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Eusociality is not a major evolutionary transition, and why that matters

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Abstract

Major evolutionary transitions (METs) across Earth's biological history describe fusions of lower-level entities into higher-level individuals (evolutionary transitions in individuality: ETIs) as well as novel forms of information storage and transmission (Information Leaps). Obligate eusociality is frequently listed as a MET—most often in the context of being an ETI and with an extrapolation that the ETI requires inclusive fitness maximization for all parties. However, obligate eusociality neither fundamentally alters how information is stored and transmitted nor meets the various criteria proposed for an ETI. We argue that rather than representing a higher-level individual, the evolution of non-reproductive worker castes is more analogous to a novel 'organ' that maintains homeostasis and nurtures the gonadal tissue of mated queens. Worker castes benefit queens by performing dangerous but necessary functions such as foraging, while enabling the gamete-producing functions to be kept relatively safe. This is an ecologically successful and significant evolutionary innovation, which can be thought of as a major competitive transition (MCT). In this context, we hypothesize that worker castes are most likely to evolve through parental manipulation. Employing such a MCT perspective generates a broad series of predictions about eusocial life histories.

Keywords Eusociality · Major evolutionary transition · Relatedness · Manipulation · Individuality · Information

Introduction

There is a common perception amongst evolutionary biologists that a small number of adaptations were particularly impactful in altering the history of life on Earth. Such events have been considered 'major' transitions that differ from the millions of other fine-tuning adaptations produced through natural selection. Maynard Smith and Szathmáry (1995) coined the term "Major Evolutionary Transition" (MET) to refer to eight such events, from the origin of cells to the emergence of human language. One of their proposed METs was the formation of social groups with castes of morphologically distinct reproductive and non-reproductive specialists—as is most evident in many social insect species.

In general, Maynard Smith and Szathmáry's list included two types of MET: (1) Cases of previously free-living entities foregoing independent reproduction to band together as a single reproducing unit (such as the evolution of eukaryotes or multicellular individuals) and (2) Novel forms of storage or transmission of information (such as the emergence of DNA or human language). Later, the former were referred to as evolutionary transitions in individuality (ETIs: Michod 1999) and the latter as Information Leaps (Robin et al. 2021). Since 1995, Maynard Smith and Szathmáry's list has been amended, edited, contracted, or expanded by various authors (e.g., Bourke 2011a; Calcott and Sterelny 2011; Szathmáry 2015; West et al. 2015). Most authors still consider the evolution of morphologically sterile worker castes as a MET, which they typically describe as exhibiting a form of "eusociality" (e.g., Gardner and West 2014; Szathmáry 2015; West et al. 2015; Koonin 2016; Korb and Heinze 2016; Marshall 2016; Bourke 2019; Ågren et al. 2019; Durand et al. 2019; da Silva 2021; Kun 2021; Carmel 2023).

Nevertheless, other authors have used the term "major evolutionary transition" to refer to quite different kinds of

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adaptations. These tend to be highly advantageous to organisms and impactful to Earth's ecosystems (so colloquially 'major'), but do not qualify as ETIs or Information Leaps. For example, Schwab et al. (2020) write: "Major evolutionary transitions, in which animals develop new body plans and adapt to dramatically new habitats and lifestyles, have punctuated the history of life. The origin of cetaceans from land-living mammals is among the most famous of these events" (pg. 10,422) (see also Aubret et al. 2007). Qiu (2008) considers the emergence of land plants as a major evolutionary transition because "it irreversibly changed the evolutionary course of life and the environment on earth" (pg. 287) (see also Van Etten and Bhattacharya 2020).

To reduce confusion across terms, Robin et al. (2021) recommended retaining Maynard Smith and Szathmáry's (1995) original definition of major evolutionary transition applied only to ETIs and Information Leaps. Additionally, they coined the term "Major Competitive Transition" (MCT) to give a conceptual home to major events such as the water-to-land and land-to-water transitions (Qiu 2008; Schwab et al. 2020). Specifically, a MCT greatly increases the ecological success and abundance of a species or clade by enabling colonization of new niches or novel ways of exploiting existing niches, potentially giving rise to adaptive radiations. Some additional examples include the emergence of flight, amniotic eggs, and inordinately large brains in *Homo sapiens*.

A fundamental difference between a major evolutionary transition (such as an ETI) and a Major Competitive Transition in the Robin et al. (2021) schema is in explaining their existence. Entire books have been written in consideration of how ETIs might overcome what appears to be a significant selective barrier—why should free-living entities give up reproduction to become sterile parts of a higher-level individual (Buss 1987; Michod 1999; Bourke 2011a; Boomsma 2023)? In contrast, MCTs are easily explained by the magnitude of direct fitness advantages they provide through improved competitive ability. For example, although there may be a multitude of questions about how functional wings have evolved, there is little mystery as to why this adaptation increased in frequency. It is important to note, however, that METs and MCTs need not be mutually exclusive. For example, the evolution of sensory systems can be considered both an Information Leap MET and a MCT (Robin et al. 2021).

