Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Insect Science

Nutritional inequalities structure worker division of labor in social insects

Alexander Walton[1] and Amy L Toth[2]

Eusocial insect societies are fundamentally non-egalitarian. The reproductive caste 'wins' in terms of resource accumulation, whereas non-reproductive workers 'lose'. Here, we argue that the division of labor among workers is also organized by nutritional inequalities. Across vastly different social systems and a variety of hymenopteran species, there is a recurrent pattern of lean foragers and corpulent nest workers. Experimental manipulations confirm causal associations between nutritional differences, associated molecular pathways, and behavioral roles in insect societies. The comparative and functional genomic data suggest that a conserved toolkit of core metabolic, nutrient storage, and signaling genes has evolved to regulate the social insect division of labor. Thus, the unequal distribution of food resources can be considered a fundamental organizing factor in the social insect division of labor.

Addresses
[1] Biological Sciences, University of Alberta, Edmonton AB T6G 2E9, Canada
[2] Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA 50014 USA

Corresponding author: Toth, Amy L (amytoth@iastate.edu)

Current Opinion in Insect Science 2023, **58**:101059

This review comes from a themed issue on **Social insects**

Edited by **Ricarda Scheiner** and **guy Bloch**

Available online 23 May 2023

https://doi.org/10.1016/j.cois.2023.101059

Introduction

Insect societies are fundamentally non-egalitarian. Among reproductive castes, there are 'haves' and 'have nots' — reproductive 'royal' castes with extremely high reproductive capacity, and non-reproductive worker castes with extremely low reproductive capacity (in some species even being functionally sterile) [1]. Reproductive caste individuals win in the game of resource accumulation. They are generally larger, have higher food intake, higher metabolism, are longer lived, and importantly, generally have more nutritional reserves (fat and protein) during both juvenile and adult stages. Furthermore, differences in diet quality/quantity can set up cascades of hormonal, metabolic, developmental, epigenetic, and gene expression differences that produce distinct castes [2].

Less recognized is the fact that there are also extensive nutritional inequalities among members of the worker caste [3]. In its most extreme form, nutritional differences during larval development can lead to distinct morphological castes (e.g. soldiers, major, and minor workers [4]). Less obviously, there is emerging evidence that even within morphologically identical worker behavioral subcastes, there are subtler nutritional inequalities that underlie the division of labor [3,5,6]. Here, we explore the generality, adaptive value, and functional consequences of these inequalities and suggest that they are fundamental to how the division of labor is organized in social insects.

Eusociality has evolved multiple times within the eusocial insects, and worker division of labor across species involves a diversity of different forms. Despite these differences, the universal challenge of resource limitation in nature brings up the possibility that there may be fundamental similarities in the physical and structural principles underlying independently evolved systems of the division of labor. For example, Oster & Wilson (1978) applied optimal foraging theory to social insects and predicted that, on a colony level, natural selection should shape group composition in social insect colonies to maximize energy intake and minimize energy loss [7]. One key prediction is that workers, and more specifically foraging workers, can function as a 'disposable caste' for the colony [8]. These individuals, performing tasks with high mortality risk and energy expenditure, can be viewed as more expendable from a colony perspective. Colonies are thus predicted to disinvest energy reserves in these individuals so that they have lower levels of stored nutrient reserves (e.g. lower fat, protein, and carbohydrate stores) than their counterparts that are found inside the nest (nest workers, nurses, and royal caste individuals).

The goal of this article is to explore three interrelated questions concerning the relationship between worker nutrition and division of labor. 1) Are nutritional differences associated with the worker division of labor across a range of eusocial insect taxa? 2) Are nutritional

Table 1

Summary of studies in social insects examining the association between the worker division of labor and internal nutrient stores.

Order	Family	Species	Citation
Hymenoptera	Vespidae	*Polybia occidentalis*	O'Donnell and Jeanne, 1995 [11]
Hymenoptera	Vespidae	*Mischocyttarus mastigophorus*	Markiewisz and O'Donnell, 2001 [12]
Hymenoptera	Vespidae	*Polistes metricus*	Toth et al. 2009 [13]
Hymenoptera	Formicidae	*Pogonomyrmex montanus, P. subnitidus, P. rugosus*	MacKay, 1983 [14]
Hymenoptera	Formicidae	*Colobus nipponicus*	Hasegawa, 1993 [15]
Hymenoptera	Formicidae	*Pogonomyrmex owyheei*	Porter and Jorgensen, 1981 [8]
Hymenoptera	Formicidae	*Pogonomyrmex badius*	Tschinkel, 1998 [16]
Hymenoptera	Formicidae	*Prenolepis imparis*	Tschinkel, 1987 [17]
Hymenoptera	Formicidae	*Leptothorax albipennis*	Blanchard et al., 2000 [10]
Hymenoptera	Formicidae	*Formica japonica*	Kondoh, 1968 [18]
Hymenoptera	Formicidae	*Tapinoma erraticum*	Meudec and Lenoir, 1982 [19]
Hymenoptera	Formicidae	*Myrmica rubra*	Brian and Abbott, 1977 [20]
Hymenoptera	Formicidae	*Temnothorax albipennis*	E. Robinson et al, 2009 [21]
Hymenoptera	Formicidae	*Dinoponera australis*	Smith et al. 2011 [22]
Hymenoptera	Formicidae	*Pogonomyrmex occidentalis, Po. barbatus, Formica fusca, Atta cephalotes, Solenopsis invicta (-), S. geminata, Pheidole spadonia, Nylanderia fulva* (+)	Silberman et al. 2016 [5]
Hymenoptera	Formicidae	*Platythyrea punctata*	Bernadou et al. 2020 [3]
Hymenoptera	Apidae	*Apis mellifera*	Toth and Robinson, 2005 [6]
Hymenoptera	Apidae	*Bombus impatiens* (-)	Couvillon et al. 2011 [23]

