

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, and it is widespread in social insects. We define two forms of metabolic division of labor, homosynergetic and heterosynergetic, we pinpoint trophallaxis, trophic eggs and cannibalism as the primary transfers underlying the homosynergetic form and discuss their evolution. We argue that homosynergetic metabolic division of labor underpins fundamental aspects of colony physiology and may be a necessary feature of superorganismal systems, impacting many life history traits. Investigating metabolic division of labor is necessary to 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 [1,2].

Metabolic division of labor is the partitioning of a given metabolic process into several elementary metabolic tasks performed by separate units within a cooperative entity. Following the two forms of major evolutionary transitions [3] – *fraternal* transitions between like units (e.g. multicellularity) and *egalitarian* transitions between unlike units (e.g. eukaryotes) – we describe two branches of metabolic division of labor: ***homosynergetic***, between like units, and ***heterosynergetic***, between unlike units. As these forms of cooperation are guided by different underlying forces and pressures, this distinction is necessary to understand the principles governing these types of metabolic division of labor. Most research on metabolic division of labor has addressed only the heterosynergetic form, primarily in microbial communities or symbioses.

Social insects engage in both forms of metabolic division of labor. Leaf-cutting ants' exchanges with their fungus gardens [4] and carpenter ants and their obligate endosymbiont *Blochmannia* [5] both represent well-studied examples of ***heterosynergetic*** metabolic division of labor in social insects. In this review we instead focus on the less explored and amorphous ***homosynergetic*** metabolic division of labor, which we propose to have been key to the major evolutionary transition to superorganismality. In insect societies, colony-level social physiology [2,6,7] relies on the partitioning of physiological tasks among colony members**.** Although earlier studies have explored social physiology and physiological castes [2,7,8], these processes have not yet been viewed through the lens of metabolic division of labor, nor have the implications metabolic division of labor on social evolution been considered.

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 metabolic pathways across individuals. The partitioning of metabolic tasks across individual units requires the *transfer* of metabolites, including digestive intermediates, between cells, tissues or individuals [2,7], allowing metabolic 'short-cutting' on the collective scale. Thus, for a system to use metabolic division of labor, at minimum the system needs a *processor*, a *user* and a direct or indirect *transfer* of metabolized material from the processor to the user. The transfer can be synchronous (direct passage) or asynchronous (externally stored) [9]. In homosynergetic metabolic division of labor, dissociation of producer and user allows signature asymmetries to come about between otherwise like units (e.g. germline and soma [10]).

Homosynergetic metabolic division of labor occurs between the cells of multicellular organisms (if we consider the organism as a colony of cells) [11,12], between parents and offspring, 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. For example, neurons often rely on metabolic processes performed by neighboring glial cells [13]. A common trait between these examples is that highly related members produce molecules at a clear cost to themselves, yet this homosynergetic metabolic division of labor benefits the collective. Social transfers of material are frequent in social insect colonies [6,14], for example through trophallaxis or trophic eggs [9,15].

Across social insects, there are a range of degrees of homosynergetic metabolic division of labor depending on within-colony relatedness and reproductive autonomy that have greater or lesser impacts on optimization at the colony level. At the eusocial extreme, homosynergetic metabolic division of labor may be a signature of superorganismality, where it can create an integrated metabolism across the colony [1]. As such forms of cooperation evolve to become obligatory, the higher organizational unit becomes entrenched [3,16,17]. While causes for hypometric metabolic scaling of the colony remain unclear [18-20], underlying mechanisms need to be explored in light of homosynergetic metabolic division of labor. Generally, to better understand social insects and their major evolutionary transitions to superorganismality, we need a better understanding of metabolic division of labor.

1) Currencies of metabolic division of labor in social insects

Metabolized material transferred between individuals acts as a currency of metabolic division of labor, where all individuals are able to use it and it is costly to produce. We highlight three forms of transfer of metabolized material that often result in homosynergetic metabolic division of labor on the scale of the colony: **trophallaxis, trophic eggs, cannibalism (Figure 1)**.

	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* [52]	*Anoplolepis gracilipes* [24]	*Harpegnathus venator* [22]	*Apis mellifera* [62]	*Vespa orientalis* [34]	*Oocerea biroi* [39]	*All termites* [37]	*Platythyrea arnoldi* [50]	*Stigmatomma silvestrii* [45]	*Camponotus floridanus* [44]

Figure 1: Different forms of homosynergetic 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 metabolic division of 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 homosynergetic 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 endogenously produced, readily usable and storable materials. Trophic eggs have been described in ants and stingless bees [21-23]. Production and consumption of trophic eggs can be considered a form of homosynergetic metabolic division of labor (**Figure 1**). In some ponerine ants, non-reproductive workers produce trophic eggs and offer them to 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 [24,25].

