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Nutritional, endocrine, and social influences on reproductive physiology at the origins of social behavior

Karen M Kapheim

Understanding the evolutionary origins of social behavior in insects requires understanding the physiological basis for reproductive plasticity. Solitary bees and wasps, or those living in small, flexible societies, will be key to understanding how conserved pathways have evolved to give rise to reproductive castes. Nutrient-sensing and endocrine pathways are decoupled from reproduction in some life stages of social insects. Heterochrony, particularly as it is related to diapause physiology, may be an important mechanism by which this decoupling occurs. Additional research is needed to understand how these pathways became sensitive to cues from the social environment. Future research targeting species with a diversity of social behaviors and diapause strategies will be key to understanding the physiological basis of social evolution.

Address
Utah State University, Department of Biology, 5305 Old Main Hill, Logan, UT 84322, USA

Corresponding author: Kapheim, Karen M (karen.kapheim@usu.edu)

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Introduction

Variation in reproductive success is one of the defining features of sociality amongst insects, whereby some individuals lay eggs and others care for eggs laid by their nestmates. Yet surprisingly little is known about the physiology underlying this reproductive variation in most social insect species. This is particularly true for species representative of the solitary ancestors from which sociality was derived or species that represent the earliest stages of this transition, in which behavior and reproduction are flexible among castes. Understanding the factors that influence reproductive physiology in these groups will provide a foundation upon which to build our understanding of how changes in these relationships have given rise to fixed reproductive castes found among the most advanced social insect species.

Here I review recent insights into the nutritional, endocrine, and social influences on reproductive physiology in the Hymenoptera (bees, ants, wasps), with particular focus on those species that are solitary or with social organization representative of the early stages of social evolution. The physiological basis of reproductive development in ants (Family Formicidae), honey bees (*Apis mellifera*), and bumble bees (*Bombus* sp.) has been thoroughly reviewed elsewhere [1–4]. I present the highlights of this research primarily to establish the foundation for comparison to reproductive physiology in those species more closely aligned with conditions at the origins of eusociality.

Overview of reproductive physiology in non-Hymenopteran insects

Egg maturation (*i.e.*, oogenesis) involves synthesis and incorporation of essential compounds, such as hormones and nutrients necessary for development, into developing oocytes [5]. The target-of-rapamycin (TOR) and insulin/insulin-like signaling (IIS) pathways are the two most highly conserved nutrient sensors involved in regulating this process, while juvenile hormones (JH) and ecdysteroids are classes of highly conserved lipophilic hormones that interact with these nutrient sensing pathways [6]. These pathways play an important role in reproductive development in insects, but the details of how they influence each other and their relative positions within reproductive regulatory networks are highly variable across species [6].

In most insects, activation of the IIS and TOR stimulates the synthesis of JH and ecdysteroids [5,6]. The TOR pathway can be activated directly when free amino acids bind to receptors on the cellular membrane [5]. IIS is a systemic nutrient sensor, because insulin like peptides (ILPs) are released primarily from the brain and bind to insulin receptors (IRs) in the periphery (*e.g.*, ovary, fat body) in response to glucose [5,7]. The IIS also stimulates the TOR pathway via the binding of ILPs to IRs on the cellular membrane, so TOR participates in both a direct and indirect response to nutrients [6]. JH is synthesized in the corpus allatum (CA), and circulates in the hemolymph. When detected by the fat body, it triggers transcription of the *Vg* gene responsible for transcribing the yolk precursor protein vitellogenin [8]. JH is the sole regulator of *Vg* in most insects, but in some lineages (*e.g.*, Diptera), ecdysteroids are more important for egg development [6,8]. Ecdysteroids are a class of cholesterol-derived hormones that includes ecdysone (E) and 20-hydroxy-ecdysone (20E), all of which are synthesized in the ovary, and stimulate the uptake of yolk by developing oocytes [5,9]. Activation of the IIS and TOR pathways also triggers the transcription of *Vg*, and thus stimulates vitellogenesis both directly and indirectly through endocrine pathways [6,10–13].