In this paper, we question whether social insects have truly undergone a major evolutionary transition as currently defined. This first involves clarifying what is meant by "eusociality" as it relates to the concept of a MET (and whether "superorganismality" is a more descriptive term: Boomsma and Gawne 2018). Thereafter, we build the case that no social insect species has undergone a MET, either as an Information Leap or ETI. In doing so, we review various proposed criteria for defining an ETI and a common

extrapolation arising from the ETI concept that evolution of obligately sterile castes requires inclusive fitness gains for all parties.

While not an ETI, we propose the worker caste is analogous to a novel 'organ' supporting an existing individual (the queen) by gathering food and resources, maintaining homeostasis, and defending the queen's reproductive tissue. The evolution of sterile, morphologically distinct castes would, therefore, be more accurately described as a Major Competitive Transition. In focusing on the competitive advantages that morphologically distinct worker castes provide (and moving beyond a narrow ETI framework), explanations for their evolution other than the general form of Hamilton's rule become more salient. In particular, the evolution of this MCT may have proceeded through parental manipulation.

Defining eusociality

From the original definition by Batra (1966) onwards, there is little unanimity over which specific trait or sets of traits (behavioral, morphological, or both) define eusociality. In its broadest definition, eusociality includes most forms of cooperative breeding (Sherman et al. 1995; Lacey and Sherman 2005). Most authors, however, distinguish between species where the worker and queen castes are morphologically distinct from where workers and queens are not. The former (variably referred to as complex, advanced, or obligate eusociality), but not the latter (simple, primitive, or facultative eusociality), is commonly proposed to have undergone a major evolutionary transition.

Boomsma and Gawne (2018) recommend adhering to Batra's (1966) original definition of the term "eusociality," which did not include the requirement of a morphologically differentiated worker caste. For social insect species with morphologically distinct and permanently unmated worker castes, they eschew the term "obligate eusociality" in favor of "superorganismality". Although Boomsma and Gawne (2018, pg. 41) suggest these are functionally identical terms, disagreement remains (da Silva 2021), and the term itself has been used differently: e.g., "sterile workers are neither necessary nor sufficient for superorganismality" (Gardner and Grafen 2009, pg. 667). Furthermore, despite explicitly acknowledging the work of Boomsma and Gawne (2018), many scholars have continued to use "eusociality", with attending adjective modifiers such as obligate, advanced, or higher (e.g., Sumner et al. 2018; Bourke 2019; Durand et al. 2019; Pernu and Helanterä 2019; Grüter 2020; da Silva 2021).

Here, we prefer to use the term obligate eusociality over superorganismality. To label a social group as "super" is to already imply in its name that a higher level of individual has formed—a conclusion that we challenge. Furthermore, to use entirely different words for facultative sterility versus

obligate sterility (= superorganismal) functions as a linguistic segregation that implies two separate phenomena and not a continuum across one: i.e., a qualitative rather than quantitative evolutionary change in reproductive capacity. This is a proposition that needs more testing (Hunt 2007). In this paper, we will argue that neither facultatively nor obligately eusocial insects have undergone a major evolutionary transition, either as an Information Leap or an Evolutionary Transition in Individuality. We will primarily focus our discussion on obligately eusocial species, because if these do not meet the criteria for a MET then neither do facultatively eusocial species.

An Information Leap MET has not occurred

Maynard Smith and Szathmáry's (1995) original MET list included such transitions as the evolution of DNA from RNA, sexual from asexual reproduction, and human language. These involved novel forms of *storage* and/or *transmission* of information and can be called Information Leaps (Robin et al. 2021). Building from Jablonka and Lamb (2006), Robin et al. (2021) delineated four levels of information: (I) Genetic information, (II) Epigenetic information, (III) Learned information, and (IV) Inscribed information, the latter of which exists in abiotic media rather than within organisms. They classified two forms of Inscribed information: 'Iconic' and 'Instructional.' The former can be transmitted among individuals indirectly, without them meeting, but is only available locally and within a certain time frame; such as in chemical trails. The latter is language transformed into physical, symbolic formats such as writing or computer code. Finally, Robin et al. (2021) introduced Level V information. This is information generated by abiotic entities (e.g., computers and artificial intelligence), where the input-to-output process cannot be understood or duplicated by any other means. Social insects do not use Level IV Instructional or Level V information.

In addition, neither Genetic, Epigenetic, Learned, nor Iconic information first arose in the social insects, or is used in qualitatively different ways by obligately eusocial insects compared to facultatively eusocial ones or even some non-social species. It could be argued that some social insects store *more* of some types of information than other animals, e.g., through vast networks of chemical trails that rely on Iconic information (Level IV). This may enable more learning (Level III) and collective behavior. However, this information is ephemeral and disappears if not continuously reinforced. Moreover, within a single generation, such species do not learn significantly more information than other species with sensory systems and brains. Finally, collective behavior is not unique to social insects and has evolved in multiple taxa.