Trophic eggs as a form of metabolic division of labor could have evolved through the combination of worker reproduction and worker policing [22,26]. 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 then eat worker-produced eggs when 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 [15]. 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 fluid (crop milk) of bees, ants, wasps and termites contains numerous proteins and metabolites that are endogenously synthesized, and which result in homosynergetic metabolic division of labor (**Figure 1**) [26-29]. These fluids have consistent caste signatures, suggesting cross-feeding or at least differential synthesis of trophallactic proteins between castes [30]. Oral fluids of adults frequently contain larval storage proteins [9,26,31], typically only produced by larvae in solitary species [32], potentially representing a critical currency of homosynergetic metabolic division of labor in social insects.

Some social insect larvae have been shown to provide a metabolic service to adult nestmates, acting as a digestive caste [33,34]. Larva-to-adult and adult-to-larva trophallaxis occur in ants, bees and wasps. In social wasps, larval regurgitate is a major source of adult nutrition [34,35].

Anal-oral trophallaxis transmits microbes [36], but it has also been shown to transmit endogenously produced proteins and metabolites. Termites are best-studied for this form of trophallaxis [37], but it has also been documented in ants and bees (**Figure 1**) [15,38]. Another form of trophallaxis has recently been discovered wherein ant pupae secrete moulting fluid that adults and larvae drink [39]. There is some similarity in the types of proteins transmitted by moulting fluid and transmitted during oral-oral trophallaxis [24,39] indicating that more recently evolved forms of trophallaxis, e.g. oral-oral, may have co-opted molecular tools from a potentially more ancient form of social transfer, e.g. pupal moulting fluid.

Cannibalism: Why and why not homosynergetic metabolic division of labor

Cannibalism is observed in response to starvation across social insects [40-42], yet under starvation, it is difficult 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** and act as **metabolic processors** (**Figure 1**). 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 [44]. 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 larval tissue** that is then provided to other colony members including other larvae (**Figure 1**).

Larval tubercules, hemolymph feeding and non-destructive cannibalism

Macabre forms of trophallaxis that verge on cannibalism are found in early-branching and ponerine ant taxa. Reproductives of *Stigmatomma* [45,46], *Myopopone* [47], *Prionopelta* [48], and *Mystrium* [49] 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" [49], the queens engage in non-destructive cannibalism on larvae. In other ant species, mostly the genus *Platythyrea*, adults drink from evolved taps, glands or tubercles found on larvae (**Figure 1**) [50].

Why would a mother drink the blood of her young? For insects that undergo complete metamorphosis, as larvae grow, they accumulate and store nutrients as larval storage proteins 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, rich in these larval storage proteins, could allow reproductives to avoid this metabolic labor.

Larval storage proteins as a primary metabolic 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 use larval storage proteins ancestrally sourced from host-prey as a primary currency of homosynergetic metabolic division of labor [9,26, 28,231,32]. If this is the case, we predict that uptake and breakdown of larval storage proteins should occur through different molecular pathways than uptake and breakdown of exogenous sources.

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 [49], 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 [50] are not capable of creating such a network. Species that engage in frequent and redistributable social transfers are well placed to evolve homosynergetic metabolic division of labor, have the cooperation become obligate, and to undergo the major evolutionary transition toward superorganismality.

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

As with other forms of division of labor [16,17], the metabolic division of labor can likely allow the cooperative group to collectively circumvent trade-offs each entity is facing individually [16,53]. Evolutionarily, there are pre-adaptations (facilitators) that should favor the evolution of homosynergetic metabolic division of labor and there are fitness maxima (benefits) that should become available only upon its evolution.

Benefits of Metabolic division of labor

Complexification of metabolic processes

In microbial communities, metabolic division of labor increases fitness by spreading the metabolic burden across individuals or types [54], but also allows for an elongation and complexification of metabolic pathways [55]. Complex metabolic processes are costly because they require production of many different enzymes [56], which through metabolic division of labor, can be distributed over different specialist individuals. Assuming these principles apply in social insects, this could enable species to evolve more complex metabolic processes (e.g. requiring more enzymes to break down or build up) and thus adapt to new or difficult to process food sources (**Figure 2**).

