Re-thinking the social ladder approach for elucidating the evolution and molecular basis of insect societies

Timothy A Linksvayer[1] and Brian R Johnson[2]

The evolution of large insect societies is a major evolutionary transition that occurred in the long-extinct ancestors of termites, ants, corbiculate bees, and vespid wasps. Researchers have long used 'social ladder thinking': assuming progressive stepwise phenotypic evolution and asserting that extant species with simple societies (e.g. some halictid bees) represent the ancestors of species with complex societies, and thus provide insight into general early steps of eusocial evolution. We discuss how this is inconsistent with data and modern evolutionary 'tree thinking'. Phylogenetic comparative methods with broad sampling provide the best means to make rigorous inferences about ancestral traits and evolutionary transitions that occurred within each lineage, and to determine whether consistent phenotypic and genomic changes occurred across independent lineages.

Addresses
[1] Department of Biology, University of Pennsylvania, United States
[2] Department of Entomology and Nematology, University of California Davis, United States

Corresponding author: Linksvayer, Timothy A (tlinks@sas.upenn.edu)

Introduction

Insect eusociality — commonly defined by reproductive division of labor, cooperative brood care, and overlapping generations [1–3] — has a scattered distribution across aphids, beetles, and thrips, but is especially common in the traditionally recognized social insects; termites, ants, corbiculate bees, and vespid wasps [4]. The most complex forms of eusociality (labeled 'advanced eusociality', 'obligate complex eusociality', 'hypersociality', 'superorganismality') [1,5], characterized by strong queen-worker dimorphism and colonies made up of dozens to millions of individuals evolved in only these four lineages: approximately 150 million years ago in the termites [6], 150 mya in the ants [7], an estimated 87 mya in the corbiculate bees [8], and at least 80 mya in the vespid wasps [9]. Societies with less complex forms of eusociality (often labeled 'primitive eusociality', 'incipient eusociality' [2,10,11]) characterized by no or very little queen-worker dimorphism and colonies usually made up of a few to dozens of individuals also evolved independently in several other hymenopteran lineages, including 45 mya in xylocopine bees [2,12], at least twice independently 35 and 20 mya in halictid bees [13,14], as well as in stenogastrine and *Microstigmus* wasps [15].

Researchers have long asserted that studying extant species with relatively simple forms of eusociality can provide general insight into the initial steps of eusocial evolution that likely occurred in the long-extinct ancestors of lineages with more complex forms of eusociality. For example, Evans [16] developed a hypothetical scenario of 13 phenotypic steps for vespid wasp sociality, or "rungs of a social ladder" [16], by arraying known extant wasp species into a putative evolutionary series based on their phenotypes. He posited that the ancestors of extant vespid wasps passed through this series of transitional forms during the evolutionary origin and elaboration of eusociality [16,17]. Similarly, Haskins and Haskins [18] and Haskins [19] proposed that ant researchers might be able to elucidate early stages of ant social evolution by studying extant ant species in genera such as *Myrmecia*, *Nothomyrmecia*, and *Amblyopone*, which were previously believed to be morphologically and behaviorally 'primitive', and also phylogenetically 'basal' (i.e. sister to the rest of ants) [20].

We refer to this line of reasoning and general approach as 'social ladder thinking'. As we describe below, social ladder thinking remains very widespread throughout the social insect literature, including in comparative genomic research. Social ladder thinking appears to have strongly impacted conceptualizations of social insect evolution, which in turn have shaped research questions, research approaches, and the interpretation of research results. We critically discuss the underlying assumptions of the social ladder approach, which are often only made implicitly, and we contrast it with 'tree thinking' [21,22], based on modern evolutionary biology, in particular phylogenetic comparative methods [23–26].