All species listed showed lower nutrient stores in foragers compared to non-foragers, except (-) indicates no significant difference between foragers and non-foragers in nutrient stores, (+) indicates a non-significant trend toward lower nutrient stores in foragers.

differences causally associated with different behavioral roles within societies? 3) Are core molecular mechanisms related to nutrient storage, mobilization, food searching, and hunger regulators of the worker division of labor? We conclude that strong support for all three questions reveals nutritional inequality is a core part of how the division of labor is organized in insect societies.

Part 1: are nutritional asymmetries associated with worker division of labor?

Within hymenopteran social insects, the division of labor between foragers and non-foragers is a near-universal feature. Despite the fact that foragers are collecting food and thus have ready access to it, we predict foragers to be nutritionally deprived compared to non-foragers, relying on rapidly metabolized carbohydrates for flight energy rather than lipid stores. Why? Colonies that distribute nutrient resources away from foragers and into non-foraging nest workers stand to benefit energetically for several reasons. First, lean foragers can be more efficient with less weight to carry around on foraging trips, even small amounts of extra weight during locomotion are energetically costly, especially for flying species [9]. Second, the reduction of nutritional reserves in the abdomen, for example, limiting the volume of the fat body, leaves more room for foragers to store liquid food in the crop [10]. Finally, since foragers have high mortality, the death of lean foragers minimizes the amount of energy lost at a colony level [8].

In reviewing the literature, we found evidence from three families of Hymenoptera (Table 1): 3 species of wasps in the Vespidae, 22 species of ants in the Formicidae, and 2 species of bees in the Apidae, that support the lean forager prediction. In honey bees, the lipid in the fat body of nurses was 2x that of foragers, and lipid stores declined before the onset of foraging [6]. Among wasps, *Polybia occidentalis* foragers have low lipid levels, and this also declines before the onset of foraging [11]. *Mischocyttarus mastigophorus* female fat body condition is negatively correlated with outside performance and positively correlated with time spent on the nest [12] (Table 2).

In ants, *Pogonomyrmex montanus*, *P. subnitidus*, and *P. rugosus* foragers die more quickly under starvation and have lower fat content than the nest workers [14]. The foraging workers are 40% leaner than the nest workers in *Pogonomyrmex owyheei* [8], and the young workers *P. badius* at the bottom of the nest have 30% fat, the older workers near the top of the nest have less than ~23% fat, foragers always have less than 10% [16]. In *Prenolepis imparis*, the callow workers act as 'corpulents', with 60% fat stores, lose this fat after brood rearing, and then become foragers [17]. In *Leptothorax albipennis*, the foraging tendency is negatively correlated with the amount of lipid storage [10]. Kondoh (1968) found two distinct subtypes of *Formica japonica* workers exist: lean and corpulent; only lean workers are found outside of the

Table 2

Studies demonstrating that experimentally altering the worker's nutritional state results in changes in behavior and/or division of labor.

Order	Family	Species	Finding	Citation
Hymenoptera	Vespidae	*Ropalidia marginata*	Low food increases foraging and aggression directed at foragers	Lamba et al. 2008 [24]
Hymenoptera	Vespidae	*Polistes metricus*	Starvation causes increased foraging	Daugherty et al. 2011 [25]
Hymenoptera	Vespidae	*Polistes fuscatus*	Starvation causes reduced aggression	Walton and Toth 2021 [26]
Hymenoptera	Formicidae	*Linepithema humile*	Low sucrose fed (lean) workers more likely to engage in foraging compared to high sucrose fed (fatter) workers	Grover et al. 2007 [27]
Hymenoptera	Apidae	*Apis mellifera*	Experimentally reduced lipid stores cause increased foraging	Toth et al. 2005 [28]
			Food stress affects queen pheromone response	Walton et al. 2018 [29]
Hymenoptera	Apidae	*Ceratina calcarata*	Female offspring more aggressive with higher levels of pollen provisions as larvae	Lawson et al. 2017 [30]

nest foraging [18]. Similarly, in *Temnothorax albipennis*, lean individuals are more likely to exit the nest (forage) [21]. In *Dinoponera australis*, the probability of foraging and foraging effort is associated with decreased fat storage in workers [22]. In morphologically distinct workers of the ant *Colobopis nipponicus*, the majors (which do not forage) had higher fat content than the minors[15]. Comparing eight ant species (*Pogonomyrmex occidentalis*, *P. barbatus*, *F. fusca*, *A. cephalotes*, *S. invicta*, *S. geminata*, *Pheidole spadonia*, and *Nylanderia fulva*), foragers from six of these species had a lower lipid and/or carbohydrate levels (and another had a non-significant trend in the same direction) compared to brood workers [5]. In *Platythyrea punctata*, lipid stores change with the division of labor from corpulent to lean and, in reverted nurses, back to corpulent [3].