Building asymmetry through dissociation of metabolic costs and benefits

Homosynergetic metabolic division of labor can minimize metabolic costs for reproductives, relegate those costs to more disposable workers or larvae, thus maximizing the lifespan and egg production of reproductive(s), beneficial to colony fitness (**Figure 2,** [57]). For instance, the process of digestion is metabolically costly but essential for nutrient intake. Thus, allocating metabolic costs related to digestion of exogenous macronutrients to the worker caste while transferring processed nutrients to the queen caste should optimize egg production, minimize metabolic costs to queens, and increase queen lifespan [9,58,59].

When social insects use metabolized materials to rear their young, it allows manipulative or directive signals to hitchhike through the social transfer [9]. The royal and worker jellies that are synthesized by honeybee nurses are highly elaborated cocktail of proteins and macromolecules that steer larvae toward queen or worker fates, respectively [60-62]. These jellies include both signals and nutrition allowing the colony to manipulate larval diet quality and thus build adaptive asymmetries within the collective (e.g body size, longevity; **Figure 2,** [57]). Over the ant phylogeny, passive larval morphologies, indicating worker-controlled feeding through trophallaxis or trophic eggs, correlate with larger queen to worker body size dimorphism [57].

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 the laying of trophic eggs, both behaviors that likely evolved originally for another purpose (**Figure 2**). Oral-oral trophallaxis evolved primarily in ant lineages exploiting a sugary liquid diet notoriously low in nitrogen [63]. Such a low-quality diet should favor the evolution of metabolic division of labor, both heterosynergetic with microbes and homosynergetic to build more complex macromolecules from minimal building blocks. Worker reproduction and policing likely facilitated the evolution of trophic eggs [21,22]. 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.

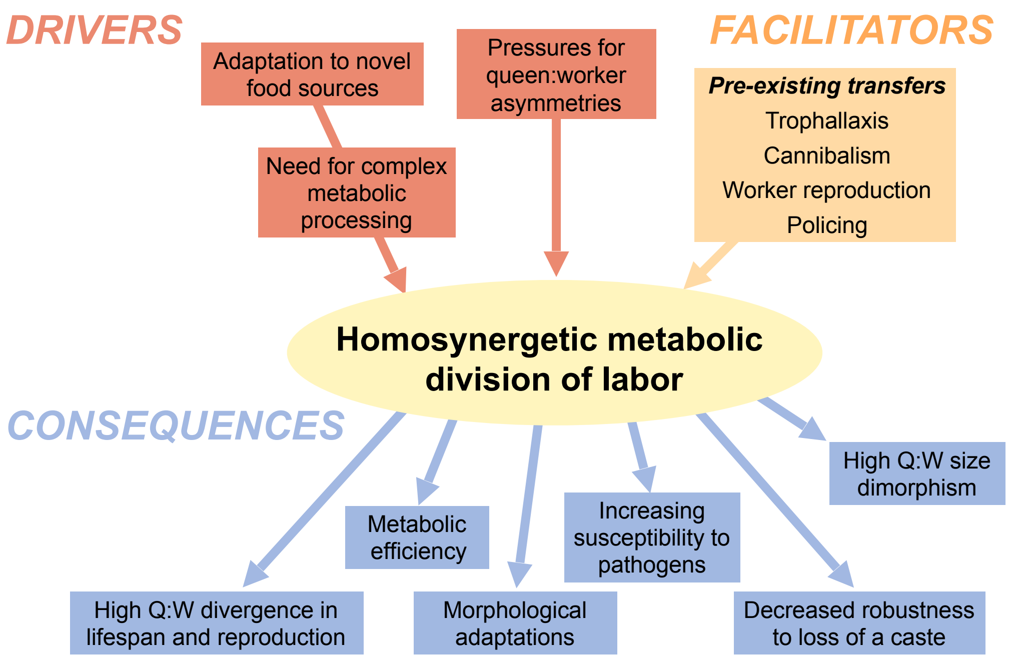

Figure 2: Diagram depicting hypothesized evolutionary drivers (red boxes) and facilitators (orange box) for homosynergetic metabolic division of labor to emerge as well as some

predicted consequences (blue boxes) of homosynergetic metabolic division of labor on life history traits of individuals and of the colony.

3) Consequences of metabolic division of labor on life history

Increased metabolic efficiency with colony size

As in solitary organisms, metabolic rate scales hypometrically at the level of the colony [19,20,64], where smaller colonies have higher metabolic rates. Yet in contrast with solitary species, in social insect colonies this association cannot be explained by constraints in resource supply or by changes in surface to volume ratio. Instead, the social synergy hypothesis [20,64] explains the hypometric scaling with the idea that larger colonies are energetically more efficient. In line with this theory, stronger homosynergetic metabolic division of labor should allow larger colonies to optimize their energetic yield, therefore reducing their metabolic rate.