In summary, there is little to suggest that social insects increase their access to or ability to use information to a degree that would rank as an Information Leap. Thus, if they have undergone a MET, it must be an Evolutionary Transition in Individuality. Indeed, when 'eusociality' or 'obligate eusociality' appears on lists of METs, it is almost always in the context of being an ETI (e.g., Bourke 2011a; Gardner and West 2014; West et al. 2015; Marshall 2016; Ågren et al. 2019; Bourke 2019; Durand et al. 2019; Korb and Heinze 2019; Kun 2021; da Silva 2021; Carmel 2023).

Obligate eusociality is not an ETI

Across eight separate lists of METs, the evolution of eukaryotes with mitochondria, multicellularity, and eusociality are the only phenomena that all the authors agree are METs and may involve a change in individuality (Herron 2021). Authors do not, however, always define an Evolutionary Transition in Individuality in the same way, as shown in four examples ranging from very broad to rather restrictive.

- "[A]n evolutionary process that results in a new population of evolutionary individuals... Because individuality comes in degrees, and any line we draw will be arbitrary." (Herron 2021, pg. 7).
- "[T]he evolution of a higher-level biological unit out of formerly-free living units." (Okasha 2022, pg. 2).
- "[I]nseparability ... seems irreversible and may mark the point where a group of individuals becomes a new individual at a higher hierarchical level." (Carmel and Shavit 2020, pg. 1).
- "[E]volutionary changes in hierarchical complexity that involve both a loss of independent breeding and higher-level adaptations to more inclusive levels of organization ... [and is] evolutionarily irreversible." (Boomsma and Gawne 2018, pg. 30).

Summing across the definitions, an ETI can be concluded as potentially having four criteria: (1) The immediate ancestral state consisted of free-living entities, from which a higher-level unit emerged; (2) This higher-level unit is inseparable; (3) The higher-level unit is evolutionarily irreversible; and (4) The former, lower-level entities have lost all ability to independently reproduce. Criteria (1) and (4) are very clear in their defining characters, but (2) and (3) are less so, with potentially variable levels of separability or reversibility, respectively.

First, consider how separability varies across proposed ETIs. A mitochondrion cannot survive outside of the eukaryotic cell, and almost all eukaryotic cells could not survive the loss of their mitochondria. Moreover, the fusion between cells and their mitochondria is extended to the genomic level, as mitochondrial DNA is transferred

into the nuclei, forming a dual origin but unified single nuclear genome (Nonacs and Tolley 2014). Hence, almost all eukaryotic cells are truly inseparable.

In the realm of multicellular organisms, simple ones that lack tissues and organs are relatively easily divisible and some species even switch between uni- and multicellularity throughout their lives (Staps et al. 2022). Thus, only complex multicellularity is commonly regarded as an ETI (Robin et al. 2021; Rose and Hammerschmidt 2021). Nevertheless, complex multicellular species have variable degrees of separability. Among animals, an adult flatworm can be cut into pieces with each piece surviving, while vertebrates might only be separable at the blastocyst stage of development (Vauvert et al. 2018).

Social insect groups exhibit an even higher degree of separability. Clearly distinct individuals can move between groups at will. Nest drifting, wherein workers move from their natal nest to another, is common across many species including those with morphologically distinct worker castes (Sumner et al. 2007; Nonacs 2017, 2023). Carmel and Shavit (2020) replace the colloquial definition of inseparability with the following specific criterion: “In social colonies, inseparability is inferred when queen-replacement is not possible” (pg. 4). However, queen replacement occurs in many obligately eusocial taxa that have been considered ETIs, such as ants and honey bees. Moreover, in unicolonial ant species, queens and workers regularly move between nest groups such that the entire colony can occupy an area hundreds of square kilometers in size (Moffett 2012). Would this now be the “inseparable” individual? Overall, if a nest or colony is to be considered a higher-level individual, it must be in a context in which the component parts can subdivide or fuse, and are often interchangeable across other such individuals.

Second, consider the criterion of evolutionary irreversibility. The observation that obligately eusocial species have never reverted back to a casteless or solitary ancestral state is presented as strong evidence for the occurrence of an ETI (Boomsma and Gawne 2018; Boomsma 2023). However, to claim that an *obligately sterile* worker caste is an irreversible ETI (Boomsma and Gawne 2018) is to imply that this is an absorbing state. Yet many species that were once obligately eusocial have lost the queen caste and the workers have reverted to being able to reproduce (Rabeling and Kronauer 2013; Majoe et al. 2021). Thus, in these cases there is a reversal from ‘post-ETI with obligately sterile workers’ to a pre-ETI state (sensu Boomsma and Gawne 2018). A further reversal to a completely solitary lifestyle seems highly unlikely—not necessarily because an ETI has occurred, but because a solitary lifestyle may well be a poor strategy against competitors in the environment. Likewise, many other species that have not undergone ETIs rely heavily on their group members, populations, and communities

for survival (e.g., humans: Robin et al. 2021; Denton et al. 2023).

