

Climate-mediated behavioural variability in facultatively social bees

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Social organisms are some of the most pervasive on earth, with the origin of sociality considered a major evolutionary transition. Previous studies suggest a role for both genetic and environmental factors in the transition from solitary to social living, with the relative contributions of these factors varying among taxa. Eusociality has arisen up to 11 times in the Hymenoptera. Four of these origins occurred within the bees, plus many probable reversions, making them ideal to understand the influence of genes and environment on social behaviour. We used a well-supported phylogeny with broad taxonomic coverage of the globally distributed bee genus *Ceratina* to test whether climate and sociality are correlated. *Ceratina* was most probably social ancestrally and originated in tropical Africa, with subsequent dispersals into temperate regions corresponding to shifts to solitary living. These findings highlight the utility of facultatively social lineages, such as *Ceratina*, for assessing the relative importance of phylogeny and ecology in the evolution of social complexity.

ADDITIONAL KEYWORDS: *Ceratina* – ecological context – Hymenoptera – latitude – social behaviour – tropical

INTRODUCTION

Social organisms make up some of the most successful lineages on earth, yet eusociality has arisen only a few times (Wilson, 1971). Both genetic and environmental variation have been attributed to the evolution of social behaviour (Rehan & Toth, 2015), but empirical studies are few, and the relative contributions of phylogeny and selection vary among taxa (Jetz & Rubenstein, 2011; Purcell, 2011; Sheehan *et al.*, 2015; Lukas & Clutton-Brock, 2017). To understand the influence of environment on the expression of social phenotypes, clades that exhibit lability in their sociality offer unrivalled potential for comparative study (Rehan & Toth, 2015).

Behaviour may vary with environmental conditions, genotypes or genotype–environment interactions (Wong & Candolin, 2015), but a set of preconditions relating to both mother and nest longevity appears fundamental to social behaviour and the extent of plasticity (Andersson, 1984). Mothers that are long lived

can progressively provision and interact with mature offspring, and remaining loyal to a nest across time impedes predation and facilitates care to reduce offspring mortality (Sakagami & Maeta, 1977). In selective environments, these preconditions may enable cooperative behavioural responses that favour population persistence and the evolution of genetic modifiers that enhance their expression (West-Eberhard, 2003).

Although species may possess all precursors for social behaviour to arise, the ecological context represents a strong predictive factor in its evolution. Comparative studies investigating congeneric and conspecific variation suggest that sociality closely tracks geographical and climatic gradients, with primitively social species more likely to be found at lower latitudes and elevations (Purcell, 2011). Social phenotypes may adapt to a broader range of conditions, enabling expansion of their distribution beyond the capacity of solitary nesting individuals (Sun *et al.*, 2014; Brooks *et al.*, 2017). The demands of both reproductive and foraging behaviours mean that environments presenting a combination of selective pressures, such as floral resource and nest site availability, are likely to be constraining for solitary nests in unpredictable conditions.

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Lineages that are facultatively social, where females are totipotent and capable of acting solitarily or as a social reproductive or helper, represent prime targets to uncouple the importance of genetic and environmental components in shaping the evolution of sociality. Bees of the genus *Ceratina* (Apidae: Xylocopinae) exhibit remarkable social variability, covering the full spectrum from solitary to eusocial behaviour, with numerous facultative social species. *Ceratina* are long lived and nest loyal, with mothers exhibiting prolonged mother–offspring interaction, often feeding young adults before overwintering or dispersal (Sakagami & Maeta, 1977). This genus originated in Africa ~56 Mya before radiating globally (Fig. 1) and comprises 17 Old World subgenera and six New World subgenera of ~200 described species (Michener, 2007). With social forms generally appearing to be correlated environmentally, the ceratinine bees enable us to test whether warming climates lead to evolutionary transitions to sociality.

MATERIAL AND METHODS

ANCESTRAL STATE

Ancestral state reconstructions were determined for key nodes of the phylogenetically robust maximum

credibility tree produced by Rehan & Schwarz (2015) for *Ceratina*. These nodes represent either major biogeographical shifts or changes in sociality for key clades, summarized in the Supporting Information (Table S1).