Body size variation and differential allocation of metabolic costs between queen and workers

Metabolic division of labor can lead to an unequal allocation of colony-level metabolic costs and benefits between individuals, and as such, it can accentuate asymmetries between colony members. The cheap worker hypothesis [65], while proposed without metabolic division of labor in mind, is likely underpinned by the ability of such species to dissociate costs and benefits across a colony's individuals. These asymmetries have developmental and life history consequences [57-59] including the adult size dimorphism and differences in longevity and fecundity between reproductives and workers (**Figure 2**).

Asymmetries in both cost and resource allocation across the colony can come about through many mechanisms. For costs, at the individual level, metabolic scaling varies phylogenetically and between castes [18,20,66], suggesting species-specific and caste-specific variation in the tradeoff between metabolic investment in colony fitness versus individual maintenance [66]. Such variation in metabolic scaling relations may indicate species where metabolic division of labor is redistributing worker and queen metabolic costs. For resource allocation, termite workers do not produce uric-acid oxidase, preventing them from using stocks of uric acid as a source of nitrogen; instead this enzyme is highly abundant in reproductives, who can then metabolize uric acid received by trophallaxis from non-reproductives and use this nitrogen source for reproduction [29].

Reinforcement of superorganismality

Homosynergetic metabolic division of labor leads to *increasing interdependence* between colony members [2,17], entrenching and reinforcing the higher-level individual. The gradient of reproductive autonomy across individuals in social insect species [67] likely parallels the degree of homosynergetic metabolic division of labor a species uses (based on proxies of dimorphism, [57] or metabolic rate [66]). As Michod & Nedelcu 2006 [68] and Strassmann & Queller 2009 [3] indicated, the fraternal transition to (super)organismality is characterized by high cooperation and low reproductive autonomy. Increasing use of homosynergetic metabolic division of labor represents both an increase in cooperation and a decrease in any form of autonomy.

Development of anatomical structures

Metabolic division of labor can favor the specialization of anatomical structures that enable the necessary transfer [2,8] (**Figure 2**). For trophallaxis, the proventriculus separating the crop from the midgut is highly elaborated in ants that engage in trophallaxis [15]. Glands can also be highly elaborated – for example, the hypopharyngeal and mandibular glands of honeybee workers are where most royal jelly proteins are synthesized [69,70]. The anatomy of other exocrine glands in 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

Metabolic division of labor can lead to metabolic interdependence [2,17]. While this interdependence can create an evolutionary point-of-no-return, it may also 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 [9].

Conclusion

Homosynergetic metabolic division of labor is widespread and understudied in social insects, despite the fact that it underlies major features of colony physiology.

This is a novel view of social insect colonies, as metabolically networked individuals. Future research needs to explore the importance of metabolic division of labor for colony fitness to ultimately establish its role in social insect life-history evolution.

Studying homosynergetic metabolic division of labor across social insects should inform our understanding of superorganismality, and the major evolutionary transitions in individuality that have occurred multiple times across social insect lineages. In contrast to multicellular systems where metabolic division of labor occurs between different cells or tissues, in social insects, metabolic division of labor occurs between distinct and accessible individuals, making social insects an excellent study system to explore networked metabolism.

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** In this article the authors have characterized the proteomic composition of the ant-pupal moulting fluid and investigated its function within the colony in five species of ants. They found that the pupal fluid is rich in nutrients and endogenously produced proteins. This fluid is drunk by adult workers but also by early-stage larvae and it is essential for their growth and survival. This work demonstrates the active role of the pupae in ant colonies and brings to light a new type of trophallaxis.