Social ladder thinking remains widespread in social insect research

The notion that steps in evolutionary transitions to complex eusociality can be elucidated by studying extant species considered to have 'primitive' or 'transitional' phenotypes (e.g. some halictid and xylocopine bees, some

polistine wasps) continues to be very broadly embraced, including in the context of comparative genomic and transcriptomic studies [11,27], and has been discussed in terms of the social ladder hypothesis, after Evans [16] and Evans and West-Eberhard [17]. For example, Rehan and Toth [11] states that "primitively eusocial species are useful for elucidating transitions", and Dew *et al.* [28] asserts, "Facultatively social species allow for empirical examination of the factors underlying evolutionary transitions between primitive and complex forms of sociality".

Other researchers [29–31], acknowledging that it is impossible to directly study the evolution of traits that evolved millions of years ago, explicitly argue that a powerful workaround is to pick an extant 'ancestor proxy' species that has certain ancestral traits (e.g. solitary life history) and assume that it is a living representative of the long-extinct ancestor of a second extant, phylogenetically related species with certain derived traits (e.g. complex eusociality). Comparisons between the two extant species are then made as a means to elucidate the evolution and molecular underpinnings of the derived trait(s) [29–31]. We note that this approach immediately begs the question of which extant species might be a good (or the best) ancestor proxy, given that any evolutionary or genetic inferences may strongly depend on the specific choice, since species often vary widely due to local adaptation, historical contingency, and so on.

While studying species with relatively simple societies to elucidate the evolution of species with more complex forms of eusociality may appear to be a very intuitive and attractive approach, we suggest that this approach is potentially problematic for several reasons. First, the idea that one extant species or lineage is generally phenotypically 'primitive' or ancestral and reflects the ancestor of a second more phenotypically 'advanced' or derived species is a widespread evolutionary misconception that is referred to as the 'primitive lineage fallacy' [32,33]. Briefly, terms such as 'ancestral' and 'derived' are only meaningful when applied to specific character states in a given phylogenetic context. All extant species or lineages possess mixtures of ancestral and derived character states and no extant species or lineage is generally 'primitive' or 'ancestral' relative to another lineage [21,32–34].

That said, such an approach could still be more-or-less valid if one strong assumption was true: that there is a more-or-less constrained phenotypic trajectory (i.e. a single 'social ladder') going from solitary life to complex eusociality that was consistently followed across independent origins of eusociality (Figure 1a,b). If this assumption was true, different lineages would be expected to follow similar phenotypic trajectories; and moreover, different species representing the same 'step' (regardless of phylogenetic relationship) along the constrained path might be directly comparable among each other, even if one was extant and

one was long extinct. Furthermore, if this assumption was true, then all species with phenotypically similar forms of eusociality (e.g. all species classified as being 'primitively eusocial'), might have experienced similar causal genetic changes, as a result of passing through the same predictable evolutionary steps (i.e. rungs on a 'social ladder'). These genomic similarities underlying the evolution of social complexity might then be predicted by some aspect of phenotypic resemblance (e.g. as characterized by the traditional categories of sociality; subsociality, primitive eusociality, advanced eusociality), regardless of the details of evolutionary history or phylogenetic independence, natural history, specific traits involved, etc. [35–37]. Whether the signal of these genomic similarities would actually be empirically detectable is another issue.

Empirical and theoretical reasons to doubt social ladder thinking

However, there are several compelling reasons to think that this assumption is not correct. In general, phenotypic evolution is not thought to be strongly constrained in such a way that a predictable and stepwise trajectory is consistently followed across independent lineages. Indeed, phenotypic evolution within a lineage usually does not occur along a linear path, but instead, many alternate combinations of traits are explored over evolutionary time in a bush-like fashion, often involving historical contingency (Figure 1c,d) [38,39]. This general conclusion is also supported by studies seeking to formally test the question of whether similar paths through phylomorphospace have been taken during the evolution of convergent morphology [40]. Patterns of social complexity within and among extant eusocial lineages also point away from a single predictable route that was consistently followed. For example, the diversity of trait combinations and life histories among extant species classified as having primitive or facultative eusociality demonstrates that there are many alternate ways to make a living as a simple eusocial species, and careful empirical studies of these species suggest an array of distinct, perhaps lineage-specific selective benefits and costs to eusocial life [10,41–47]. Similarly, extant species with phenotypically complex forms of eusociality also show a diverse array of combinations of traits associated with social complexity (e.g. colony size, degree of queen-worker dimorphism, number of worker subcastes, number of pheromones and exocrine glands, etc.), suggesting that an array of possible trait combinations and phenotypic evolutionary trajectories existed historically [48–51]. Available comparative genomic studies also support the conclusion that independent origins of eusociality largely involve distinct genetic changes [37].

