Metabolic division of labor in social insects

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Abstract (120 words max)

Social insects are known for reproductive and behavioral division of labor, but little attention has been paid to metabolic forms of division of labor. Metabolic division of labor is the partitioning of complementary metabolic tasks between individuals within the colony, and it is widespread in social insects. Here we pinpoint trophallaxis, trophic eggs and cannibalism as the most well-studied transfers underlying metabolic division of labor in social insects and discuss their evolution. We argue that metabolic division of labor underpins fundamental aspects of colony physiology and may be a necessary feature of superorganismal systems, impacting many life history traits. It is critical to investigate metabolic division of labor to better understand major evolutionary transition(s) to superorganismality in social insects.

Keywords
Social physiology; auxotrophy; cross-feeding; superorganism; ants, royal jelly

Introduction

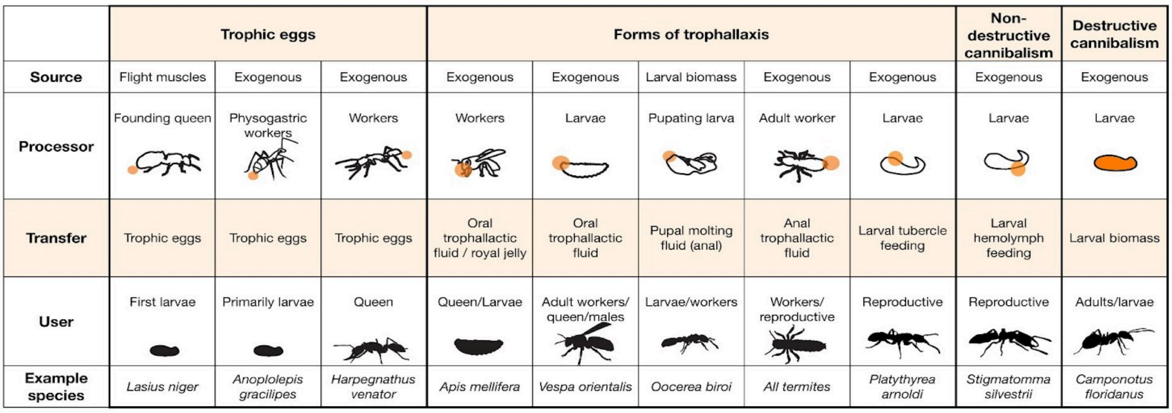
Division of labor is a central aspect of living organisms and can be observed across levels of biological organization: between organelles within a cell, between cells within a multicellular organism, between microbes in a community and between multicellular organisms within a social group [1]. Social insects display many types of division of labor including the dissociation of reproduction between workers and reproductives, task specialization within the worker caste, and also **metabolic division of labor.** While most research has focused on behavioral and reproductive division of labor, less attention has been paid to metabolic division of labor, a potentially defining feature of advanced eusociality.

We define **metabolic division of labor** as the partitioning of a given metabolic process into several elementary metabolic tasks performed by separate units within a cooperative entity. Broadly, metabolic division of labor allows the decoupling of breakdown of incoming food (catabolism) and synthesis of endogenous molecules (anabolism), although there can be much finer subdivisions of subsections of metabolic pathways across individuals. Separating metabolic tasks across individual units requires the *transfer* of metabolites between cells, tissues or individuals. Thus, for a system to have metabolic division of labor, the system needs a *processor*, a *user* and a direct or indirect *transfer* of metabolized material from the processor to the user. The transfer of metabolized material can be synchronous (direct passage) or asynchronous (externally stored) [2]. Dissociation of producer and user allows signature asymmetries to come about between units (e.g. germline and soma, [3]).

