j.tree.2021.04.002

References

1. Molet, M. *et al.* (2012) Evolution of novel mosaic castes in ants: modularity, phenotypic plasticity, and colonial buffering. *Am. Nat.* 180, 328–341
2. Rajakumar, R. *et al.* (2018) Social regulation of a rudimentary organ generates complex worker-caste systems in ants. *Nature* 562, 574–577
3. Wheeler, D.E. (1991) The developmental basis of worker caste polymorphism in ants. *Am. Nat.* 138, 1218–1238
4. Ward, P.S. (1997) Ant soldiers are not modified queens. *Nature* 385, 494–495
5. Trible, W. and Kronauer, D.J. (2017) Caste development and evolution in ants: it's all about size. *J. Exp. Biol.* 220, 53–62
6. Baroni Urbani, C. (1998) The number of castes in ants, where major is smaller than minor and queens wear the shield of the soldiers. *Insect. Soc.* 45, 315–333
7. Wheeler, D.E. and Nijhout, H.F. (1983) Soldier determination in *Pheidole bicarinata*: effect of methoprene on caste and size within castes. *J. Insect Physiol.* 29, 847–854

8. Emlen, D.J. and Nijhout, H.F. (2000) The development and evolution of exaggerated morphologies in insects. *Annu. Rev. Entomol.* 45, 661–708
9. Trible, W. and Kronauer, D.J.C. (2021) Hourglass model for developmental evolution of ant castes. *Trends Ecol. Evol.* 36, 100–103
10. Feener, D.H. *et al.* (1988) Curvilinear allometry, energetics and foraging ecology: a comparison of leaf-cutting ants and army ants. *Funct. Ecol.* 2, 509–520
11. Molet, M. *et al.* (2009) Shift from independent to dependent colony foundation and evolution of 'multi-purpose' ergatoid queens in *Mystrium* ants (subfamily Amblyoponinae). *Biol. J. Linn. Soc.* 98, 198–207
12. Kikuchi, T. *et al.* (2008) Small queens and big-headed workers in a monomorphic ponerine ant. *Naturwissenschaften* 95, 963–968