Consider also that other events that are commonly regarded as Evolutionary Transitions in Individuality may not be totally irreversible. For instance, a widely accepted ETI-defining event is the mitochondrial symbiosis during the transition from prokaryote to eukaryote (Margulis and Fester 1991; Zachar and Boza 2020; Kun 2021). However, even this event can be reversed. Karnkowska et al. (2016) discovered a eukaryotic species, *Monocercomonoides*, without mitochondria. Their data support the conclusion that the mitochondria were lost over evolutionary time, rather than absent in the ancestral state.

Finally, in the broadest sense, evolutionary irreversibility seems to be more a feature of long-term genetic change, per se, than a diagnostic character for an ETI (i.e., Dollo’s Law: Simpson 1953). Cetaceans have not evolved back into terrestrial artiodactyls. *Homo sapiens* will not evolve back into *H. erectus*. Irreversibility would seem more a function of the length of time since a change occurred and the amount of genetic differentiation thereafter, than whether or not a species is undergoing an ETI. Clearly, even if all proposed ETIs are irreversible, not all irreversible adaptations are ETIs. Thus in our opinion, irreversibility of any evolved feature is the weakest and least convincing evidence for an ETI.

Interestingly, to propose that obligate morphological caste evolution is the ETI immediately contradicts criterion (1). Such workers never existed as free-living, non-social individuals. Here, the comparison to complex multicellularity is most apt. The evolution of a new tissue layer or organ system within a complex multicellular individual is not considered to have created a novel, higher-level individual. Such new tissues or organs evolve within the existing state of individuality to the benefit of the gametic tissue. Similarly, the emergence of a worker caste supports the gamete production of an existing complex multicellular individual (the would-be queen). Furthermore, worker castes follow an analogous developmental ontogeny as body organs. Larvae, like replicating tissue cells (Sun et al. 2021), have their developmental options continually narrowed until they can become only one thing, such as a worker. Just as for organs like livers and kidneys, a worker’s remaining fitness-enhancing option is to maximize the success of the collective and therefore the gamete producers.

This leaves only the fourth ETI criterion to consider, namely that former, lower-level entities have lost all ability to independently reproduce without the higher-level entity. As discussed above, workers and body organs were never free-living organisms that subsequently “lost” reproductive abilities. Furthermore, queens of many obligately eusocial species still produce their first cohort of offspring when initiating a new colony in the absence of any worker presence (e.g., ants: Hölldobler and Wilson 1990). Their retained

ability to reproduce apart from the higher-level entity is a clear violation of criterion (4).

Finally, because we are proposing that obligate eusociality is a variant of complex multicellularity instead of a *new* ETI, another possible phrasing of criterion (4) is: Does reproduction by an obligately eusocial group differ from that of a non-eusocial, multicellular individual due to the input from a higher level of individuality? During reproduction in all social and nonsocial species, offspring receive genetic material from at most two parents. No additional amount of or novel ways of transmitting Level I and II genetic and epigenetic information across generations occurs in any social insect species relative to what solitary complexly multicellular individuals can do. Thus, there is no fundamental change in reproduction due to a higher level of individuality. There is no ETI.

In the following section, we address a fifth concept that has become tightly linked with Evolutionary Transitions in Individuality, but is by no means a universally accepted criterion—inclusive fitness maximization.

ETIs and inclusive fitness gains

In conjunction with accepting that obligate eusociality is an ETI, many authors also either explicitly or implicitly assert that the evolution of higher-level individuality is best explained through inclusive fitness theory. For example, Bourke (2011b) explicitly emphasizes the need for fitness goals and outcomes to all align: “Societies are stable to the extent that the inclusive fitness optima of their members coincide. This in turn provides the rationale for the entire ‘major transitions’ view of evolution, whereby the origin of novel types of group in the history of life (e.g. genomes within cells, multicellular organisms and eusocial societies) can be explained as the result of their previously independent constituent units achieving a coincidence of inclusive fitness optima through grouping” (pg. 3315). More implicitly, Carmel and Shavit (2020) regard inclusive fitness as “one of the most widely accepted explanations of... the change in individuality that occurs through major evolutionary transitions” (pg. 2), while Pull and McMahon (2020) state that: “The major evolutionary transitions framework explains, via inclusive fitness theory, how new levels of biological individuality... can emerge.” (pg. 1).

