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Peer Review

Review of: "Programmed Cell Death and the Origin of Wing Polyphenism in Ants: Implications for Major Evolutionary Transitions in Individuality"

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Review of: **Programmed Cell Death and the Origin of Wing Polyphenism in Ants: Implications for Major Evolutionary Transitions in Individuality**

Authors: **Hanna, Boudinot, Liebig, Abouheif**

I find the data, methods, analyses, and the taxon-specific conclusions to be convincing. It seems highly probable that programmed cell death (PCD) was already occurring early in the evolution of the social ants. PCD is clearly a mechanism involved with why worker-destined larvae fail to develop wings. Relative to this conclusion, I have only one objection. The authors state that the immediate ancestor to the ants was a solitary wasp species. To my knowledge, we do not know anything conclusive about the social state of this presumed ancestor. Yes, it was likely a wasp, but nothing relative to its behavior. In other words, the ancestor of the ants may have already exhibited facultative eusociality like that observed in the polistine wasps. In short, social behavior may have predated winglessness. If one equates sociality with being a major transition, then it may have occurred before and independent of evolving wingless workers. We do not know, and the authors' cladograms cannot resolve this.

The above point is one of several reservations I have about placing this study in the context of being a Major Evolutionary Transition (MET). First off, the authors claim that “eusociality” is a MET without defining what level of it equates with becoming a MET-level phenomenon (see Boomsma, 2023 for why this matters), nor do they define what constitutes a MET and why wingless offspring would be one. METs, as proposed in the literature, are either lower-level entities fusing into a single

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higher-level one (an ETI: Evolutionary Transition in Individuality), or Information Leaps in terms of increasing the information content available to organisms. Recent papers by Robin et al. (2021) and Nonacs and Denton (2023) argue strongly that the social insects are neither an ETI nor an Information Leap and, therefore, do not meet a definition of a MET. Instead, worker castes are more analogous to the evolution of a novel organ; and the evolution of any other specific multicellular organ has never been proposed to be a MET. Indeed, wing discs exist in all Hymenoptera and, therefore, PCD in ant worker wing discs is literally just a modification of an already evolved and existing tissue. It is neither an ETI nor an Information Leap.

Furthermore, PCD is a widespread phenomenon in multicellular organisms. It may be critical to the evolution of complex multicellularity of tissues and organs – which does generally meet the definition of a MET (Robin et al. 2021). Hence, what happened in ants is not a novel MET, but the elaboration of one aspect facilitated by the earlier complex multicellularity MET. In the Introduction, the authors give examples of PCD in Dictyostellium and yeast producing multicellular organizations. However, no one is claiming these to be METs. So, why would it be one in ants? Finally, the authors concede in the Discussion that winglessness (likely with PCD) has also evolved in solitary species (e.g., the velvet ants – which are actually wasps). Therefore, observing that PCD and winglessness occurred in the evolutionary history of ants cannot by itself conclude that a MET has occurred. This is not to say that a wingless worker caste is evolutionarily unimportant, given ants' eventual ecological success. However, to the degree that PCD played a role, the creation of a wingless caste may be better described as a Major Competitive Transition (MCT: see Robin et al. 2021).

In my opinion, the work here should really minimize or drop the MET context relative to their findings, and instead, frame the results as to what they mean as regards the evolution of obligate eusociality; assuming here that wingless individuals become reproductively-limited helpers at the nest – as is the case in all ant species. There is great disagreement as to whether obligate eusociality (sometimes called superorganismality) evolves through altruism (i.e., daughters gain more inclusive fitness by helping mothers than by founding their own nests – the monogamy hypothesis of Boomsma, 2023), or through parental manipulation where offspring help because it is the best inclusive fitness option left to them when placed in a bad situation (Nonacs and Denton 2023). Your results would seem to me to very much favor the latter scenario, where depriving your daughters of wings strongly affects their ability to individually succeed (and would not be affected by how often the female has mated)!

To summarize, this work adds a likely mechanism to our understanding of how obligate eusociality may have evolved in the ants. However, even if we use the widest possible definition of a MET, one that includes a facultative level of eusocial organization, the authors cannot conclude that PCD was the critical factor. It is quite possible that PCD produced a wingless worker caste only after social behavior was present.

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Respectfully submitted,

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Declarations

Potential competing interests: No potential competing interests to declare.