Metabolic division of labor occurs between the cells of multicellular organisms [4,5], within microbial communities [6-8] and between colony-members in social insect colonies. In multicellular organisms, certain cells produce and secrete molecules into the extracellular space or bloodstream, these molecules travel through the body and are taken up by other cells where they act or are used. In microbial communities, related or unrelated microbes secrete signals or waste-products into the medium and other microbes take these up and use them. An important difference is that the cells of a multicellular organism are clonal and produce such molecules at a clear metabolic cost to themselves, while in microbial communities, cross-feeding is more often a form of opportunism, recycling or tit-for-tat cooperation. Social transfers of material are frequent in social insect colonies [9,10], for example through trophallaxis or trophic eggs [11,2]. Across social insects, there are likely a range of degrees of metabolic division of labor depending on within-colony relatedness and reproductive opportunity, from simple recycling to full altruistic cooperation. At the eusocial extreme, fully altruistic metabolic division of labor may be a signature of superorganismality, where it creates an integrated metabolism across the colony in a major evolutionary transition in individuality [1]. To better understand social insects and their major evolutionary transitions to superorganismality, we need a better understanding of metabolic division of labor.

1) Forms and currencies of metabolic division of labor in social insects

We highlight three forms of transfer that often result in metabolic division of labor: **Trophallaxis, trophic eggs, cannibalism (Figure 1)**. In most cases, social transfer behaviors that came to mediate metabolic division of labor likely evolved originally for another purpose [2,12].



	Trophic eggs			Forms of trophallaxis					Non-destructive cannibalism	Destructive cannibalism
Source	Flight muscles	Exogenous	Exogenous	Exogenous	Exogenous	Larval biomass	Exogenous	Exogenous	Exogenous	Exogenous
Processor	Founding queen	Physogastric workers	Workers	Workers	Larvae	Pupating larva	Adult worker	Larvae	Larvae	Larvae
Transfer	Trophic eggs	Trophic eggs	Trophic eggs	Oral trophallactic fluid / royal jelly	Oral trophallactic fluid	Pupal molting fluid (anal)	Anal trophallactic fluid	Larval tubercle feeding	Larval hemolymph feeding	Larval biomass
User	First larvae	Primarily larvae	Queen	Queen/Larvae	Adult workers/ queen/males	Larvae/workers	Workers/ reproductive	Reproductive	Reproductive	Adults/larvae
Example species	*Lasius niger*	*Anoplolepis gracilipes*	*Harpegnathus venator*	*Apis mellifera*	*Vespa orientalis*	*Oocerea biroi*	*All termites*	*Platythyrea arnoldi*	*Stigmatomma silvestrii*	*Camponotus floridanus*

Figure 1: Different forms of metabolic division of labor in social insects grouped into the three main types of social transfer (Trophic eggs, Trophallaxis and its various forms, and Destructive and Non-destructive cannibalism). For division of metabolic labor to occur, the system requires a *processor*, a *user* and a direct or indirect *transfer* of metabolized material from the processor to the user. Here, we highlight ten examples of metabolic division of labor in social insects cited throughout the text and here classified according to their method of transfer. Source refers to the source material that is transformed or metabolized.

Trophic eggs

Trophic eggs are a high-quality processed food source, where the producer has transformed exogenous food into endogenous, readily usable and storable materials. Trophic eggs are frequently observed in ants and stingless bees [13,14]. Production and consumption of trophic eggs can be considered a form of metabolic division of labor (**Figure 1**); in some ponerine ants, non-reproductive workers produce trophic eggs and offer them to the reproductives. In invasive yellow crazy ants, larvae are exclusively fed with trophic eggs produced by a special caste of physogastric workers, themselves receiving food from other workers via trophallaxis [15,16].

Trophic eggs as a form of metabolic division of labor could have come about through the combination of worker reproduction and worker policing [13,14]. In species with totipotent workers or where workers have ovaries, it can be in a worker's interest to perform the metabolic labor of transforming exogenous food into eggs. Dominant individuals eat worker-produced eggs through policing and this provides a metabolic 'shortcut' relative to feeding on solely exogenous food. Thus, with these two behaviors in place, all elements required for metabolic division of labor are fulfilled (**Figure 1**).

Trophallaxis

Trophallaxis is the direct ingestion by one individual of material excreted, secreted or regurgitated by another, and these behaviors occur under various forms and between various partners [11]. All forms of trophallaxis can transmit metabolized material between individuals and have the potential to enable metabolic division of labor (**Figure 1**).

Oral-oral trophallaxis, where one individual regurgitates and the other drinks, occurs in many ants, bees, wasps and termites. The trophallactic fluids (crop contents) of bees, ants, wasps and termites contain numerous proteins and metabolites that are endogenously synthesized, and which likely constitute a form of metabolic division of labor (**Figure 1**)[17-20]. These fluids have consistent caste signatures, suggesting cross-feeding or at least differential synthesis of trophallactic proteins between castes [21]. Oral fluids of adults frequently contain larval storage proteins [17,21], typically only produced by larvae in solitary species [22].