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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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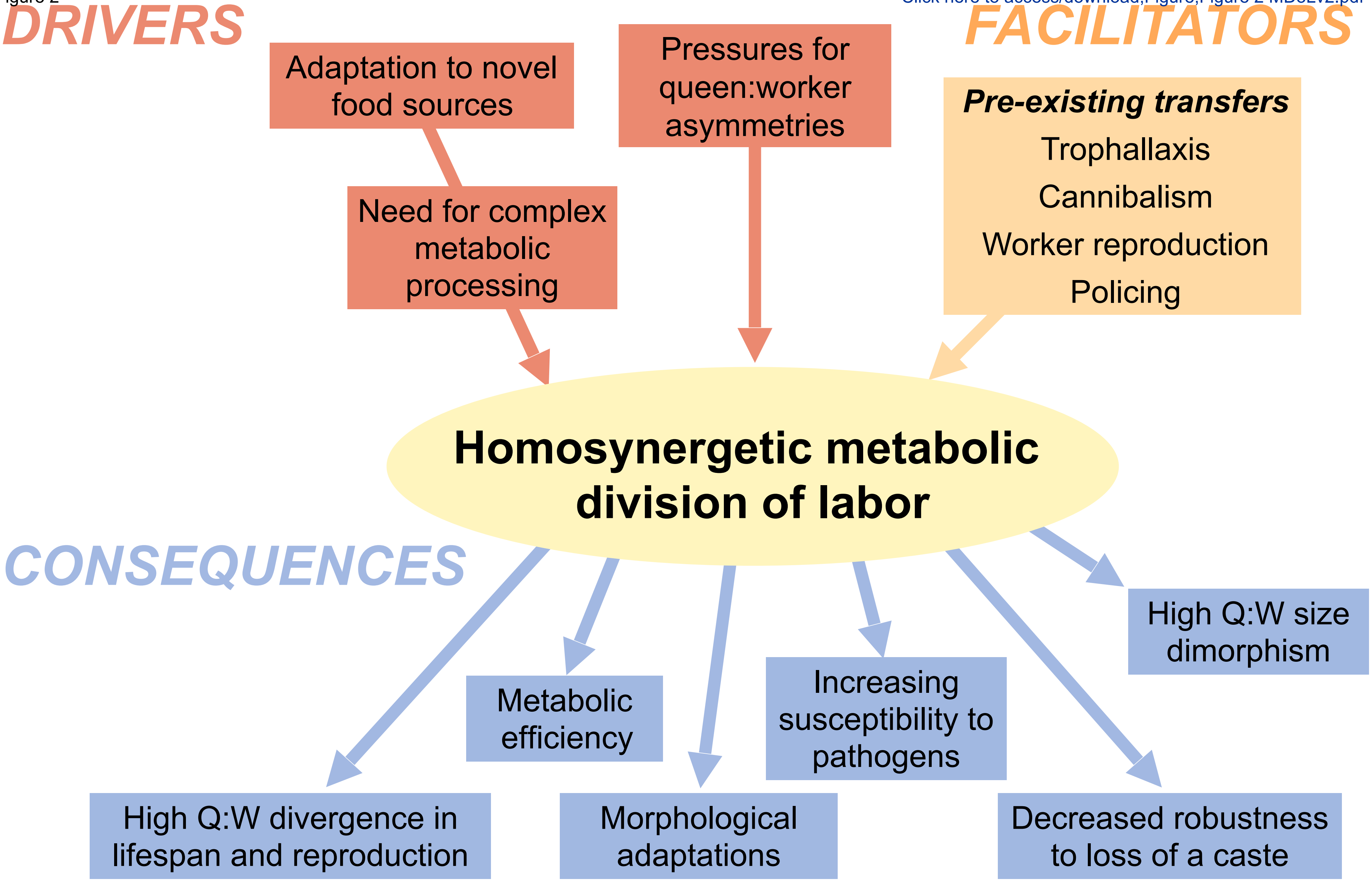
	Trophic eggs			Forms of trophallaxis					Non-destructive cannibalism	Destructive cannibalism
Source	Flight muscles	Exogenous	Exogenous	Exogenous	Exogenous	Larval biomass	Exogenous	Exogenous	Exogenous	Exogenous
Processor	Founding queen	Physogastric workers	Workers	Workers	Larvae	Pupating larva	Adult worker	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 [52]*	*Anoplolepis gracilipes [24]*	*Harpegnathus venator [22]*	*Apis mellifera [62]*	*Vespa orientalis [34]*	*Ooceraea biroi [39]*	*All termites [37]*	*Platythyrea arnoldi [50]*	*Stigmatomma silvestrii [45]*	*Camponotus floridanus [44]*

Figure 2



DRIVERS
Adaptation to novel food sources
Need for complex metabolic processing
Pressures for queen:worker asymmetries
FACILITATORS
Pre-existing transfers
Trophallaxis
Cannibalism
Worker reproduction
Policing
Homosynergetic metabolic division of labor
CONSEQUENCES
High Q:W divergence in lifespan and reproduction
Metabolic efficiency
Morphological adaptations
Increasing susceptibility to pathogens
Decreased robustness to loss of a caste
High Q:W size dimorphism