Notably, lineages with species classified as having relatively simple forms of eusociality often seem to have maintained similar degrees of social complexity for tens of millions of years [12,52]. These results indicate that

Figure 1
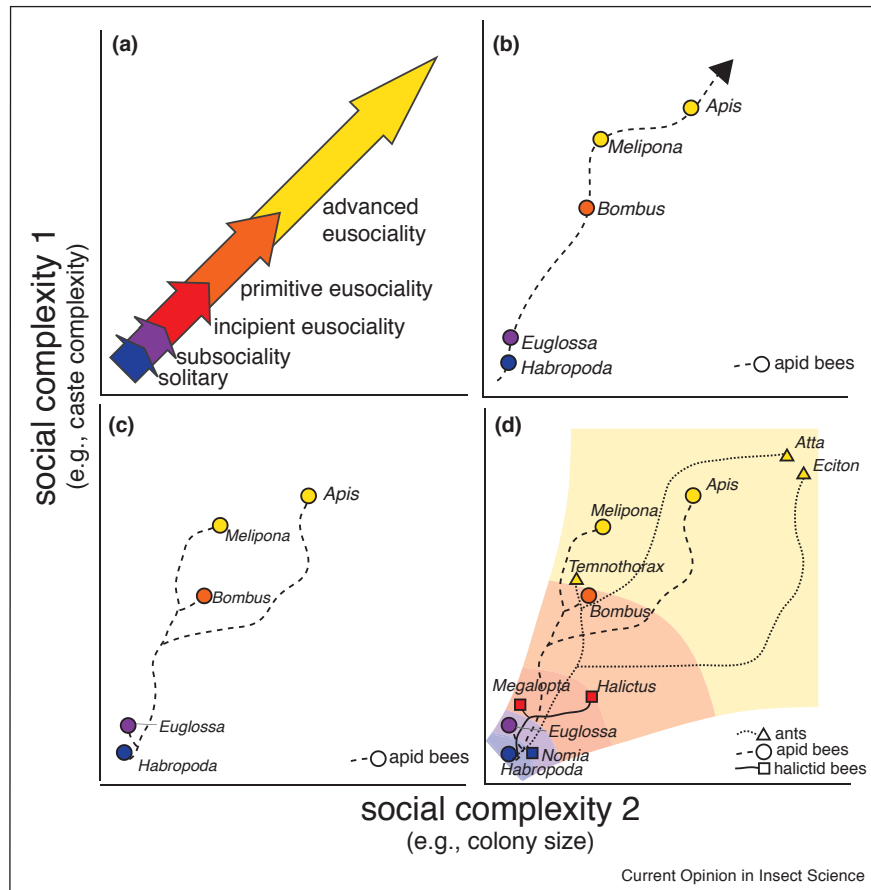
(a) According to a social ladder conceptualization, populations are assumed to transition progressively through a stepwise sequence of phenotypic categories [11,16] along a more-or-less linear trajectory through trait space. Here, we visualize trait space as two axes of social complexity (e.g. log colony size on the X-axis and a continuous measure of the complexity of the caste system on the Y-axis), but additional traits (e.g. number of social signals) could be used to quantify social complexity, so that in reality the relevant trait space is multidimensional. Note that the phenotypic categories have various alternate definitions and labels in the literature, and there has also been renewed discussion about whether the ancestors of eusocial lineages were always subsocial at some point, as illustrated here [1,2,10]. **(b)** Social ladder thinking seems to assume that all populations would fit on a highly constrained evolutionary trajectory (dashed arrow) through trait space, so that populations can only move up (or down in some cases [11]) the trajectory, corresponding to an overall increase (or decrease) in social complexity. Extant groups (e.g. various apid bee genera, illustrated here) at different locations in trait space are then assumed to reflect different stages of social evolution [11,16]; the ancestors of groups with higher social complexity is assumed to have historically passed through locations in phenotypic space occupied by groups with lower social complexity; and extant groups with lower social complexity are assumed to reflect the ancestor of groups with higher social complexity [30,31]. Note that in reality, the apid groups illustrated here vary widely in measures of social complexity, so that for example, the illustrated location of *Melipona* in trait space might reflect the location of a single species or the genus mean, but other related species and genera would likely be in different regions of trait space. This suggests that at best, extant groups might only somewhat lie on a linear trajectory that might only somewhat reflect historical evolutionary trajectories. **(c)** If the actual phenotypic trajectories that were taken historically by the ancestors of each group of extant apid bee genera could be inferred and plotted (e.g. with a phylophenospace approach [40]), we hypothesize that they would resemble something like the branching pattern illustrated here, and not a constrained linear trajectory. **(d)** If additional groups (e.g. ants, halictid bees) are also added, we would expect to observe lineage-specific patterns. Note that the ancestors of groups with relatively high social complexity still presumably historically passed through lower levels of social complexity, as illustrated by the colored regions in trait space. However, we hypothesize that in contrast to a strict social ladder conceptualization, the convergent evolution of social complexity involved many alternate paths (e.g. compare the imagined paths of the ancestors of *Atta* and *Eciton*), so that extant groups with lower levels of social complexity are only superficially similar to the ancestors of extant groups with higher social complexity. We also note that this superficial similarity is also likely to decrease as more and more traits (including those unrelated to social complexity) are considered.