We also note that although the nutrient-depleted forager pattern is supported by 27 species, there are two exceptions. Silberman (2016) found no correlation between the behavior and nutrient stores in *Solenopsis invicta* ants [5]. In the bumble bee *Bombus impatiens*, there was no difference in the nutritional state between nest workers and foragers [23]. However, we note that both species have large variations in worker body size, which itself still stems from differences in larval nutritional state [31]. Thus, it is possible that in systems with the size-based division of labor, early life nutritional differences, which are manifested as differences in adult size, are stronger determinants of adult behavioral task performance than adult nutritional differences.

How worker nutritional inequalities come about is an important question. Multiple different mechanisms may be in play, including dietary shifts over the lifetime (e.g. worker honey bees cease eating pollen when they begin foraging [32]), metabolic demands of work causing depletion of nutrient stores (e.g. metabolism of fat in honey bee workers to produce wax and brood food) and in some species, differential food sharing and/or transfer. For example, in *Tapinoma erraticum*, old ants (which tend to be foragers) are donors of food, whereas young ants (which work in the nest) are recipients [19]. *Myrmica rubra* ants inside the nest are more well-nourished and draw food stores away from nutrient-depleted foragers [20].

Part 2: do nutritional differences cause behavioral differences in societies?

Despite the large number of correlative studies cited above, there have been far fewer studies that address causality (Table 2). For those that do, there is accumulating evidence that across multiple, independently evolved lineages, diet and nutritional manipulations cause individuals to fill different roles in insect societies. However, the specific type of behaviors and the

direction of influence of nutritional state can vary between and within species (e.g. life stage).

In the paper wasps of the family *Vespidae*, where a worker's behavioral caste is often flexible and may shift or regress throughout her lifetime [33], nutritional inequalities are proving to be a major organizer of labor [34]. In *Polistes metricus*, starvation caused a reduction in lipid stores and an increase in foraging behavior [25]. Similarly, in the sister taxa *P. fuscatus*, nutritional deprivation decreased dominance-related aggressive interactions between nest-mates [26]. A causal relationship between nutritional state and worker behavior is also evident, though not necessarily in the same direction, in the paper wasp *Ropalidia marginata* where starvation increased foraging activity and aggression directed at foragers [24]. Conversely, a surplus of food led to a decrease in intranidal aggression [35].

In social bees, nourishment also causally influences behavioral variation. In the subsocial carpenter bee *Ceratina calcarata*, depriving daughters of pollen induced worker phenotypes (small, non-aggressive subordinates), whereas pollen supplementation caused daughters to behave like solitary bees [30,36]. In the honey bee *Apis mellifera*, lipid depletion is a proximate causal determinant of foraging onset [28]. Honey bees reared as larvae in pollen-stressed colonies initiated foraging earlier as adults (though less successfully than their counterparts from unstressed colonies) [37]. Moreover, worker larval nutritional deprivation caused an increase in retinue behavior (i.e. responsiveness to queen mandibular pheromone) [29]. However, an *in vitro* manipulation of honey bee larval diet quantity did not affect the likeliness to perform nursing or foraging (possibly due to compensatory food intake as adults) [38]. As with social wasps and bees, the nutritional state can determine worker social behavior in some ant groups. For example, a reduction in available sucrose food resources caused a significant decrease in aggression and overall activity in Argentine ant (*Linepithema humile*) workers though reducing their access to insect prey (i.e. protein) did not affect aggression [27]. Further research, across life stages and lineages with various forms of sociality, is necessary to elucidate the relationship between nutritional inequality and behavioral organization in insect societies.

While the aforementioned studies demonstrate causality on a broad scale (i.e. diet or nutritional manipulations influence worker behavior), more work is needed to better elucidate the physiological, molecular, and neurological pathways that connect nutritional state and worker behavior. While a large number of social insect studies show nutritional differences correlating with the division of labor, and show that diet/food manipulations affect behavior, in general, the field lacks studies that identify and manipulate these candidate genetic and physiological pathways to test their role in regulating behavior via nutritional input (causatively).

Part 3: do core nutrition/feeding-related genes regulate social traits?