Social insect larvae have been suggested and shown to provide a metabolic service to adult nestmates, acting as a digestive caste [23,24]. Larva-to-adult and adult-to-larva trophallaxis occurs in ants, bees and wasps. In social wasps, larval regurgitate is a major source of adult nutrition [24,25].

Anal-oral trophallaxis transmits microbes, but it has also been shown to transmit endogenously produced proteins and metabolites [26]. Termites are best-studied for this form of trophallaxis [27], but it has also been documented in ants and bees (**Figure 1**) [11,28]. A new form of trophallaxis has recently been discovered wherein ant pupae secrete pupal moulting fluid that adults and larvae drink [26]. This fluid is quite similar to that passed during oral-oral trophallaxis [17,26] indicating that more recently evolved forms of trophallaxis, e.g. oral-oral, may have co-opted similar currencies from a more ancient form of social transfer, e.g. pupal moulting fluid.

Cannibalism: Why and why not metabolic division of labor

Cannibalism is observed in response to starvation across social insects [29-32] Under starvation, it is hard to argue that cannibalized larvae were initially produced for this purpose. But beyond response to suboptimal conditions, there is evidence that larvae are a form of **live food storage** or act as **metabolic processors** (**Figure 1**). Larval cannibalism (up to a rate of 66% [33]) is observed outside of starvation or stressful conditions in several species of ants and wasps [34,35]. In the ant *Camponotus floridanus* higher production of larvae in response to high food availability does not result in a higher number of pupae but in an increase in larval cannibalism [36]. If such cannibalism is a form of metabolic division of labor, the larvae would be both processors and the mode of transfer. Thus, in addition to simple storage, cannibalized larvae could represent a metabolic caste specialized in the **transformation of exogenous material into larvae tissue** that is then provided to other colony members including other larvae (**Figure 1**). Difficulties in demonstrating larval cannibalism as an adaptation for metabolic division of labor include 1) measuring the proportion of larvae produced solely to be cannibalized, and 2) the experimental manipulation of cannibalism. While larval cannibalism has been documented in many social insect species, its importance under non-starvation conditions must be better understood.

Larval tubercules, hemolymph feeding and non-destructive cannibalism

Macabre forms of trophallaxis that verge on cannibalism are found in early-branching ant taxa – larval hemolymph feeding. Reproductives of *Stigmatomma* [37,38], *Myopopone* [39], *Prionopelta* [40], and *Mystrium* [41] pierce the larval cuticle at specific site and drink larval hemolymph through small cuts, using larval “secretions” as primary food source. In these “Dracula ants” [41], the queens engage in non-destructive cannibalism of larvae. In other ant species, mostly of the genus *Platythyrea*, adults drink from evolved taps, glands or tubercles found on their larvae (**Figure 1**) [42].

Why would a mother drink the blood of her young? For insects that undergo complete metamorphosis, as larvae pass through the stages of growth they must accumulate and store nutrients to provide resources for metamorphosis. If larvae perform the metabolic labor of transforming exogenous nutrients into the ideal composition to build new ant biomass, drinking their hemolymph would allow reproductives to avoid this metabolic labor.

Larval storage proteins as currency for Hymenoptera

The Hymenopteran evolutionary history (parasitic wasps), the habit of feeding on larval and pupal fluids (both rich in larval storage proteins), and the presence of larval storage proteins in adult oral secretions collectively suggest that social Hymenoptera may rely on the currency of larval storage proteins ancestrally sourced from prey [17,19,21,22,43].

Consequences for superorganismality across forms

Some forms of social transfer allow each individual to take in, contribute and *redistribute* materials. This not only rapidly distributes materials across exceptionally large colonies [44], but also enables a *networked* social circulatory system. Social transfers that do not allow such a redistribution (once-in-a-lifetime transfers e.g. pupal moulting fluids, transfers during claustral founding [45]) are not capable of creating such a network. Species that engage in frequent and redistributable social transfers are well placed to evolve altruistic metabolic division of labor, as observed in multicellular systems, and to undergo the major evolutionary transition toward superorganismality.