extant species and lineages with relatively simple forms of eusociality should be understood as having successful alternate life history strategies when compared to extant species with more complex forms of eusociality. These results are not consistent with the notion that species with relatively simple forms of sociality are in any way transitional or on their way to evolving more complex forms of eusociality.

Thus, we believe that there is little theoretical or empirical reason to think that there is a single phenotypic route involving predictable evolutionary changes (i.e. a 'social ladder') across independent origins and elaborations of eusociality, and there is also little theoretical or empirical reason to think that extant species with simple forms of eusociality are representative of the ancestors of extant lineages with complex eusociality. At the least, we argue that the idea of a single stepwise phenotypic trajectory from simple to complex societies should be treated as a hypothesis that researchers should seek to evaluate empirically in comparison to alternate hypotheses (Figure 1), for example, using formal phylogenetic comparative approaches [40].

Overall, we believe that lineages with both phenotypically simple and more complex forms of eusociality should be studied *in their own right*, in order to elucidate phenotypic and genetic changes that occurred in the ancestors of each lineage, but not as a means to attempt to elucidate general evolutionary steps that occurred in other lineages. Subsequently, the complementary aim of identifying phenotypic and genetic changes that have repeatedly been involved during the evolution of eusociality in independent lineages can be tackled. We emphasize that each of these steps requires broad sampling, in order to make rigorous inferences about likely ancestral states (i.e. using formal phylogenetic comparative methods) [23–26]. Fortunately, such broad sampling will be facilitated by decreasing sequencing and computational costs, and advances in phylogenomic approaches [53,54], although limited available phenotypic data (e.g. measures of colony size and other aspects of social complexity, basic natural history data, etc.) will likely remain a major constraint.

We have argued that extant eusocial species from lineages with relatively simple forms of social complexity cannot be considered to be living representatives of the long-extinct ancestors of lineages with more complex forms of eusociality. However, we also emphasize that decades of research focused on lineages with relatively simple societies highlight many important insights about how these societies function and evolve [44,55,56]. Socially polymorphic species, and closely related species differing in social organization, present especially exciting study systems, for example for elucidating the genetic underpinnings of variation in social organization within these lineages [56,57]. We simply emphasize that great care must be taken before concluding that results from these lineages inform the genetic basis and evolution of eusociality in other lineages.