There is mounting evidence that conserved insect nutrient-sensing genes have been co-opted in social insect evolution to regulate social behavior [39,40]. Insulin-like peptides (Ilps) are well known to be associated with feeding regulation in solitary species [41,42], and a growing number of studies implicate them in the regulation of the forager division of labor. Ilp expression varies between foragers and nurses in honey bee brains, where insulin-like peptide 1 (Ilp1) expression is higher in foragers whereas insulin-like peptide 2 (Ilp2) expression is higher in nurse bees [43]. Similarly, in *Polistes metricus* wasps, *Ilp2* brain gene expression is higher in satiated non-foragers than in starved foragers [25]. In *Diacamma* ants, where colonies consist of monomorphic individuals and reproduction is performed by dominant gamergates, fat body *Ilp1* expression is higher in dominant ants [44]. Causality has been demonstrated only in the honey bee system in which inhibition of the insulin-related target of rapamycin delayed the onset of foraging behavior [43].

In addition to Ilps, several other neuropeptides are associated with the regulation of social food-seeking and forager division of labor. *Neuropeptide F* (NPF) was shown to be associated with honey bee foraging [45]. Another neuropeptide, tachykinin has been associated with honey bee response thresholds to task-related stimuli [46] and *Acromyrmex* ant worker aggression [47]. Additionally, *tachykinin* and NPF brain gene expression were positively correlated with an increase in aggression within satiated *Polistes fuscatus* paper wasp nests [26]. Moreover, the neuropeptide *Corazonin*, which contributes to the regulation of metabolism in *Drosophila* [48], stimulates hunting behavior and inhibits ovary activation in *Harpegnathos saltator* worker ants [49].

Storage proteins and their genetic regulation are important to the organization of social traits. The egg-yolk precursor vitellogenin is a major regulator of insect physiology and has been well-studied in social insects for its role in behavioral ontogeny [50,51]. In honey bees, RNAi-mediated knockdown of vitellogenin gene expression causes rapid onset of foraging and a bias for nectar foraging [52,53]. In a currently unpublished study from *Polistes fuscatus* paper wasps, knockdown of vitellogenin expression in worker head fat body decreased aggression toward conspecifics (Walton et al., *in prep*), reinforcing the role of vitellogenin in the regulation of social behavior in multiple lineages of social Hymenoptera. In addition to vitellogenin, hexamerins are some of the most abundant storage proteins in insects,

commonly associated with diapause phenotypes [54,55]. In social insects, they are also likely important regulators of the division of labor. Hexamerins have been implicated in reproductive caste bias during larval development in *Polistes* wasps [56,57]. In *Reticulitermes* and *Macrotermes* termites, hexamerins are also causally related to soldier caste differences, and show differential expression between forager and builder castes [58,59].

In summary, these studies suggest a common theme of core nutrient-sensing, storage, and feeding-related genes being associated with worker subcaste differentiation and the division of labor; we note; however, that outside of honey bees, there have been few studies testing causality. Across lineages of social insects, some of the same genes and pathways (e.g. insulin pathway, feeding neuropeptides, storage proteins) are associated with social behaviors, including foraging, aggression, and nest construction. This suggests that genes with ancestral roles related to nourishment and food-seeking may have been co-opted in social contexts for the regulation of both food-related (foraging) and non-food-related (aggression and building) worker behaviors.

Part 4: synthesis and conclusions

We find supportive evidence from over 30 different hymenopteran social insect species representing multiple origins of sociality of a strong pattern in which differences in the worker behavioral role are associated with differences in individual nutritional state. We note that across these diverse systems, nutritional inequalities are found in multiple different systems of the division of labor (reproductive, morphologically-based, dominance-based, age-based). Thus, with a few possible exceptions (two genera with morphologically distinct workers, *Bombus* and *Solenopsis*), there is a widely shared pattern in which worker division of labor is structured along nutritional lines, specifically, in which nutritionally deprived individuals engage in foraging behavior. We suggest the 'lean forager syndrome' is more robust for systems with morphologically identical workers; other regulating mechanisms may be more important for species with morphologically distinct workers.

