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The evolution of eusociality in allodapine bees: workers began by waiting

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Understanding how sterile worker castes in social insects first evolved is one of the supreme puzzles in social evolution. Here, we show that in the bee tribe Allodapini, the earliest societies did not entail a foraging worker caste, but instead comprised females sharing a nest with supersedure of dominance. Subordinates delayed foraging until they became reproductively active, whereupon they provided food for their own brood as well as for those of previously dominant females. The earliest allodapine societies are, therefore, not consistent with an ‘evo-devo’ paradigm, where decoupling of foraging and reproductive tasks is proposed as a key early step in social evolution. Important features of these ancestral societies were insurance benefits for dominants, headstart benefits for subordinates and direct reproduction for both. The two lineages where morphologically distinct foraging worker castes evolved both occur in ecosystems with severe constraints on independent nesting and where brood rearing periods are very seasonally restricted. These conditions would have strongly curtailed dispersal options and increased the likelihood that dominance supersedure occurred after brood rearing opportunities were largely degraded. The origins of foraging castes, therefore, represented a shift towards assured fitness gains by subordinates, mediated by the dual constraints of social hierarchies and environmental harshness.

Keywords: forager castes; social evolution; evo-devo

1. INTRODUCTION

Eusocial insects comprise a major faunal element in most terrestrial ecosystems, yet their evolutionary origins are very few [1]. This means that an ecologically very successful strategy is, paradoxically,

unlikely to evolve. Two broad approaches have been used to explore how eusociality has arisen. One approach emphasizes ecological factors and kin selection as key evolutionary drivers (e.g. [2]), whereas a more recent, ‘evo-devo’, approach emphasizes developmental genetics and how queen and forager castes may be understood in terms of the decoupling of gene suites controlling elements in the developmental groundplans of solitary antecedents [3].

These two approaches, one stressing ecological factors and the other developmental genetics, have the potential to bring very different insights to the origins of eusociality [3]. However, both approaches posit historical scenarios, and assessing these require that we have some knowledge of the evolutionary events leading up to eusociality. A critical issue is whether a key feature of early societies involved rearrangements of elements in the developmental groundplans of solitary ancestors.

Bayesian methods (e.g. [4]) can be used to infer the nature of early insect societies, but with the caveat that there is sufficiently informative social variation among extant taxa to have confidence that signals of likely ancestral states can be captured. Allodapines meet this requirement, and sociality in species in this group ranges from largely subsocial to highly eusocial [5]. Social nesting, where two or more females help rear brood in a nest, is ancestral for allodapines and has never been entirely lost, probably because of the vulnerability of brood to orphaning and enemies-at-the-nest [6]. Because allodapine larvae are not enclosed within protective cells and are progressively provisioned, they require adults to be present throughout their development.

In all allodapines, females emerge as adults in the company of other, older females. Once females reach adulthood they can either disperse or remain in their nest, whereupon there are three broad options available, depending on species [7]: (i) in *Macrogalea* and in some species of *Exoneurella*, females can commence reproduction without any apparent social constraints; (ii) in most other species, females join a reproductive hierarchy where they delay foraging roles until they also lay eggs; and (iii) in some species, including the two highly eusocial species, females can assume a foraging role without becoming reproductive. We call these three strategies *Reproduce*, *Wait* and *Forage*, respectively. Although *Waiting* involves eventual direct reproduction, it may also entail allo-parental care, both immediate and delayed. While *Waiting*, females could help in nest maintenance or other intra-nidal tasks (e.g. [8]), and after assuming dominance, food they bring back to the nest could be used by their own brood as well as any remaining brood from previously dominant females. Allodapine broods are reared in a communal tunnel where they are in physical contact and able to move, so that food brought into the nest is available to all larvae that are present [9].

Here, we ask whether newly emerging females in early allodapine lineages were likely to adopt *Reproduce*, *Wait* or *Forage* roles. Each of these strategies could have very different implications for understanding the origins and subsequent elaboration of sociality.