If there is no consistent social ladder, are there no shared features underlying the convergent evolution of eusociality?
We have also argued that the specific phenotypic routes historically taken by different eusocial lineages are likely to be largely distinct (see Figure 1c,d), so that a social ladder perspective, assuming more-or-less consistent steps taken in a progressive way across lineages, is likely to be incorrect and misleading. That said, we certainly acknowledge that previous research focused on drawing general conclusions based on broad comparisons across eusocial lineages has made important contributions, for example, by highlighting general principles governing how societies evolve [1,4,11,44,50,58–61].

Even though the specific phenotypic routes are likely to be largely distinct between lineages, the convergent evolution of suites of traits characterizing eusociality (e.g. reproductive caste) in different insect lineages is likely *to some degree* to involve similar genes or gene pathways. The important empirical question is: to what degree [50,62]? Each lineage that independently evolved eusociality shares a common ancestor, and thus shares common physiological and developmental features. These shared features have been referred to as 'groundplans' [63–65] or 'toolkits' [61] and are hypothesized to be important for the convergent evolution of eusociality. For example, it certainly seems reasonable to expect that independent origins of an egg-laying caste in two different insect lineages might both involve changes in molecular pathways regulating female insect reproductive development and physiology [63]. Similarly, widely conserved insect pathways such as insulin/TOR signaling pathways that mediate physiological responses to the nutritional environment, and endocrine pathways such as JH/ecdysone involved in insect development must be involved to some degree in the evolution of insect polyphenisms, including social insect queen-worker caste dimorphism [50,62,66,67].

Indeed, previous studies found evidence for a small amount of overlap in genes or functional classes of genes with caste-associated expression patterns [68]. A recent study specifically designed to attempt to assess the degree of overlap in the transcriptomic underpinnings of caste-based division of labor in the honey bee *Apis mellifera* and the pharaoh ant *Monomorium phaoronis* found that the proportion of shared genes with shared caste-biased expression in the abdomen was somewhat similar ($\sim$0.3 versus $\sim$0.4) as the proportion of shared genes with shared differential expression across development, which appears striking given that development is considered to be strongly conserved [69]. Future studies including many more species will be necessary to determine how general these patterns are. Overall, these studies suggest that the convergent evolution of eusociality has likely involved the recruitment of some overlapping sets of genes in lineages with independent origins and elaborations of eusociality, together with many genes showing lineage-specific patterns of expression as well as taxonomically restricted genes [70–73]. Such studies point to the potential to elucidate both the shared and distinct genetic features involved in the independent origin of eusociality in different lineages.

Conclusions

We have discussed limitations with the approach of seeking to elucidate general early steps in eusocial evolution by studying extant species with relatively simple forms of eusociality. We suggest that there are no compelling empirical or theoretical reasons to think that extant species with relatively simple forms of eusociality can serve as stand-ins to understand the evolutionary steps taken by the long-extinct ancestors of species with more complex forms of eusociality. Instead, we argue that species from all eusocial lineages should be broadly sampled and studied in their own right. Phylogenetic comparative methods can make the most of data from such broad sampling, combined with phylogenetic information, to make inferences about ancestral traits as well as historical evolutionary changes for these character states [23–26]. Indeed, such phylogenetic comparative methods have been widely used to elucidate ancestral states and historical transitions for traits related to sociality and social complexity in various social insect lineages, including vespid wasps [9,74], allodapine bees [52], and ants [49,75], as well as in other social lineages such as snapping shrimp [76], and primates [77,78]. These approaches have also increasingly been used to infer and reconstruct ancestral genome content [79], which might provide further clues for evolution of shared and distinct eusocial features across lineages. We also echo previous authors emphasizing the importance of carefully defining social complexity based on specific traits, as these traits often differ between eusocial lineages, and small shifts in trait definitions can have large impacts on evolutionary inferences [2,3,10]. Finally, we stress that researchers must very carefully interpret and present the results of all such comparative studies, along with assumptions and caveats when attempting to make general conclusions about eusocial evolution.

Conflict of interest statement

Nothing declared.

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