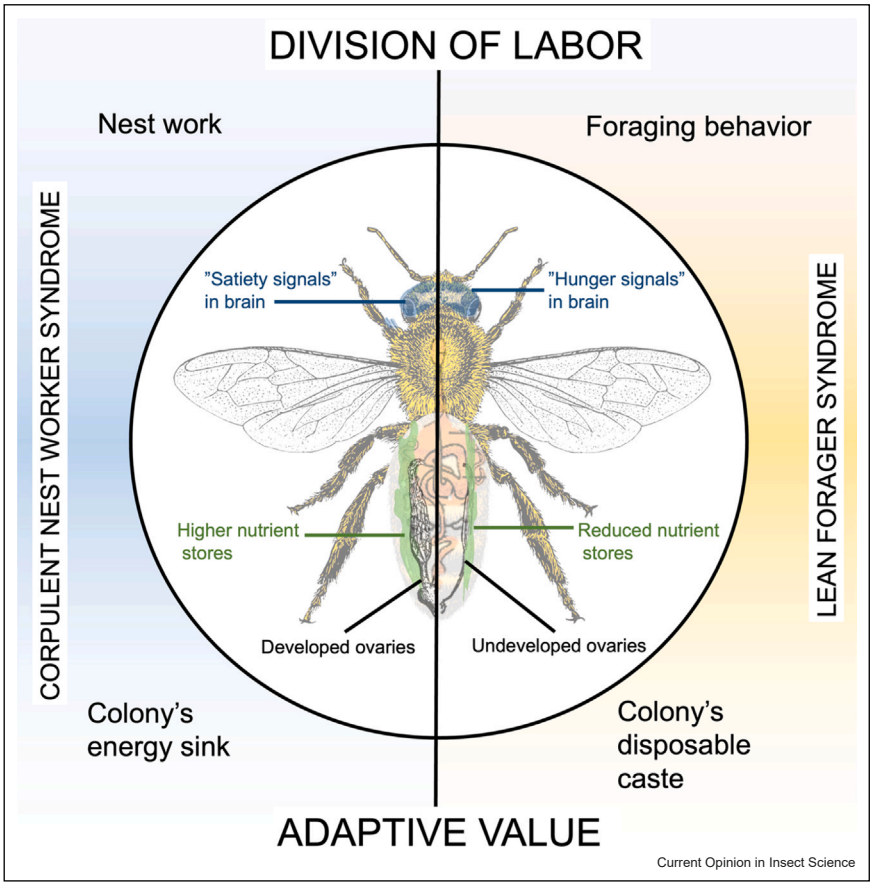
The existence of nutrient-depleted foragers was consistent across most species examined. In some species, foragers not only have depleted nutrient stores, but this depletion occurs (at least partly) before the onset of foraging behavior. For example, in *Prenolepis imparis*, corpulent workers lose massive amounts of their energy stores during a period of brood rearing before becoming foragers [17]. This may be so extreme that foragers can be seen as 'running on empty'. Lipid stores can be so depleted that workers of some species must depend entirely on circulating carbohydrates to fuel locomotion [60]; however, this may not apply equally to all taxa [11,16].

An equally important part of the lean forager syndrome is the implied converse, the corpulent nest worker. Because nest workers have a higher nutritional state, they may function as living vessels for the storage of colony energy. This is seen to an extreme degree in the ants, in which replete workers remain in the nest and store liquid food in their crops [61]. Recent work has identified the existence of 'fat body repletes' in several species of ants, in which lipid stores in the fat body are hypertrophied to an extreme degree (*Monomorium pharaonis:* [62]; *Prenolepis imparis:* [17]; *Myrmecocystus mexicanus:* [63]).

Several lines of evidence suggest the lean forager-corpulent nest worker pattern is adaptive (Figure 1). First, this pattern has convergently evolved multiple times. The lean syndrome may be another manifestation of the 'disposable caste' phenomenon [8]. While this has been invoked to explain patterns of age-related division of labor (e.g. sending out the oldest workers to die), it applies equally well to understand nutritional asymmetries. Colonies should send out the most nutrient-depleted individuals to die so that the colony loses less of its precious energy reserves. Finally, the lean foragers may also be more energetically efficient. Studies have documented up to a 2x difference between nest workers and foragers in weight/lipid weight [6]. When multiplied over many foraging trips and many workers, lean foragers carrying less body weight on foraging trips could indeed save their colonysubstantial energy [9]. Furthermore, the corpulent nest workers could serve as a valuable sink of colony energy. Energy stored in (often) young, well-protected workers can safeguard a substantial part of colony energy stores during nest evacuation or relocation.

This adaptive pattern may have another evolutionary function to orchestrate behavioral maturation. Studies suggest that 'hunger signals' in the brain may be the important regulators of social foraging across multiple independent origins of eusociality. Nutrient depletion before the onset of foraging could act as a cue to the individual to leave the nest and begin foraging behavior [6]. Although foraging by hungry animals may seem obvious, the interesting twist is that social insect foragers are generally eating very little of the food they collect; the vast majority is brought back to the colony to feed colony mates or contribute to colony food caches. In support of this, studies reviewed above from ants, bees, and wasps suggest canonical feeding regulation genes including the insulin pathway, neuropeptides such as *tachykinin*, NPF, and *corazonin*, and the storage proteins vitellogenin and hexamerins, as well as others are associated with different forms of foraging division of labor. This suggests that a core part of the 'toolkit' for the division of labor in eusocial insects is based on core feeding and nutrition genes found in solitary insects [40].

Figure 1



Schematic summary of the skinny forager/corpulent nest worker pattern, which is underlain by differences in physiology (fat and carbohydrate stores, ovary development), and brain gene expression and chemistry (e.g. expression of hunger signals such as NPF). This nutritional inequality not only structures the division of labor among nestmates within a social insect colony but can also have an adaptive value for colonies in terms of storing energy and saving on energy costs.