A character matrix allowing multiple states for 99 taxa was compiled for two traits: (1) sociality, simplified to either solitary or social ($N = 34$ species: eight solitary and 26 social); and (2) climate, reduced to temperate or tropical ($N = 99$ species: 18 temperate, 73 tropical and eight species that occur in both temperate and tropical climates; see Supporting Information, Table S2). Behavioural data for *Ceratina* largely comprise anecdotal observations (Sakagami & Maeta, 1977), which limited our classification of solitary taxa to only known obligate single foundress, including subsocial species, whereas social species included all varieties of multi-female cooperative nesting. Using the MultiState function in BayesTraits (Pagel *et al.*, 2004), the two traits were mapped across 200 random post-burn-in trees from Rehan & Schwarz (2015) to accommodate phylogenetic uncertainty.

Analyses were repeated five times to account for potential instability in marginal likelihood estimation from the harmonic mean, which was assessed across each run to confirm stability. As the harmonic mean is a running total, the best run was determined through

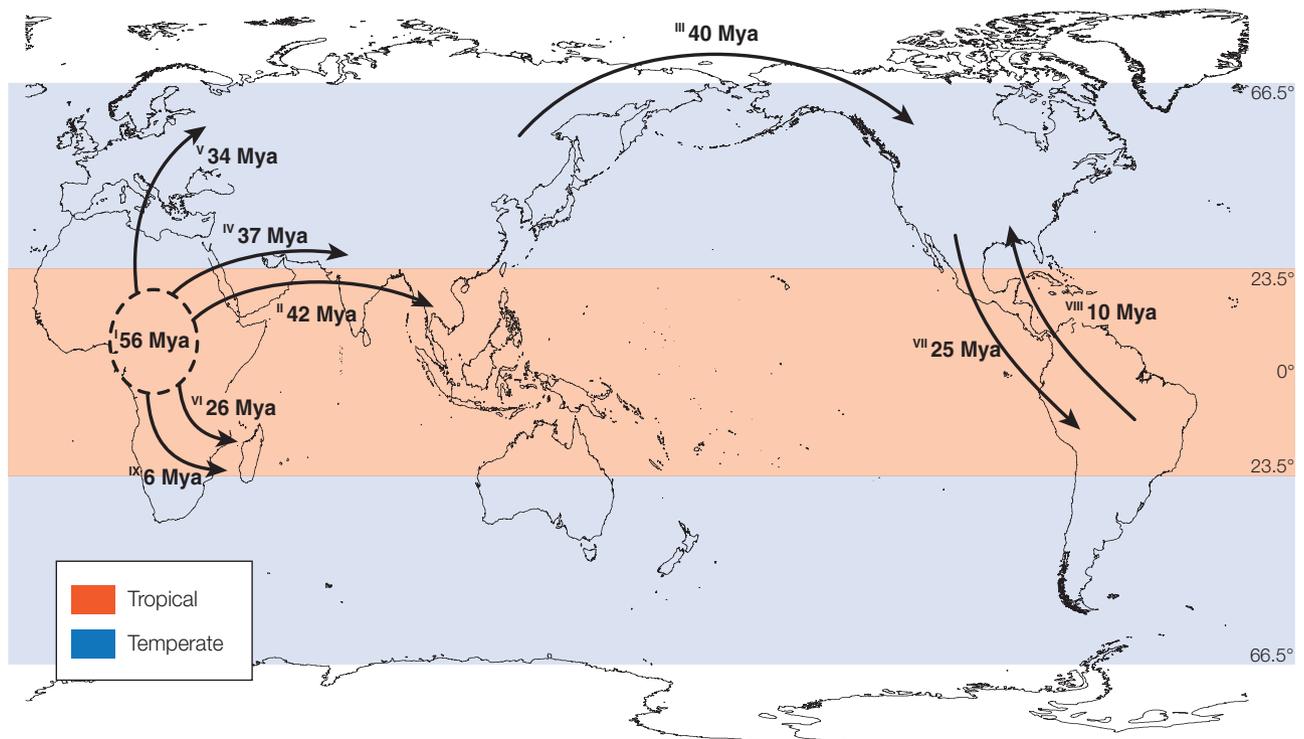


Figure 1. Map showing ages of *Ceratina* radiation through global climate zones. *Ceratina* had a tropical African origin, followed by cosmopolitan distribution. Species are currently distributed across both tropical and temperate biogeographical zones world-wide.