It is important to note that inclusive fitness theory is widely believed to be capable of explaining *all* adaptations—not just ETIs. For example, over 100 authors (Abbott et al. 2011) contend that: “Inclusive fitness is as general as the genetical theory of natural selection itself. It simply partitions natural selection into its direct and indirect components” (pg. 1). What they are referring to is the general form of Hamilton’s rule (Birch 2014), which is derived in such a way that the dependent variable (the change in frequency of

cooperators) is used to ‘predict’ the same dependent variable—meaning that the rule is always true (Nowak et al. 2017).

Why is a rule that applies equally well to all adaptations (on par with the theory of natural selection itself), so commonly associated with ETIs in particular? Maximizing inclusive fitness cannot specifically define an ETI, just as ‘natural selection occurs’ cannot usefully define a MET. A possible reason for the association between ETIs and inclusive fitness theory is that the latter can be *useful* for understanding ETIs; i.e., it seems counterintuitive why somatic cells or workers would willingly give up direct fitness unless this somehow increased their inclusive fitness. This is in contrast to major competitive transitions, whose evolution can easily be explained by referencing direct fitness advantages.

If being explicable only by indirect fitness gains were to be a shared feature across obligate eusociality and all other ETIs, this could be a rationale for associating them together as representing the same phenomenon. Thus, despite failing any or all currently proposed criteria for an ETI, adding “coincidence of inclusive fitness optima through grouping” as a 5th possible criterion could redefine obligate eusociality as an ETI. This criterion, however, could apply equally well to facultative eusociality and many other examples of cooperative behavior.

This propensity for excessive generality from inclusive fitness theory limits it as an informative explanation for obligate eusociality and ETIs, in general. For example, Corning and Szathmáry (2015) write: “the assertion that the goal of an evolutionary agent is to ‘maximize its inclusive fitness’ is not very helpful... Especially in relation to the discussion about the major transitions, consider again the stochastic corrector model [for understanding the ETI of protocells]. It is a continuous-time, fully dynamic model with reproducing and dying-out groups... Once you solve the group selection model you can always post hoc make up one using inclusive fitness, but this produces no additional information” (pg. 53). Szathmáry (2015) also notes that in general, the egalitarian ETIs in which unlike units fuse together (e.g., the transition to eukaryotes from prokaryotes) can be explained without invoking inclusive fitness theory. Indeed, as the relatedness between the unlike units is zero, one only needs to examine direct fitness benefits and costs to determine if the adaptation should increase in frequency. Similarly, the exact role that kin selection plays and the effects it might have had throughout the evolution of wasp sociality (relative to group-level benefits) have been questioned (Hunt 2007). While Hamilton’s General Rule will always hold, explanations that are more specific to the adaptations of interest are clearly more useful than this particular rule that applies to any adaptation.

Therefore, we can simplify the problem of how obligate sterility evolved by posing a series of straightforward and

specific questions and possible answers. How can groups increase their functioning efficiency (Oster and Wilson 1978)? By a division of labor with specialized castes where one caste (the queens) is reproductive and the other (the workers) is completely or mostly sterile and obliged to do all the functions that maximize group survival. Who stands to gain the most from being part of a group with such a division of labor (Beekman and Ratnieks 2003)? It is the fecund queens and not the sterile workers. Indeed, in measuring benefits, costs, and relatedness in *Lasioglossum malachurum*, Richards et al. (2005) found that workers would benefit more from direct reproduction than by investing in their queen's reproduction. Who might have the power to manipulate developmental trajectories to create a coincidence of shared goals in such groups (Huisken and Rehan 2022)? It is parents that can control how much and what type of food their future offspring receive. Thus follows that a simpler and more specific hypothesis for the evolution of all levels of eusociality is parental manipulation. In the case of social insects, the end result is a Major Competitive Transition, which is due to being able to segregate and safely isolate the gametic tissue from the dangerous tasks of foraging and bodily defense.

Obligate eusociality as a MCT

Discarding the proposition that obligate eusociality is an ETI and considering if it is a Major Competitive Transition immediately draws attention to two evolutionary questions: what process or processes can lead to the loss of reproductive totipotency in some group members, and does such a change increase the competitive ability of the group? Here, we propose that obligate sterility could evolve via parental manipulation, where some offspring are constrained in their development to the degree that becoming sterile workers is the only remaining viable option. This hypothesis leads to a broad series of predictions (Table 1). Moreover, if manipulation is evident across all levels of eusociality from the most facultative to the most obligate, then perhaps it ought to be the null hypothesis for the proposed transition events within that spectrum, against which all other hypotheses are compared.