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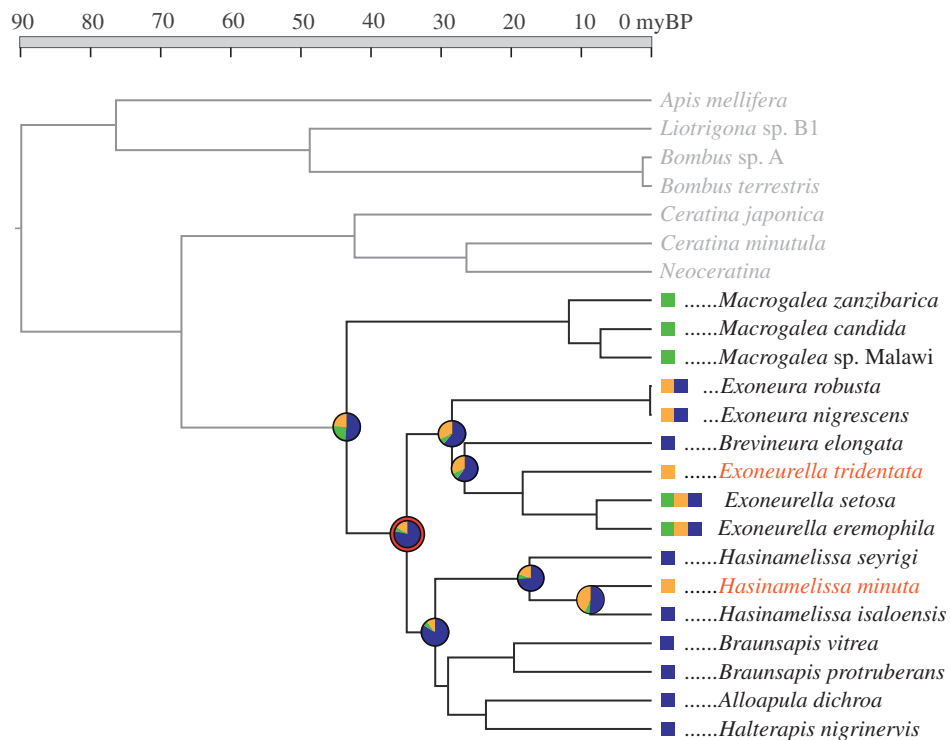


Figure 1. Chronogram of allodapine species with pie charts indicating probabilities for alternative subordinate strategies at key nodes. Grey branches denote non-allodapine species that were not used for inferring ancestral social states. Coloured squares indicate strategies adopted by subordinate females, and two or more squares indicate polyphenism of strategies. The red circle indicates the most recent common ancestor of the two species with true worker castes, *E. tridentata* and *H. minuta*. Newly emerged female strategy: green squares, *Reproduce*; brown squares, *Forage*, blue squares, *Wait*.

2. MATERIAL AND METHODS

We used detailed published studies (see electronic supplementary material) to identify strategies adopted by newly emerged females in 16 species covering all major allodapine clades. Social organization tends to be phylogenetically conserved within allodapine genera [10] and less detailed studies (e.g. [11]) do not suggest forms of sociality that differ in structure from our included species. In some allodapines, newly emerging females can adopt two or more of the *Wait*, *Reproduce* and *Forage* strategies; e.g. in *Exoneurella setosa* they can adopt any one of the three strategies [12]. Only two allodapines, *Exoneurella tridentata* and *Hasinamelissa minuta*, show the hallmarks of highly eusocial behaviour: queen-worker dimorphism with sterility or near-sterility of workers [5].

We developed phylogenies of these 16 species, but when doing so we included additional species (see electronic supplementary material), for which detailed social data were not available, to avoid long-branch attraction for thinly sampled clades. We used halictine bees as the outgroup and included corbiculate and ceratine species to provide fossil calibration points. These taxa were all deleted from trees before inferring ancestral allodapine social traits. We used the same gene fragments (*COI*, *cytb* and the F2 copy of *EF-1 α*) and Bayesian protocols as Chenoweth *et al.* [6], outlined in the electronic supplementary material. After phylogenetic analyses, allodapines lacking social data were pruned from trees, and the resulting phylograms were transformed into chronograms using the same calibration points and method for estimating divergence dates as Chenoweth *et al.* [6], also outlined in the electronic supplementary material.

