Interplay of Nutrition and Environment: a Major Factor behind Social Evolution in Insects

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ABSTRACT

The social insect species exhibiting overlap of generations, cooperative brood care and reproductive caste differentiation are termed as eusocial. If morphological caste difference exists then they are termed as highly eusocial while primitively eusocial are the ones having morphologically identical queen and worker castes. Little is known about division of labor among members of species lacking a distinct queen caste. Obvious interest crops up for the processes in primitively eusocial species resulting in some individuals becoming reproductive queens while others ending up as sterile workers. The presence of sterile worker caste that makes it possible for the fertile queen to produce large number of offsprings is an important feature of insect societies. The evolutionary mechanisms of natural selection responsible for such sterility and other, less extreme forms of altruism have long been considered as a paradox. To explain this paradox, three theories namely kin selection, parental manipulation and mutualism have been suggested. But one factor i.e. nutrition has not been given due importance in relation to caste determination. Experimental and correlative studies indicate that pre-imaginal caste – determination is based on the nutritional differences during larval development. Environmental availability of food materials also has a role to play in the shaping of the life cycles and thus the social way of life for various insects. So, in this review, we try to bring forward the implications which nutrition along with the environment has on subfertility and the evolution of eusocial behaviour.

Keywords: Social insect, nutrition, environment, pre-imaginal caste differentiation.

1. INTRODUCTION

A deep understanding of the nutritional state and nutritional needs of an organism is important to understand its development, physiology and behaviour as nutrition during development can be responsible for physiological, morphological and behavioural differences as adults. Dietary variation acts as a major factor leading to within and among species physical differences [1] and is also thought of as a driver of life history evolution [2]. An example of such an organisation are the insect societies which have attracted the attention of biologists for centuries as they represent one

of the major transitions in evolution. [3]. Eusocial insect castes exhibit alternative adult phenotypes differing greatly in size, longevity and fecundity [4]. One of the most challenging areas of modern biology is to understand the forces that mould the evolution of social behaviour. To meet this challenge a whole new field of socio-biology has developed [5]. There are three reasons for social insects being the focus of special attention in this context [6]. Firstly, the most extreme form of social behaviour such as the presence of sterile workers is shown by social insects. Secondly, various stages in the course of evolution from solitary to highly eusocial are exemplified by these insects. Thirdly, social insects are characterized by a special category of genetics called haplodiploidy which brings asymmetry in the genetic relatedness among parents and offsprings on one hand and among siblings on the other thus pushing them towards sociality. These factors present the organisation of insect society to be having an unreal quality even to the most experienced observers. Ever since Darwin, the evolution of such sterile individuals in social insect colonies has been a major evolutionary puzzle. [7]. In order to solve this puzzle it is essential to elucidate the proximal mechanisms by which complex social behaviours such as those forming the basis of colony defence, division of labour and nest construction were produced. It has been a topic of argument among many authors that dietary variation formed the fundamental basis of evolution of eusociality [6,8-10]. It has been suggested that the sterile workers resulted from “trophic castration” i.e. low quality diet resulting in reproductive incapability.

It becomes clear in many species that nutritional differences play a fundamental role in the development of worker and sexual castes by looking at the difference in the size of these castes indicating they have received quantitatively different diets during developmental period [11]. In ants, it has been found that different castes have different body composition because they assimilate nutrients from different trophic levels [12]. In Termites [13] and social aphids [14] also nutritional component appears to be involved in caste determination. If there are nutrients which limit development of organ sytems specific to one caste such as wings, fat bodies and reproductive tissues then caste determination may depend upon receiving different type of diet during development. Additionally, if one caste, like the gynes, require higher levels of a particular nutrient then an alternative food source rich in that particular nutrient may be used for provisioning them. Evolution of sociality may or may not be underpinned by withholding of nutrients but differentially provisioning larvae so that only specific ones receive nutrients essential for sexual development , maybe an upstream driver of caste determination in many eusocial taxa [15]. All these studies point towards the possibility that environmental variation in availability of basic nutrients may have a sound impact on the production of these very diverse phenotypes. Therefore, caste determination in social taxa may be based on an interplay between environmental availability, differential provisioning and nutrition working in coalition with a shared molecular kit for sociality. [16,17]

So, in this review, we present the works shedding light on this link.

2. THE INSECT SOCIETY

The insect species in which individuals share resources and reproduce cooperatively are known as social insects. There is a characteristic morphology, behaviour, life-history pattern and internal organization of the insect colony and thus it represents a level of organisation above the individual organism [6]. Profound bias in reproduction is one of the hallmarks of insect societies. Some individuals (the workers) are sterile or have relatively low reproductive potential while others (typically the queens) are extremely fecund. There is competition for reproductive dominance between adult females; subordinates perform nest maintenance and brood care activities but do not reproduce in primitively social species. Alternative developmental processes, initiated during pre-adult stages cause make the females to develop into either queens or workers in more advanced social systems. To understand how such complex social systems evolved among insects, many theories have been put forward. Some of the main theories are:

- Inclusive fitness and kin selection theory [18-20]
- Theory of mutualism [21]
- Theory of reciprocal altruism [22]
- Theory of subfertility /parental manipulation [23]

But none of these theories were able to pin-point exactly how sociality evolved. The main reason or trigger for the social evolution in insects is not clear but many other factors have been explained which are thought to be working behind the scenes for the act of caste development in social taxa.