2) Why metabolic division of labor has evolved and how?

Benefits of Metabolic division of labor

Circumvent trade-offs

As with other forms of division of labor, the benefits of metabolic division of labor within a cooperative group include the increase in task performance due to task specialization, the reduction in costs related to switching between tasks, and the ability to collectively **circumvent trade-offs** each entity is facing individually [46].

Complexification of metabolic processes

In microbial communities, metabolic division of labor increases the yield of a reaction by reducing metabolic burden [47], and allows for an elongation of metabolic pathways [48]. If these principles apply in social insects, we would expect that the **need for complex metabolic processes should favor the emergence of metabolic division of labor.** Therefore, in species feeding on a low-quality diet requiring ample processing to create social insect biomass, metabolic division of labor should be necessary for colony productivity (**Figure 2**). For example, to build insect biomass, nectar and honeydew are likely much lower quality than are insect prey, and require more molecular processing to satisfy larval needs for growth. Colonies of species feeding on low-quality diets tend to be much larger [12], possibly indicating a need for more metabolic laborers. In contrast to nectar and pollen, the royal jelly synthesized by honeybee nurses is a highly elaborated cocktail of proteins and macromolecules [49,50]. Thus, metabolic division of labor may be an adaptive mechanism to manipulate larval diet quality and thus build adaptive asymmetries within the collective (e.g body size, longevity; **Figure 2,** [51]).

Building asymmetry through dissociation of metabolic costs and benefits
Metabolic division of labor can minimize metabolic costs for reproductives, relegate those costs to more disposable workers or larvae and thus maximize the lifespan and egg production of the reproductive(s), beneficial to colony fitness (**Figure 2,** [51]). For instance the process of digestion is metabolically costly but essential for nutrient intake. Thus allocating metabolic cost related to digestion of exogenous macronutrients to the worker caste and the intake of processed nutrients to the queen castes would optimize egg production while minimizing metabolic costs to queens [21,52,53].

Resilience to variation in food availability
Variation in food availability in the environment is another factor that can promote the emergence of colony-level metabolic division of labor. Metabolic division of labor can buffer environmental variability by building up energy storage in times of wealth to be used in times of scarcity (**Figure 2**).

Facilitators of the emergence of metabolic division of labor

As metabolic division of labor requires the transfer of metabolites from producer to a user, its emergence relies on mechanisms of transfer, such as trophallaxis or trophic eggs, both social transfer behaviors that likely evolved originally for another purpose (**Figure 2**). Trophallaxis evolved primarily in ant lineages exploiting a sugary liquid diet notoriously low in nitrogen [12] – such a low-quality diet should favor the evolution of metabolic division of labor (as discussed above). Worker reproduction may have facilitated the transfer of metabolized products between individuals through the evolution of trophic eggs [13,14]. Whether larval cannibalism is a primitive form of metabolic division of labor is debatable, but it may have led to the evolution of hemolymph drinking.