Whereas ETIs are defined with respect to organismal complexity, with the exclusion of ecological ramifications (e.g., Szathmáry 2015), intrinsic to the MCT framework is the need to identify how having reproductive and non-reproductive castes is competitively advantageous within an ecosystem. In other words, a MCT must be 'major' in the colloquial sense of the word: it must greatly increase the abundance and ecological success of the species, possibly producing adaptive radiations and enabling novel niches to be exploited. Therefore, rather than passing over why is eusociality so successful, a MCT approach also generates

predictions about the taxonomic distribution of eusociality and about a variety of life history characteristics that are adaptive for increasing group-level, and thus parental, reproductive success (e.g., the prevalence of low within-group relatedness due to behaviors such as polygyny and worker drifting; Table 1). Thus, considering the evolution of social insects as a MCT that can occur within complex multicellular species is a broadening perspective that connects the interplay of many aspects of their biology, rather than restricting it to an ETI framework that is based on inclusive fitness generalities.

Conclusions

MET, ETI, MCT, eusociality and superorganismality are terms and not real objects. They are definitions that reflect a given author's opinions and prejudices. As such, a variety of definitions exist in the literature and no one definition is more correct than any other. Their inherent value resides in how they organize one's thinking relative to the phenomena being considered. In this light, our argument for treating highly ecologically successful transitions to eusociality (both facultative and obligate) not as METs but rather as MCTs is as follows.

The brilliant evolutionary innovation that gave social insects a tremendous competitive advantage is physically separating the germ line from a large portion of the soma. This allows the evolutionary future of the individual to be placed as much as possible out of harm's way, while a large portion of the body executes the dangerous tasks required for survival and reproduction. For a typical metazoan animal, a grievous injury to some body part may result in the demise of the germ line as well. For a eusocial organism, injured soma can be replaced at a lower cost, decreasing the risk that the entire individual dies. Much of the main body, namely the large 'worker organ,' is expectedly disposable and replaceable.

Secondarily, eusociality allows the somatic body to be a chimera of multiple fathers, or if also admitting drifters, a product of multiple mothers and fathers. This occurs at no cost to the germ line represented by the queen's gametes and those of her mates. Indeed, to the degree that a diverse group improves group functioning and success, it will increase parental fitness. Furthermore, whatever the queen's life expectancy is—short or bordering on decades—the reproductive potential of the workers can be adjusted to match: from totipotency if extremely short to complete sterility if very long. Manipulation can work to produce the most successful version of a MCT.

Thus, eusociality as a Major Competitive Transition can link both a viable evolutionary mechanism supported by considerable evidence at all levels of social complexity

Table 1 Predictions about facultative and obligate eusociality derived from a MCT perspective, and not from the classical MET one. We pose 11 specific predictions across 6 areas of eusocial life history and behavior. Note that the availability of data to test predictions varies. Thus, some are more speculative about what future research may find

A. The taxonomy and genomics of eusocial species

Taxonomic rationale: Workers must be relatively cheap to make, yet be able to do enough useful work (e.g., gathering resources) to exceed their replacement cost. Hence, workers would be a “disposable caste” (Porter and Jorgenson 1981) that functions as a somatic organ

Genomic rationale: ETI and MCT scenarios may be expected to differ in genomic signatures for the appearance of novel gene regulatory networks (GRNs) through step-wise modes of evolution (Boomsma 2023)

Prediction A1: Only in small-bodied species with rapid generation times and continuous reproduction would a eusocial life history generate enough competitive advantages to evolve

Evidence for A1: Of the 21 taxa listed as being farther along a eusociality continuum or superorganismal by Boomsma and Gawne (2018; Fig. 2, pg. 42), arthropods comprise 18 of them, including all of those classified as superorganismal. Of the remaining three, two are small mammals (mole rats) and the other is *Himasthla* trematodes

Prediction A2: If the development of obligately sterile castes differs qualitatively from facultative castes as an ETI, then unique GRNs should be found disproportionately in obligately sterile species (Boomsma 2023). Alternatively, if sterility levels fall along a continuum as fitting a MCT, then GRNs are equally likely to evolve at any point in the progression from rudimentary cooperation between a mother and a totipotent daughter worker, to morphologically distinct castes with an absolutely sterile worker caste

Evidence for A2: A review by Sumner et al. (2023) found the evidence too scarce for a definitive conclusion. Many genomic differences exist between ants and solitary insects suggestive of steps, but this provides no insight into whether these changes were spread across the continuity of eusocial evolution, or were strongly clustered at a special transition point. Overall, step-wise evolution is evident across the entire span of eusociality from extant ants (e.g., a recently evolved supergene in *Solenopsis invicta*) to the transition from solitary to social life histories in corbiculate and carpenter bees (Shell et al. 2021)

B. Parental manipulation is evolutionarily plausible

Rationale: The cost/benefit ratio for manipulative traits is significantly less than for the evolution of offspring cooperative traits. Mothers need to gain only one more offspring for every two grandchildren lost by forcing offspring to become sterile helpers. Conversely, for daughters to willingly help requires producing one full sibling to replace each offspring lost. Ergo, mothers require only a 50% group productivity increase to favor manipulation while daughters incur a fitness cost with any group productivity increase below 100%. Furthermore, fitness interests of offspring manipulated into sterility will become aligned with their mother's objective—to maximize overall group success. Finally, manipulation is equally advantageous with monandry or polyandry and requires no specific mating system preconditions to evolve