The influence of nutrient stores on the organization of the division of labor promises to be a fruitful line of inquiry for future investigations. However, the field could benefit from more work addressing causal associations between specific physiological and molecular mechanisms and worker behavior. In addition, we urge further considerations of evolutionary scenarios on resource availability and the evolution of sociality, especially comparing mechanisms from related solitary and social species (across a social spectrum) within a phylogenetic context. This can help tie in how nutritional asymmetries may have contributed to the evolution of sociality. Along those lines, more work on the potential importance of resource limitation in driving the evolution of cooperation among social insects may be informative.

Data Availability

No data was used for the research described in the article.

Declaration of Competing Interest

None.

Acknowledgements

We thank Guy Bloch and Ricarda Scheiner for the invitation to present on this topic and write a review on it; Gene Robinson for early inspiration; Susan Fahrbach for a long-ago insect physiology assignment that spurred thinking on this topic; and the National Science Foundation, Grant 1827567 from the EDGE Program for funding.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. O'Donnell S: **Caste, social insects**. Encyclopedia of Social Insects. 2020,.

2. Thompson GJ, Chernyshova AM: **Caste differentiation: genetic and epigenetic factors**. Encyclopedia of Social Insects. 2021,:165-176.

3. •• Bernadou A, Hoffacker E, Pable J, Heinze J: **Lipid content influences division of labour in a clonal ant**. *J Exp Biol* 2020, **223**:jeb219238.
Establishes a causal role of nutritional state for the worker division of labor in an ant species with morphologically identical workers. Lipid stores decrease as ants transition from nursing to foraging and increase again in experimentally reverted nurses.

4. Psalti MN, Libbrecht R: **Caste Differentiation**. Encyclopedia of Social Insects. Springer; 2020.

5. Silberman RE, Gordon D, Ingram KK: **Nutrient stores predict task behaviors in diverse ant species**. *Insectes Sociaux* 2016, **63**:299-307.

6. Toth AL, Robinson GE: **Worker nutrition and division of labour in honeybees**. *Anim Behav* 2005, **69**:427-435.

7. Oster GF, Wilson EO: Caste and Ecology in the Social Insects. Princeton University Press; 1978.

8. Porter SD, Jorgensen CD: **Foragers of the harvester ant, Pogonomyrmex owyheei: a disposable caste?** *Behav Ecol Sociobiol* 1981, **9**:247-256.

9. • Combes SA, Gagliardi SF, Switzer CM, Dillon ME: **Kinematic flexibility allows bumblebees to increase energetic efficiency when carrying heavy loads**. *Sci Adv* 2020, **6**:eaay3115.
This experimental study tracked metabolic rate and aspects of flight kinematics (flapping frequency, stroke amplitude) in bumble bees that were either carrying light loads or heavy loads. They uncovered unexpected costs of load-carrying in terms of increases in flapping frequency when carrying heavy loads.

10. Blanchard GB, Orledge GM, Reynolds SE, Franks NR: **Division of labour and seasonality in the ant *Leptothorax albipennis*: worker corpulence and its influence on behaviour**. *Anim Behav* 2000, **59**:723-738.

11. O'Donnell S, Jeanne RL: **Worker lipid stores decrease with outside-nest task performance in wasps: implications for the evolution of age polyethism**. *Experientia* 1995, **51**:749-752.

12. Markiewicz DA, O'Donnell S: **Social dominance, task performance and nutrition: implications for reproduction in eusocial wasps**. *J Comp Physiol A* 2001, **187**:327-333.

13. Toth AL, Bilof KBJ, Henshaw MT, Hunt JH, Robinson GE: **Lipid stores, ovary development, and brain gene expression in Polistes metricus females**. *Insectes Sociaux* 2009, **56**:77-84.

14. MacKay WP: **Stratification of workers in harvester ant nests (*Hymenoptera: Formicidae*)**. *J Kans Èntomol Soc* 1983, **56**:538-542.

15. Hasegawa E: **Caste specialization in food storage in the dimorphic antColobopsis nipponicus (Wheeler)**. *Insectes Sociaux* 1993, **40**:261-271.

16. Tschinkel WR: **Sociometry and sociogenesis of colonies of the harvester ant, *Pogonomyrmex badius*: worker characteristics in relation to colony size and season**. *Insectes Sociaux* 1998, **45**:385-410.

17. Tschinkel WR: **Seasonal life history and nest architecture of a winter-active ant, *Prenolepis imparis***. *Insectes Sociaux* 1987, **34**:143-164.

18. Kondoh M: **Bioeconomic studies on the colony of an ant species, *Formica japonica* Motschulsky: 2. allometric study of the body weight and the corpulency relating to the body size of workers**. *Jpn J Ecol* 1968, **18**:171-179.

19. Meudec M, Lenoir A: **Social responses to variation in food supply and nest suitability in ants (*Tapinoma erraticum*)**. *Anim Behav* 1982, **30**:284-292.

20. Brian MV, Abbott A: **The control of food flow in a society of the ant Myrmica rubra L**. *Anim Behav* 1977, **25**:1047-1055.