We used a Bayesian method, *BAYESMULTISTATE*, for exploring ancestral character states. Various priors were explored, with the criterion that acceptance rates are bounded by 20 and 40 per cent [13]. A rate deviation prior of 15 with an exponential (0, 10) reverse jump hyperprior met this requirement, but trials using gamma priors with similar acceptance rates produced almost identical results. We used 40×10^6 iterations with a burn-in of 10×10^6 , sampling every 1000th generation. Likelihoods of alternative ancestral states were assessed using Bayes Factor (BF) tests, ‘fossilizing’ each strategy for each relevant node in turn [13]. Fossilized runs took longer to plateau than for unfossilized analyses and we used $1-2 \times 10^9$ iterations, choosing post-burn-in periods on the basis of harmonic mean

plots. All fossilized runs were replicated at least twice to check for the consistency of results, but no discrepancies were found.

3. RESULTS

Our results are summarized in figure 1, where the relative likelihoods of alternative ancestral strategies (*Reproduce*, *Wait* and *Forage*) are summarized using pie charts. Charts are given for ancestral nodes leading to the two highly eusocial species, *E. tridentata* and *H. minuta*, but only where BF tests (electronic supplementary material, table S2) supported one strategy over both alternatives. Our analyses indicate that each of these species was preceded by greater than or equal to four antecedent nodes with support for *Waiting*. These included the root allodapine node and the most recent common ancestor (MRCA) for these eusocial species. One complication is the possibility of polyphenism of strategies at internal nodes, as happens in some extant species. We explored the likelihood of ancestral polyphenism by coding extant species as monophenic or polyphenic and then used the same ‘fossil’ protocol as above to infer ancestral states. We found that monophenism was more probable in both the root node and the MRCA for the two highly eusocial species (BF = 3.294 and 2.556, respectively).

4. DISCUSSION

It has been hypothesized that origins of worker castes may be explained by the decoupling of separate

elements in developmental groundplans of solitary ancestors (e.g. [14,15]), such as gene networks for oviposition and foraging. In this way, castes could arise from differential expression of behaviours that were, to a large extent, present before the origin of sociality. If such decoupling of elements is the key to the origins of sociality, as suggested by the evo-devo paradigm, we would expect to see signs of this in the earliest allodapine lineages. We found no evidence for this. Instead, those early societies were more likely to comprise female assemblages where foraging and reproduction were not decoupled, and where the joint activation of oviposition and foraging, characteristic of solitary-nesting females, waited on dominance supersedure. This does not mean that the eventual appearance of highly eusocial behaviour did not entail the developmental shifts envisaged by evo-devo, but it does mean that substantial evolutionary time occurred between the origin of sociality and the later origins of foraging castes.

Our analyses indicate that *Waiting* by subordinates was the ancestral trait and persisted in most lineages for greater than 40 Ma. *Waiting*, therefore, exhibits substantial evolutionary stability. We suggest this is owing to three features: (i) subordinates do not take on a foraging role until they are reproductive, so that associated risks are delayed until foraging also reaps direct fitness benefits; (ii) any brood from previously dominant females that are still present after supersedure will benefit from alloparental care by newly dominant females, providing indirect 'headstart' benefits [16]; and (iii) dominant females may gain 'insurance benefits' [17] by tolerating the presence of *Waiting* females, who could complete the rearing of orphaned brood when the dominant dies.

Interestingly, both highly eusocial species, *E. tridentata* and *H. minuta*, occur in arid ecosystems where nesting sites are scarce and where rainfall is highly seasonal and very limited [18,19]. Scarcity of nesting sites would lower the rates of successful dispersal, and seasonally restricted rainfall means that, by the time *Waiting* subordinates attain dominance, there may be few floral resources to begin a new round of brood rearing. Given these constraints, assumption of a *forage-now* role might become the best strategy for gaining indirect fitness via 'assured fitness returns' [20].

Assuming a foraging role while waiting in a reproductive queue may have important consequences for future strategies. Foraging entails physiological and mortality costs, and these are likely to reduce the likelihood of attaining future dominance, leading to a trade-off between future direct fitness and more-immediate assured indirect fitness. For example, allocation of physiological resources to foraging would leave fewer reserves for later ovarian development, and predation risks during foraging would lower the likelihood of surviving until dominance supersedure becomes possible. Such trade-offs could canalize the worker strategy: as a subordinate strategy becomes increasingly honed for foraging and its assured fitness returns, the possibilities for assuming reproductive dominance would lessen. This scenario

is not inconsistent with evo-devo, but it does suggest an important role for ecological selective factors in the eventual origins of foragers.

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