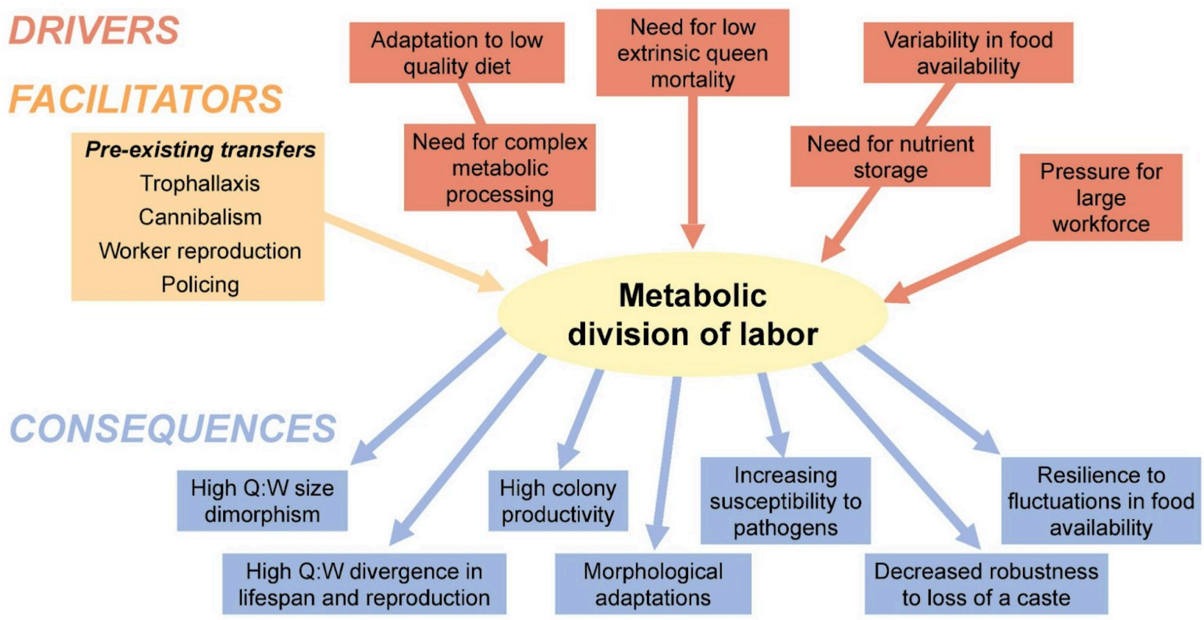


Figure 2: Diagram depicting different evolutionary drivers (red boxes) and facilitators (orange box) for metabolic division of labor to emerge as well as the consequences (blue boxes) of metabolic division of labor on life history traits of individuals and of the colony.

3) Consequences of metabolic division of labor on life history

Queens and workers divergence in body size, lifespan and reproduction

Metabolic division of labor leads to an unequal allocation of metabolic costs and benefits between individuals, and as such, it can accentuate asymmetries between colony members. These asymmetries can have developmental and life history consequences [51-53] including the adult size dimorphism or differences in longevity and fecundity between reproductives and workers (**Figure 2**). Termites workers are lacking of uric-acid oxidase which prevent them from using stocks of uric acid as a source of nitrogen; instead this enzyme is highly abundant in reproductives which can thus metabolize uric acid that they receive from non-reproductives and use this nitrogen source for their reproduction [20].

Reinforcement of superorganismality

Colony level-metabolic division of labor leads to increasing interdependence between colony members, and thus reinforces the higher-level individual, the colony or superorganism. In larvae of species that are fed by trophallaxis, larval development is dependent on trophallactic fluid metabolites and proteins provided by workers, as in the case of the honeybee [50].

Development of anatomical structures

Metabolic division of labor can favor the specialization of anatomical structures that enable the transfer (**Figure 2**). For trophallaxis, the proventriculus separating the crop from the midgut is highly elaborated in ants that engage in trophallaxis [11]. Glands can also be highly elaborated, for example, the hypopharyngeal and the mandibular glands of honeybee workers is where most proteins in royal jelly are synthesized [54,55]. The anatomy of different exocrine glands in other social insects engaging in trophallaxis should be investigated in relation with metabolic division of labor to reveal signs of morphological adaptation.

Costs of metabolic division of labor

As a results of task specialization, metabolic division of labor can lead to metabolic interdependence. While this interdependence can create an evolutionary point of no return, it may, on the other hand, reduce the resilience of the colony to internal or external stressors. Another cost related to the transfer of material is the higher risk of pathogen transmission and therefore, metabolic division of labor is expected to evolve together with immune defense mechanisms [2].

Conclusion

Division of metabolic labor is likely widespread in social insects and underlies colony physiology, but further studies are needed to understand its use and implications. New social transfers and forms of metabolic division of labor are still being discovered, even today [26].

Given the novelty of this view of social insects, we need to explore the importance of metabolic division of labor to colony fitness in order to ultimately establish its role in social insect life-history evolution.

The fact that metabolic division of labor occurs so broadly in social insects will also inform our understanding of superorganismality, and the major evolutionary transitions in individuality that have occurred multiple times across social insect lineages. As opposed to multicellular systems where metabolic division of labor occurs between cells, in social insects it occurs between distinct and accessible individuals, making social insects a good study system to explore networked metabolism.

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Author contribution

A.C.L. and M.A.N. collaborated in the writing of the manuscript, on its revision, and in the study of the literature.

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