21. Robinson EJH, Richardson TO, Sendova-Franks AB, Feinerman O, Franks NR: **Radio tagging reveals the roles of corpulence, experience and social information in ant decision making**. *Behav Ecol Socio* 2009, **63**:627-636.

22. Smith CR, Suarez AV, Tsutsui ND, Wittman SE, Edmonds B, Freauff A, Tillberg CV: **Nutritional asymmetries are related to division of labor in a queenless ant**. *PLoS One* 2011, **6**:e24011.

23. Couvillon MJ, Jandt JM, Bonds J, Helm BR, Dornhaus A: **Percent lipid is associated with body size but not task in the bumble bee Bombus impatiens**. *J Comp Physiol A* 2011, **197**:1097-1104.

24. Lamba S, Chandrasekhar K, Gadagkar R: **Signaling hunger through aggression — the regulation of foraging in a primitively eusocial wasp**. *Naturwissenschaften* 2008, **95**:677-680.

25. Daugherty THF, Toth AL, Robinson GE: **Nutrition and division of labor: effects on foraging and brain gene expression in the paper wasp *Polistes metricus***. *Mol Ecol* 2011, **20**:5337-5347.

26. •• Walton A, Toth AL: **Resource limitation, intra-group aggression and brain neuropeptide expression in a social wasp**. *Funct Ecol* 2021, **35**:2241-2252.
This study shows that nutritional restriction causes a reduction in intranidal aggression in paper wasp colonies and that changes in nutritional environment and social behavior correlate with brain gene expression of the neuropeptides *tachykinin* and *neuropeptide-F*.

27. Grover CD, Kay AD, Monson JA, Marsh TC, Holway DA: **Linking nutrition and behavioural dominance: carbohydrate scarcity limits aggression and activity in Argentine ants**. *Proc R Soc B: Biol Sci* 2007, **274**:2951-2957.

28. Toth AL, Kantarovich S, Meisel AF, Robinson GE: **Nutritional status influences socially regulated foraging ontogeny in honey bees**. *J Exp Biol* 2005, **208**:4641-4649.

29. Walton A, Dolezal AG, Bakken MA, Toth AL: **Hungry for the queen: honeybee nutritional environment affects worker pheromone response in a life stage-dependent manner**. *Funct Ecol* 2018, **32**:2699-2706.

30. Lawson SP, Helmreich SL, Rehan SM: **Effects of nutritional deprivation on development and behavior in the subsocial bee *Ceratina calcarata* (Hymenoptera: Xylocopinae)**. *J Exp Biol* 2017, **220**:4456-4462.

31. Chole H, Woodard SH, Bloch G: **Body size variation in bees: regulation, mechanisms, and relationship to social organization**. *Curr Opin Insect Sci* 2019, **35**:77-87.

32. Crailsheim K, Schneider LHW, Hrassnigg N, Bühlmann G, Brosch U, Gmeinbauer R, Schöffmann B: **Pollen consumption and utilization in worker honeybees (*Apis mellifera carnica*): dependence on individual age and function**. *J Insect Physiol* 1992, **38**:409-419.

33. Matthews RW, Ross KG: The Social Biology of Wasps. Cornell University Press; 1991.

34. • Hunt JH: **Origin of an evolutionary novelty: the worker phenotype of eusocial wasps**. *Insect Soc* 2021, **68**:303-318.
This report synthesizes JH Hunt's career-spanning research on the division of labor in social wasps. The author proposes an explanation for the evolution of the worker phenotype as a result of a confluence of elements of wasp biology, including behavior, development, and nutrient dynamics.

35. Premnath S, Sinha A, Gadagkar R: **Regulation of worker activity in a primitively eusocial wasp, *Ropalidia marginata***. *Behav Ecol* 1995, **6**:117-123.

36. Lawson SP, Ciaccio KN, Rehan SM: **Maternal manipulation of pollen provisions affects worker production in a small carpenter bee**. *Behav Ecol Socio* 2016, **70**:1891-1900.

37. Scofield HN, Mattila HR: **Honey bee workers that are pollen stressed as larvae become poor foragers and waggle dancers as adults**. *PLOS ONE* 2015, **10**:e0121731.

38. Schilcher F, Hilsmann L, Ankenbrand MJ, Krischke M, Mueller MJ, Steffan-Dewenter I, Scheiner R: **Honeybees are buffered against undernourishment during larval stages**. *Front Insect Sci* 2022, **2**.

39. Toth AL: **To reproduce or work? Insect castes emerge from socially induced changes in nutrition-related genes**. *Mol Ecol* 2017, **26**:2839-2841.

40. Toth AL, Robinson GE: **Evo-devo and the evolution of social behavior**. *Trends Genet* 2007, **23**:334-341.

41. Chowański S, Walkowiak-Nowicka K, Winkiel M, Marciniak P, Urbański A, Pacholska-Bogalska J: **Insulin-like peptides and cross-talk with other factors in the regulation of insect metabolism**. *Front Physiol* 2021, **12**:701203.

