Size and shape in *Formica* ant workers

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Allometry is the study of scaling relationships, especially between body size and the measurements of different body parts, or between body size and fundamental physiological traits, such as metabolic rate or lifespan (Shingleton 2010). Allometry began as the study of developmental relationships among body parts; differences in the growth rates of different body parts as individuals grow result in different body shapes or morphology by adulthood. For instance, if limbs grow relatively faster during development, then larger individuals will end up with proportionately longer legs compared to some other size measure (e.g. total body length), whereas those whose limbs grow relatively slowly would end up with proportionately shorter legs. Allometry now describes broader scaling relationships, including comparisons of relative proportions of body parts across species. When the proportions of body parts correlate with crucial aspects of an animal's life history, interspecific comparisons may help to illuminate how natural selection produced both morphology and behaviour.

In insects, body size influences individual fitness in myriad ways: for instance, larger females have an advantage in aggressive encounters, can lay more eggs, and may be more likely to survive hibernation. In social insects, large size is generally associated with higher rankings in dominance hierarchies and in eusocial insects, is clearly associated with caste. The size difference between queens and workers is a fundamental aspect of social insect castes; queens are so predictably larger than workers that the absence of a size difference is considered to be notable. Queen-worker size differences are clearly associated with reproductive division of labour, and when there are size-based allometries during development, this can produce morphological differences between castes. Some social insects, including thrips, aphids, termites, stingless bees, and ants, may produce distinct size-based worker morphs, such as soldiers, which

are morphologically specialized for tasks such as colony defense. In such cases, individual workers follow different developmental programs, such that discrete subcastes exhibit distinct scaling relationships. This is referred to as 'non-linear allometry'. Alternatively, when all individuals follow the same developmental program, consistent scaling of body parts with body size can still produce different morphologies for different-sized individuals, a situation referred to as 'linear allometry'. When body parts scale with a slope of 1 in a log–log comparison, all individuals have the same relative proportions, regardless of size, which is known as 'isometry'.

One way of investigating the nature of developmental programs that produce different morphologies associated with different tasks is to investigate body size allometries in species with behavioural task specialization. Two recent papers from Jessica Purcell's lab illustrate this approach. In the first paper, behavioural observations demonstrate that in four species of *Formica* ants, workers do exhibit size-based task partitioning (West and Purcell 2020). These species of *Formica* do not exhibit morphologically specialized subcastes but do exhibit variation in worker size, so linear allometries could produce size-based morphological variation that might be functionally associated with size-based task partitioning. In the second paper, in this issue of *Insectes Sociaux*, Tawdros, West, and Purcell (Tawdros et al. 2020) investigate this possibility, and also propose a general framework for investigating how variation in body size, size scaling relationships, and behaviour may be associated in social insects without morphological subcastes. The framework comprises three questions: Are workers variable or uniform in size? If variable, do they exhibit isometric or allometric scaling? If allometric, is the allometry linear or non-linear?

Tawdros et al. answered these questions with six linear measures of worker ant body parts, including heads, thoraces, legs, and antennae. Coefficients of variation varied from 6.75 to 16.35, suggesting moderate levels of worker size variation compared to ant species with extreme morphological differentiation among worker subcastes, but considerably more variation than would be apparent in eusocial

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species such as honeybees. Having established then that workers do exhibit size variability, the next questions pertain to scaling relationships. Comparing body parts to head width, a standard measure of body size in many studies of social insects, most scaling relationships were allometric, and the allometries were linear. This suggests that size variation could produce at least subtle differences in morphology among small and large workers. Interestingly, all four *Formica* species exhibited similar scaling relationships, perhaps suggesting allometries based on an ancestral body plan and development program that continues to constrain worker morphology.

The research framework proposed by Tawdros et al. could easily be applied to other kinds of social insects. It might be especially interesting to apply this program to social insect groups that are becoming models for understanding significant social evolutionary transitions. For instance, in bees, it

would be possible to compare size-based scaling relationships in species with facultative versus obligate sociality, or between closely related eusocial and solitary species, to better understand the extent to which castes are behaviourally or morphologically defined.

References

- Shingleton A (2010) Allometry: the study of biological scaling. *Nat Educ Knowl* 3:2
- Tawdros S, West M, Purcell J (2020) Scaling relationships in *Formica* ants with continuous worker size variation. *Insect Soc*. <https://doi.org/10.1007/s00040-020-00779-0>
- West M, Purcell J (2020) Task partitioning in ants lacking discrete morphological worker subcastes. *Behav Ecol Sociobiol* 74:66. <https://doi.org/10.1007/s00265-020-02845-w>