comparison of the final log of 100,000,000 iterations across the five runs (see [Supporting Information, Table S3](#)). Reconstructions were explored using both Markov chain Monte Carlo (MCMC) and reverse jump MCMC (rjMCMC) approaches under uniform, exponential and γ distributions, and also γ and exponential hyperpriors that are a uniform distribution from which values are drawn to seed the values of the γ and exponential priors. This removes much of the uncertainty in applying priors and therefore limits the assumptions being made. Each of the distributions was set at 0–10, 0–30 and 0–100, totalling 105 runs for 21 prior arrangements. Comparison of harmonic means determined that an exponential hyperprior with a distribution between zero and ten was most suitable, with transition rates between each of the states left unrestricted.

CORRELATED TRAITS

We investigated whether sociality and climate were correlated by fitting independent (traits not correlated) and dependent (traits correlated) models using the DISCRETE function in BayesTraits ([Pagel & Meade, 2006](#)), before comparing estimates of the marginal likelihood for each model.

Our multi-state data matrix required conversion into discrete binary characters (sociality, $N = 34$ species; climate, $N = 91$ species) for this analysis, meaning that the climate trait for eight taxa found in both tropical and temperate regions was removed. The same hyperprior was applied over 100 000 000 iterations and run five times, as in the reconstruction of ancestral states, with the stepping stone sampler of BayesTraits also implemented. This feature estimates the marginal likelihood by placing successively heated ‘stones’ that link the posterior with the prior ([Xie *et al.*, 2011](#)), providing an alternative estimate for us to test independent and dependent models.

A log Bayes factor (log BF) was then calculated from both methods of marginal likelihood estimation ([Supporting Information, Table S4](#)), for the best of the five runs, in the equation $\log BF = 2(\log \text{marginal likelihood complex model} - \log \text{marginal likelihood simple model})$, to test for evidence of trait correlation.

RESULTS

ANCESTRAL STATES

The ancestral state of the ceratinines ([Fig. 2; Supporting Information, Fig. S1](#): node *e*) was reconstructed as most likely to be social and found in the tropics (see [Supporting Information, Table S3](#)). Likewise, the ancestors representing the first two dispersals out of Africa to Asia (nodes *a* and *f*) were likely to be social with tropical origins based on the data available.

Clades of more recent African/Oriental representatives (node *g*) and African/Malagasy subgenera (node *i*) also probably had a social ancestor with a tropical origin. In contrast, the ancestor of the Palaearctic (and Malagasy) clade (node *h*) was confidently recovered as solitary and of temperate origin.

Dispersal into the New World (node *b*) was associated with a social and tropical ancestral state. The subsequent dispersal into South America (node *d*) was also tropical but solitary, a probable consequence of absent behavioural data in clade representatives. The clade comprising the back migration into North America (node *c*) then corresponds to a shift to a temperate environment and retains a solitary ancestral state.

CORRELATED TRAITS

The correlated evolution of social state with climate was supported by evolutionary models with very strong evidence from both harmonic mean ($\log BF = 27.75$) and stepping stone sampling ($\log BF = 10.34$) methods used to estimate the marginal likelihood. Transition rates of the dependent model were highest (3.05) from tropical to temperate for solitary species and from temperate to tropical for social species (see [Supporting Information, Fig. S2](#)).

DISCUSSION

Our results demonstrate that ceratinine bees occupying tropical climates are more likely to exhibit social behaviour but form solitary nests in temperate areas. Sociality is strongly constrained by development time and season length ([Purcell, 2011](#)). In bees, the shorter season length of higher elevations and latitudes can force reversion to a univoltine life cycle ([Sakagami & Maeta, 1977](#)), producing a single brood per year. Relative to highly social species, the longer egg-to-adult development periods of facultatively social species require correspondingly longer breeding seasons ([Schwarz *et al.*, 2007](#)). The climate of lower elevations and latitudes relaxes this constraint to permit the production of their second brood. Consequently, for many facultatively social species the interplay of climate and breeding season length probably determines their voltinism.