Variation in how these pathways regulate reproductive physiology within and among species likely promotes and enables the immense diversity of reproductive strategies found among insects. This is likely a prerequisite for the origin of social insect castes, among which nutrient-sensing and endocrine pathways can function independently of each other and are decoupled from reproduction in some individuals.

Nutritional influences on caste-related reproductive physiology may be constrained by diapause

Among the Hymenoptera, the nutritional influences on reproductive development are best understood in two species: honey bees that live in highly eusocial societies and bumble bees that are obligately eusocial, but go through a solitary phase during nest initiation each year. In these species, nutrition plays an important role in caste determination, and in parallel, reproductive development, but with some important differences. In the earliest stages of honey bee development, the relationship between the IIS, TOR and the lipophilic endocrine pathways are mostly similar to patterns observed in other insects. Early stage larvae destined to become queens receive more of the highly proteinaceous royal jelly, which leads to elevated JH titers via activation of the IIS and TOR pathways [4,14–16]. However, the regulatory relationship between nutrition, IIS, and reproduction is drastically altered among later larval stages and adults. Among fourth and fifth instar larvae, expression of both insulin receptor genes and *tor* are down-regulated in queen-destined larvae [4,17]. Although adult queens continue to have better access to nutritious royal jelly, and thus more nutrient stores than workers, they have lower expression of IIS genes [18].

In contrast, bumble bee reproduction seems to be mediated by a conserved relationship between nutrition and physiology. In the European buff-tailed bumble bee (*Bombus terrestris*), *ILP*, *insulin-like growth factor-1* (*IGF-1*), and several hexamerin protein storage transcripts are more abundant in reproductive queens than in workers or virgin and diapausing queens [19,20•]. Conversely, insulin receptors *InR-1* and *InR-2* are down-regulated in reproductive queens, which is consistent with known feedback responses within an activated IIS [20•].

This difference in the relationship between nutrient-signaling and reproductive physiology in honey bees and most other insects, including bumble bees, is generally assumed to be a product of advanced stages of eusocial evolution [1,21]. While this is likely true, there is another difference between honey bees and most other insects in which reproductive physiology has been studied—diapause (Figure 1). Unlike bumble bees and many other insects, honey bees are able to survive the winter on food stores in the hive, and thus avoid diapause. In most other temperate insects, however, nutrient signaling also plays a major role in diapause [22,23]. In fact, genes involved in diapause regulation in bumble bee queens also tend to be differentially expressed between queens and workers [23]. This suggests the effects of nutrition on reproductive physiology and the evolution of social castes is likely constrained by diapause requirements.

Clues regarding how the influence of diapause has shaped the relationship between nutrition and reproduction over the course of social evolution come from studies in species with more flexible social organization. Paper wasps in the vespid subfamily Polistinae live in small groups with a reproductive division of labor and cooperative brood care. Unlike for obligately eusocial species, polistine castes are not morphologically specialized, and they retain totipotency throughout their lifetimes. This flexibility provides insight into physiological changes that accompany the earliest stages of caste evolution. Among new nest foundresses, workers, and queens of *Polistes metricus*, lipid stores and ovary development are positively correlated, and are also correlated with expression of IIS genes [24]. Consistent with this, *hexamerins* and several genes in the IIS are up-regulated in queen-destined larvae, as compared to worker-destined larvae [25,26]. Nutrient restriction of lab-reared larvae led to significant up-regulation of genes involved in lipid metabolism, though the resulting transcriptional profile was only partially similar to that of workers [27•]. A separate study with a similar experimental design found significant effects of larval diet on reproductive development at emergence [28••]. When protein was restricted for larvae-rearing foundresses, offspring emerged with traits very similar to that of workers, including more developed ovaries, than when protein was unrestricted or supplemented. *P. metricus* gynes (*i.e.*, females that will become nest foundresses the following spring) emerge from development with inactivate ovaries, ready to overwinter in diapause, while worker ovaries are somewhat activated at emergence, since they do not overwinter [29]. Indeed, ovarian development among *Polistes dominula* workers has been shown to depend on diet upon emergence [29]. Collectively, these results suggest larval diet has more direct influence over diapause requirements than reproductive development in *Polistes* wasps, but diet directly influences reproductive physiology in adults.

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