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Digest: Evolution of eusociality favored by split sex ratios under worker-control*

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Eusociality has repeatedly independently evolved in ants, bees, and wasps (Hymenoptera), leading to the idea that haplodiploidy may be an important driving factor in this group. Using a modeling approach, Quiñones et al. show that split sex ratios and worker control of sex ratios (achieved by removal of male brood) can promote the initial evolution of helping raise offspring of related individuals. However, over time, these factors can result in social polymorphism, that is, a mix of solitary and social nests, or to eusocial colonies with three different strategies, namely those that produce mostly females, mostly males, or a balanced sex ratio.

The conditions that allow the evolution of eusociality, that is, the existence of unmated and mostly sterile workers, are the subject of continuing debate. Hamilton's foundational research showed that the evolution of sterility (or forgoing the ability to reproduce) can be selected if the sterile individuals instead help their close relatives to raise offspring (Hamilton 1964a,b). Thus relatedness (r) is key to the evolution of eusociality. This insight, and the observation that eusociality evolved independently many times in the haplo-diploid Hymenoptera (i.e. ants, bees, wasps), inspired the "haplodiploidy hypothesis." It posits that hymenopteran workers would gain by raising sisters ($r = 0.75$, due to haplodiploidy) instead of conceiving their own offspring ($r = 0.5$), and that this scenario facilitates the evolution of eusociality. However, this benefit of a higher relatedness between sisters can be cancelled out by a lower relatedness between sisters and brothers, reducing any relatedness "advantage" for haplodiploids in the context of evolving eusociality. This holds true for any population sex ratios, including female bias, because a female bias increases the reproductive value of males, cancelling out any relatedness benefit (Craig 1979). There is, however, the possibility to specialize in producing one sex within a nest (while the population sex ratio remains unaltered), creating so-called "split sex ratios," which indeed could promote the evolution of eusociality under certain circumstances (Gardner et al. 2012). Assuming additional conditions, for example, lifetime monogamy and determination of offspring sex by mothers (often met in Hymenoptera), haplodiploidy can then effectively facilitate the evolution of eusociality.

Using mathematical theory, including deterministic models and individual-based simulations, Quiñones et al. (2020) investigate the effect of worker control over sex ratios on the evolution of eusociality. In these models, designed to match typical life histories of subsocial bees and wasps, both the tendency to stay and help at the mother's nest (rather than to disperse and reproduce) and the helpers' tendencies to bias sex ratios toward females (by selectively killing male brood, a behavior known as fratricide) were allowed to co-evolve.

Quiñones and colleagues found that, under the model's assumptions, fratricide facilitates the evolution and initial spread of helping behavior (because resources are invested in additional sisters). Social nests (with workers) thus produce only females, whereas solitary nests (without workers) specialize in male production. Therefore, fratricide leads to split sex ratios without depending on partial polygamy.

A female-biased sex ratio in turn facilitates both the evolution of fratricide and the evolution of helping, whereby the sex ratio has a stronger effect on the evolution of helping than fratricide.

*This article corresponds to Quiñones, A. E., G. J. B. Henriques, and I. Pen. 2020. Queen-worker conflict can drive the evolution of social polymorphism and split sex ratios in facultatively eusocial lifecycles. Evolution. https://doi.org/10.1111/evo.13844.

Interestingly, in the long run, fratricide does not lead to fixation of helping, but to different life histories, depending on the efficiency of workers in helping. If fratricide does not evolve, the life history becomes that of a univoltine eusocial species. Fratricide leads to the evolution of social polymorphism, with split sex ratios between solitary nests producing only males and social nests producing only females, or a fully eusocial life history with three types of social nests (those containing mostly males, mostly females, or both at roughly the same rates). One striking outcome is that social polymorphism is not necessarily just a transitionary state en route to full eusociality, but may well be a stable result of evolution.

As with all models, the results depend strongly on the underlying assumptions and simplifications. For instance, worker reproduction (by arrhenotoky, i.e., males produced from unfertilized eggs) is widespread in social insects and may lead to different selection pressures on queens and workers (Wenseleers et al. 2013). Likewise, queens manipulating their daughters to stay as helpers (e.g., by castrating them via malnutrition) might facilitate the evolution of helping behavior. Incorporating these additional effects in refined future models may further refine our understanding.

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