A bivoltine life cycle is common to many facultatively social insect species and considered an adaptation to seasonal environments that also include tropical wet and dry periods ([Smith *et al.*, 2003; Rehan *et al.*, 2010, 2015](#)). Adults pass the unfavourable season in diapause to emerge and produce their first brood, which then help to rear the second brood and forgo reproduction. Bivoltinism is crucial to the expression of the behavioural precursors to sociality, because it allows overlapping generations and cooperative brood care ([Seger,](#)

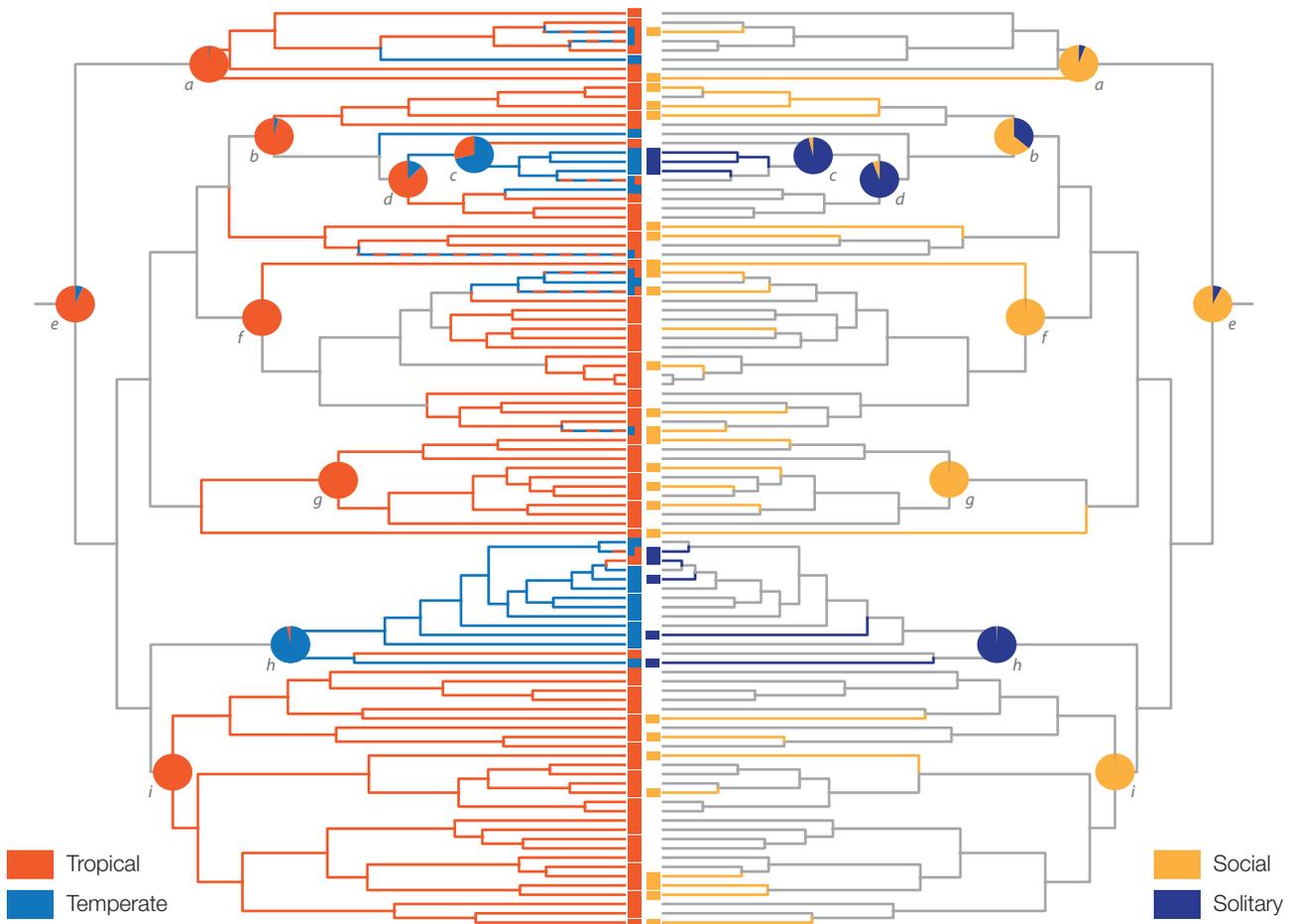


Figure 2. Comparative phylogeny of maximum credibility tree produced by Rehan & Schwarz (2015), with climate zones (left) and behaviour (right) overlaid. Biogeographical distribution is strongly correlated with social behaviour. Grey branches indicate trait state unknown.