42. Wu Q, Brown MR: **Signaling and function of insulin-like peptides in insects**. *Annu Rev Entomol* 2006, **51**:1-24.

43. Ament SA, Corona M, Pollock HS, Robinson GE: **Insulin signaling is involved in the regulation of worker division of labor in honey bee colonies**. *Proc Natl Acad Sci* 2008, **105**:4226-4231.

44. Okada Y, Watanabe Y, Tin MM, Tsuji K, Mikheyev AS: **Social dominance alters nutrition-related gene expression immediately: transcriptomic evidence from a monomorphic queenless ant**. *Mol Ecol* 2017, **26**:2922-2938.

45. Ament SA, Velarde RA, Kolodkin MH, Moyse D, Robinson GE: **Neuropeptide Y-like signalling and nutritionally mediated gene expression and behaviour in the honey bee**. *Insect Mol Biol* 2011, **20**:335-345.

46. • Han B, Wei Q, Wu F, Hu H, Ma C, Meng L, Zhang X, Feng M, Fang Y, Rueppell O, *et al.*: **Tachykinin signaling inhibits task-specific behavioral responsiveness in honeybee workers**. *eLife* 2021, **10**:e64830.
The task-specific response thresholds of behaviorally specialized worker honey bees are modified by tachykinin-related neuropeptides.

47. Howe J, Schiøtt M, Boomsma JJ: **Tachykinin expression levels correlate with caste-specific aggression in workers of the leaf-cutting ant *Acromyrmex echinatior***. *Front Ecol Evol* 2016, **4**:55.

48. Kapan N, Lushchak OV, Luo J, Nässel DR: **Identified peptidergic neurons in the *Drosophila* brain regulate insulin-producing cells, stress responses and metabolism by coexpressed short neuropeptide F and corazonin**. *Cell Mol Life Sci* 2012, **69**:4051-4066.

49. Gospocic J, Shields EJ, Glastad KM, Lin Y, Penick CA, Yan H, Mikheyev AS, Linksvayer TA, Garcia BA, Berger SL, *et al.*: **The neuropeptide corazonin controls social behavior and caste identity in ants**. *Cell* 2017, **170**:748-759e12.

50. Amdam GV, Norberg K, Fondrk MK, Page RE: **Reproductive ground plan may mediate colony-level selection effects on individual foraging behavior in honey bees**. *Proc Natl Acad Sci* 2004, **101**:11350-11355.

51. Amdam GV, Norberg K, Hagen A, Omholt SW: **Social exploitation of vitellogenin**. *Proc Natl Acad Sci* 2003, **100**:1799-1802.

52. Nelson CM, Ihle KE, Fondrk MK, Page RE Jr, Amdam GV: **The gene vitellogenin has multiple coordinating effects on social organization**. *PLoS Biol* 2007, **5**:e62.

53. Marco Antonio DS, Guidugli-Lazzarini KR, Do Nascimento AM, Simões ZLP, Hartfelder K: **RNAi-mediated silencing of vitellogenin gene function turns honeybee (*Apis mellifera*) workers into extremely precocious foragers**. *Naturwissenschaften* 2008, **95**:953-961.

54. Denlinger DL: Insect Diapause. Cambridge University Press; 2022.

55. Lewis DK, Spurgeon D, Sappington TW, Keeley LL: **A hexamerin protein, AgSP-1, is associated with diapause in the boll weevil**. *J Insect Physiol* 2002, **48**:887-901.

56. Hunt JH: The Evolution of Social Wasps. Oxford University Press; 2007.

57. Hunt JH, Amdam GV: **Bivoltinism as an antecedent to eusociality in the paper wasp genus *Polistes***. *Science* 2005, **308**:264-267.

58. • Elsner D, Hartfelder K, Korb J: **Molecular underpinnings of division of labour among workers in a socially complex termite**. *Sci Rep* 2021, **11**:18269.
The authors test historically Hymenoptera-focused hypotheses about the mechanisms of division of labor in a fungus-growing termite. Similar to findings from bees, wasps, and ants, the authors report that storage proteins underlie division of labor between termite foragers and builders.

59. Zhou X, Oi FM, Scharf ME: **Social exploitation of hexamerin: RNAi reveals a major caste-regulatory factor in termites**. *Proc Natl Acad Sci* 2006, **103**:4499-4504.

60. Lorenz MW, Kellner R, Völkl W, Hoffmann KH, Woodring J: **A comparative study on hypertrehalosaemic hormones in the *Hymenoptera*: sequence determination, physiological actions and biological significance**. *J Insect Physiol* 2001, **47**:563-571.

61. Wilson EO: **Social insects**. *Science* 1971, **172**:406.

62. Børgesen LW: **Nutritional function of replete workers in the pharaoh's ant, *Monomorium pharaonis* (L.)**. *Insectes Sociaux* 2000, **47**:141-146.

63. Burgett DM, Young RG: **Lipid storage by honey ant repletes**. *Ann Èntomol Soc Am* 1974, **67**:743-744.