Prediction B1: Mothers or workers exercise power to affect the development of offspring or siblings by pheromones, diet, epigenetic modifications, behavior, or a combination of these

Evidence for B1: In bee species where cooperation is variable, mothers differentially provision resources among female offspring, which predictably results in some daughters adopting a worker role (Kapheim et al. 2012, 2013; Huiskens and Rehan 2022). In facultatively eusocial *Polistes* wasps, a nest's first brood cohort generally become workers that are smaller in size than either the queens or the later gyne brood; handicapping them with respect to succeeding independently (Reeve 1991). In many ant and obligately eusocial wasp species, mated queens raise the first worker brood alone. These workers are often nanitic; much smaller and hence likely less fecund and incapable of being queens (relegating their fitness options to align with maximizing group-level success). Thus, it appears that across all levels of eusociality, only brood of a different species, such as inquiline parasites, can selectively escape manipulation into becoming workers and sexualize themselves to the detriment of group productivity (Nonacs and Tobin 1992)

Prediction B2: Working (where that behavior appears to be facultative and often benefiting close kin), has measurably poorer fitness outcomes relative to independent reproduction

Evidence for B2: The mean fitness of *Megalopta genalis* helpers is significantly lower than being a foundress, suggesting that helping mothers is a poor choice if voluntary. Moreover, population genetic simulations find that only maternal manipulation can invade and predict the frequencies of solitary and social females to closely match populations in nature (Kapheim et al. 2015). Similarly, Richards et al. (2005) and Rehan et al. (2014) found that, respectively, *L. malachurum* and *Ceratina australensis* workers do not reproduce enough siblings to offset the number of offspring they could have had as queens

C. Fecundity, group lifespan and the evolution of life history

Rationale: Reproductive potency can come with a cost in worker value. Resources allocated to making reproductive organs in workers that are rarely or never used because fecund queens are continually present, could be better utilized for making longer-lived or more workers (i.e., improving the MCT). Therefore, the level of reproductive capability in workers will negatively correlate with individual queen lifespan and fecundity or with an efficient mechanism that assures queens can be replaced if needed

Prediction C1: the evolution of longer-lived and higher-fecundity queens is more likely to precede the evolution of morphologically distinct castes of obligately sterile workers, rather than the presence of morphological castes being a needed precondition for lifespan and fecundity increases

Evidence for C1: Social insect queens are one of the few exceptions where a fecundity versus lifespan tradeoff is conspicuously absent. Bernadou et al. (2021) view this as a key evolutionary innovation promoting colony size increases (that correlates with morphological castes and obligate sterility). However, it remains an open question if evolutionarily obligate sterility facilitates increased fecundity and lifespan, vice versa, or both evolve in tandem

Table 1 (continued)

Prediction C2: Nesting in sites with the potential to be long-lasting creates strong selection on queen castes (i.e., to be continually present, either as long-lived, fecund queens or efficiently replaceable); which in turn selects for reduced reproductive potential in the worker caste

Evidence for C2: Nest sites that have the potential to be safe, suitable and available for many years correlate with a “space perennial” life history (Nonacs 1988, 1993a), that exhibits sequential polygyny, with multiple relatively short-lived queens that are regularly replaced by mated females recruited from within the nest or from other nests. This is often observed in termites (e.g., Kaib et al. 2001; Adams and Atkinson 2008) and ants with known nest resident times exceeding 30–40 years (Hölldobler and Wilson 1990; Van Buggenum 2022). Vespine wasp species are almost uniformly monogyne with annual life history. However, in cases where multiyear survival is possible, nests become polygynous (e.g., Ross and Visscher 1983)

D. The evolving individual

Rationale: Social insect colonies are in a constant state of genetic flux, where present group members die and are replaced by genetically different ones, including those that are the gamete-producers. That an entity could swap out its entire genome over time and yet still appear as the same ‘individual’ violates the proposed condition that an ETI creates inseparability. However, as a MCT, this allows potentially immortal ‘individuals’ to evolve and adapt to their environment through sacrificing a constant genetic identity

Prediction D1: Within-group relatedness can be a variable and continually changing value that does not affect the cooperation among group members

Evidence for D1: Within species, the genetic relatedness between group members rarely affects levels of cooperation or reproductive skew (Nonacs and Hager 2011)

Prediction D2: Unicoloniality (the lack of aggression between conspecifics from different groups) is a stable social system that will never revert to exhibiting within-group, kin-nepotistic aggression

Evidence for D2: The ecological success of known unicolonial species suggests that, in fact, it may be present in many more species than currently identified (Nonacs 2017). This awaits more data from across species