1983). Temporally split broods can then further favour helping behaviour in Hymenoptera through maternal manipulation of sex ratios between broods (Quiñones & Pen, 2017). The importance of the bivoltine life cycle suggests that a favourable climate, allowing uninterrupted development of the second brood, may have preceded the early evolution of sociality (Hunt & Amdam, 2005). For many facultatively social bee species, temperate climates allow such conditions (reviewed by Schwarz *et al.*, 2007), but the physiological threshold for *Ceratina* appears to require a warmer and/or longer active season.

The direct fitness benefits associated with solitary nesting mean that, despite favourable season length, the tropics must present considerable costs for the first brood to exhibit alloparental care when they are totipotent and not physiologically constrained to help. A combination of selective pressures may encourage daughters to remain in their natal nest to help, and mothers to allow them, through the threat of reproductive failure (Field *et al.*, 2000; Rehan *et al.*, 2014). Predation pressure

for bees is perhaps highest at lower latitudes, as found in other Hymenoptera (Jeanne, 1979), where ants are abundant and speciose (Guénard *et al.*, 2012). Solitary bee nests are also highly susceptible to parasitoids (Rehan *et al.*, 2011). By inducing individual behavioural responses that favour cooperation in the face of predation or parasitism, selection pressures may ultimately alter genotypes to provide the foundation for discrete social phenotypes across populations.

The behavioural plasticity of facultatively social individuals presents considerable insight into the thresholds of selective pressure that influence the costs and benefits of group living. With required behavioural precursors in place, selective environments may favour the evolution of obligate social behaviour. Although these will vary across species, our study underlines the importance of facultatively social species, such as the ceratinines, for understanding factors that facilitate the transition from solitary to social life.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

All tables presented in this Supporting Information are provided as worksheets within a separate excel file.

Table S1. Representatives included per key node for ancestral state reconstruction.

Table S2. Character matrix of sociality and climate states assigned to species of *Ceratina*, supported by available literature where possible, to reconstruct ancestral states. Records comprising multiple states were removed for tests of correlation between traits.

Table S3. Summary of ancestral state reconstructions for sociality and climate traits, represented by proportional probabilities, of key nodes. The italicized and greyed record indicates the best of five runs, presented in [Figure 2](#), based upon comparison of the harmonic mean, which is a running total, recorded in the final iteration. Classification of solitary taxa was confined to known obligate single foundress species, whereas social species represent all varieties of multi-female cooperative nesting.

Table S4. Summary of final iteration log for both independent (not correlated) and dependent (correlated) models with corresponding stepping stone sampler estimates of the marginal likelihood for each run. Italicized and greyed record indicates the best of five runs for each model, based upon comparison of the harmonic mean, which is a running total, recorded in the final iteration. Log BayesFactor tests determine evidence of support for the correlated model based upon comparison of the estimated marginal likelihood, from both the harmonic mean and stepping stone, for best runs. Classification of log BayesFactor scores are provided below.

Figure S1. Maximum credibility chronogram produced by [Rehan & Schwarz \(2015\)](#) with nodes included in reconstruction of ancestral states of in-group taxa (black) in this study highlighted with grey circles (labelled *a-i*) and nodes representing estimated dispersal ages presented in [Figure 1](#) indicated by red dots (I–IX). Maximum credibility values are provided above nodes, and time scale indicates millions of years since the present. Branch lengths are proportional to divergence time.

Figure S2. Transition rates matrix produced in the dependent model of evolution for sociality and climate. Horizontal arrows depict transition rates between climate states dependent on sociality as indicated by outer coloured squares; likewise, vertical arrows depict transition rates between social states dependent on the climate state of the inner squares. Arrow widths are proportional to rate.