3. HOW CASTES DEVELOP?

There has been a long standing debate on whether the castes are determined in the egg (maternal or genetic differences) or by the environment of the developing larva. In honey bees, the effect of diet on caste determination has long been known and many other related environmental factors have been described [4,8]. However, the genetic systems involved in caste determination have recently been described in a variety of species across separate origins of eusociality [24-27] and at least in two ant species maternal effects have been shown. But inspite of the recent emphasis on genetic effects responsible for caste determination, there is still lack of understanding about the simultaneous contribution of both genetic and environmental factors towards caste determination. Epigenetic effects [28] and endocrine changes in individuals that differentiate the developmental trajectories of queens and workers in honey bees are triggered due to qualitative differences in larval nutrition at critical times during development. It is quite curious that the role of qualitative diet differences in caste determination is not well understood in other social insects despite a

historic knowledge of the important role played by royal jelly in queen development in honey bees. But, trophic differences within and among species of ants [29] have been successfully explored by the use of methods such as stable isotope analysis and they may be a means of discovering cryptic differences in diet among social insect castes.

4. ROLE OF NUTRITION

In most systems of gyne determination, regardless of the level of sociality, nutritional factors play an important role. In many species, a mechanism called "**nutritional switch"** links nutrition and development. The nutritional history of larvae is translated into endocrine signals through this mechanism and this results in the coordination of subsequent patterns of differentiation. Evidences are present for the role of nutrition in gyne determination in *Apis mellifera* [30], *Bombus hypnorum and Bombus terrestris* [31] and *Myrmica rubra* [32]. The link between nutritional factors and hormonal changes has been best outlined in the honeybee. Gyne development requires royal jelly in honey bees [33]. It is thought that the food amount along with the pheromones or oral secretions fed to the larvae by the workers combine to initiate the path divergence in highly dimorphic hornets and yellow jackets. The long-standing view for the non-dimorphic polistines such as Polistes, Ropalidia and others is that the differences in the quantity of nourishment they receive during larval developmental stage acts as a nutritional switch to bias development towards one caste or the other [34].

If ample food is given to the female larvae, they develop into gynes, whereas the less well fed larvae become workers. It has been shown by food supplementation studies that colonies given nutrients ad-libitum produce higher frequencies of female offspring having gyne like traits, i.e. larger size, more fat body, greater cold tolerance and higher diapause potential than the control colonies [11]. While, on the other hand, small offspring are produced as a result of under feeding. Poor larval nutrition early in the colony cycle, due to a low worker to larva ratio produces workers while gynes are produced towards the end of the colony cycle due to improved nutrition because of an increased worker to larva ratio pointing towards a combined effect of environment and nutrition towards caste development.

In a study carried out on a social wasp it was found that different individuals produced during different stages of wasp nest have different content of nutrients and these contents were particularly different in the individuals produced during initial stages which are destined to be workers (sterile) and those produced at advance stage which are destined to be gyne (reproductive) [35]

Higher levels of lipids and K were found to be present in reproductive destined larvae. Ca was retained more in reproductive destined larvae. Higher levels of Mn were found to be present in all

the adults. Foragers had the highest level of Mn. Spring gynes had higher levels of proteins than the fall gynes or the queen stages suggesting that the gynes are accumulating proteins before nesting. In all adults Cu increased from emergence to adulthood. There was a significant increase in carbohydrates and a significant decrease in lipids from the emerging gynes to the spring gynes. After becoming queens, the protein levels recovered, indicating gynes gained proteins after emerging from diapause and there is loss of protein from foundresses as the workers are produced and regain when the workers are available. Emerging gynes had lower carbohydrates and lipids than early workers. Emerging gynes had lower protein levels than early workers but emerging gynes had higher proteins than late workers.

The results of this study compel our thought process to about the interconnected role being played by the environment and respective food availability in architechturing the basic plan of eusocial life.

5. FUTURE DIRECTIONS

Many factors contribute to the regulation of caste production and the determination of a developing individual's caste fate and the final adult size. But, queen-worker division of labor is highly influenced by nutrition. It is very surprising that apart from a few ant studies very little is known about the natural nutritional levels and nutritional fluctuations of individuals over the course of colony cycle within the insect colonies. Several works have discussed the absence of such fundamental data. At this point, the need for mapping out the natural nutritional levels during different points of the entire colony cycle i.e. "nutritional profile studies" has become more important than ever to supplement the important advancements made in the field of physiology and genomics to help us acquire a more precise understanding of the role of nutrition in social insect colony dynamics.

Nutrition appears to be the master regulator of caste production. Nonetheless, a lot of work is needed to understand the interplay between the nutrient distribution within colonies, the nutrient sensing pathways of individuals and the availability of nutrients in the environment.

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