E. Genetic diversity, group-level benefits and competitive advantage

Rationale: Genetic diversity within a cooperating group has the potential to further increase the benefits from sociality (social heterosis: Nonacs and Kapheim 2007). If diversity benefits can be gained, then the MCT expectation would be for queens to selectively favor behaviors that increase overall group diversity

Prediction E1: it is often selectively advantageous to increase genetic diversity by queens mating with multiple males

Evidence for E1: A phylogenetic analysis by Hughes et al. (2008) showed that monogamy was the most likely state in a species ancestral to the social Hymenoptera. However, another finding is that multiple mating appears to have evolved over 20 times in descendent clades (with apparently no reversals to monogamy). Tellingly, lower relatedness amongst offspring is often beneficial (Oldroyd and Fewell 2007), without lessening cooperation—as is consistently predicted across multiple mathematical models on the effects of mating frequency (Nonacs 2011, 2014, 2017, 2019; Olejarz et al. 2015; but see Davies and Gardner 2018). Interestingly, social insects differ from cooperative helping in birds, where increased extra-pair copulations do tend to reduce a male’s investment into its mate’s offspring (Møller 2000)

Prediction E2: nests or colonies often increase group-level genetic diversity by exchanging some number of their workers. This is known as drifting, where workers move from their natal group into another one that often is composed of either more distant kin or non-relatives

Evidence for E2: Drifting has been observed across the multiple social Hymenoptera species and occurs in both facultatively and obligately eusocial species (Sumner et al. 2007; Nonacs 2017, 2023; Kennedy et al. 2021; Lengronne et al. 2021). Drifters can sometimes gain inclusive fitness by helping kin, but even exchanges between unrelated groups can be favored through generalized reciprocity (Taborsky et al. 2021), involving the trading of genetic diversity (Nonacs 2023)

(parental manipulation) to an immediate fitness benefit (a competitive advantage against ecological competitors at its early evolutionary stages, as well as enabling social heterosis from increased genetic diversity in its more elaborated forms). Viewing eusociality as a Major Competitive Transition and not an Evolutionary Transition in Individuality does not mean that kin selection is implausible.

Instead, the MCT framework seeks to understand how aiding or manipulating kin (or anyone else) will evolve by accounting for the ecological success of the group against competitors.

Table 1 (continued)

F. Alternative reproductive strategies (ARS)

Prediction F1: Cohorts of offspring that have been manipulated to mature and behave as non-reproductive helpers are ripe to be exploited by both parents and non-parents. This creates opportunities for competitively advantageous exploitative strategies and life histories

Evidence for F1: The growing list of such ARS involving the benefits of having non-discriminating and cooperative workers includes:

1. Many dulotic and inquiline parasites use heterospecific workers to raise their offspring. Interestingly, the prevalence of parasitism varies greatly between Hymenoptera and termites—occurring in all major clades of the former, but almost never in the latter (Robin et al. 2021). This phylogenetic difference may reflect greater and earlier manipulation and restriction of developmental options in Hymenopteran larval ontogeny, than found in most termites
2. Colony founding in facultatively and obligately eusocial species can involve cooperation between multiple kin and non-kin foundresses (pleometrosis) (e.g., Nonacs and Reeve 1995; Shaffer et al. 2022). Pleometrosis is ‘semisocial’ cooperation between individuals of the same generation—thought to be not conducive to the formation of obligately sterile, morphologically distinct castes due to unfavorable patterns of genetic relatedness (Boomsma 2023). From a MCT standpoint, however, semisocial females ought to be equally capable of manipulating their offspring into becoming sterile helpers. In pleometrotic wasps and ants, they clearly do
3. The frequent occurrence of adoption or usurpation of another female’s nest as strategic behaviors in paper wasps, with the maturing brood becoming workers for the non-parental females (Nonacs and Reeve 1993, 1995)
4. Brood raiding and nest consolidation across incipient ant colonies—where workers may abandon their mother to join another unrelated female’s brood. The joined nest thereby quickly passes through a high mortality phase of colony life history. Although only one queen may remain at the end of the consolidation process, it pays off for all queens to enter a lottery to be that winner (Nonacs 1993b)
5. Sperm parasitism (Umphrey 2006), where *Acanthomyops* females mate with non-conspecific males to produce hybrid workers. Although no female *Acanthomyops* can be produced, males are and the hybrid workers can survive in locations where pure *Acanthomyops* workers cannot—thus expanding the species’ ecological niche
6. Dependent lineages in ants (e.g., Anderson et al. 2006; Helms Cahan et al. 2006), where females need to mate both intra- and interspecifically. The interspecific matings produce hybrid and sterile workers; and only the intraspecific matings can produce female gynes. Nevertheless, even though 50% of the workers’ genome has no inclusive fitness with sperm parasitism or in dependent lineages, this appears to have no effect on colony functioning

Declarations

Conflict of interest Neither PN nor KKD have any financial or non-financial interests that are directly or indirectly related to the work submitted for publication.

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