International Journal of Entomology Research
ISSN: 2455-4758; Impact Factor: RJIF 5.24
Received: 17-01-2020; Accepted: 18-02-2020; published: 18-03-2020
www.entomologyjournals.com
Volume 5; Issue 2; 2020; Page No. 53-56

An insight to the concept of Eusociality in insects

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Abstract
Any species in which organism interacts with another member of its own species is called social. Eusociality is more complex and defined by the presence of three basic attributes *viz*. cooperative brood care, reproductive division of labor and overlap of generations. Species that lacks one or more these three basic attributes are called presocial. Presocial can further subdivide in to subsocial and parasocial. Subsociality refers to the social behavior between parents and offspring and parasociality refers to the social behavior among members of same generation. Besides these three basic attributes, sometimes other characteristics like communal nest construction and living, altruism, swarming, territorial defense, trophallaxis, corpse management, group decision making, group communication *etc* may also present. The division of labor creates behavioral groups called castes. Eusociality is sometimes managed by a set of pheromones that alter the behavior of castes in the colony. Advanced eusocial organisms may also show morphological variations between castes. However not all eusocial insect species have distinct morphological variations between castes. Eusociality is mostly found in the phylum Arthropoda but few Chordates also express it. Overall we can say that eusocial organisms prefer the species survival over individual survival as long term survival strategy. Changing environment may cause reversal from eusociality to solitary adaptations and *vice versa*.

Keywords: eusociality, isoptera, hymenoptera, pheromones, haplodiploidy

Introduction

Any species in which organism interacts with another member of its own species is called social. Eusociality is more complex and defined by the presence of three basic attributes *viz*. cooperative brood care, reproductive division of labor and overlap of generations. Species that lacks one or more these three basic attributes are called presocial. Presocial can further subdivide in to subsocial and parasocial. Subsociality refers to the social behavior between parents and offspring and parasociality refers to the social behavior among members of same generation. Besides these three basic attributes, sometimes other characteristics like communal nest construction and living, altruism, swarming, territorial defense, trophallaxis, corpse management, group decision making, group communication *etc* may also present. The division of labor creates behavioral groups called castes. Eusocial species with a sterile caste is sometimes called hypersocial. Advanced eusocial organisms may also show morphological variations between castes. However not all eusocial insect species have distinct morphological variations between castes. Eusociality is mostly found in the phylum Arthropoda but few Chordates also express it. There are two reported species of mammal *viz*. *Heterocephalus glaber* (naked mole rat) and *Cryptomys damarensis* (Damaraland mole rat), which are considered eusocial. Even a crustacean (*Synalpheus regalis*), show eusociality. Extreme case of eusociality is seen in leaf cutter ants (*Atta*), which converts leaf fragments into gardens to grow fungi. Among phylum Arthropoda and class Insecta, order Isoptera is completely eusocial, while approximately 50 reported species of order Hemiptera are eusocial. Among order Coleoptera only single species (*Austroplatypus incompertus)* is reported eusocial. Among order Thysanoptera 6 species are reported eusocial. Among order Hymenoptera all Formicidae (ants) except few species are eusocial. Among Apidae (bees), approximately 600 reported species are eusocial and among Vespidae (wasps), approximately 700 reported species are eusocial [1].

The term ‘eusociality’ was coined by Suzanne Batra in 1966. Wilson (1971) further defined eusociality with three main attributes (cooperative brood care, overlapping generations and reproductive division of labor). Michenes (1974) further subdivide it into ‘primitive’ and ‘advanced’. Eusocial organisms live in groups and group living have its own costs and benefits. Some prominent benefits are defense against larger predators, faster and efficient foraging, communal nest construction *etc*. Some prominent costs are easy detection of group by predators, increase transmission of diseases and parasites, sharing of their own food *etc*. Isopterans and Hymenopterans are highly advanced eusocial organisms. Termite conony consists of four castes: queen, king, workers and soldiers. Queen and king are sole reproductive individuals, while soldiers (males) and workers (males and females) are sterile. Workers forage and store food and soldiers defend the colony. Termites show complex mutualism with cellulose digesting protozoa and bacteria. As they survive on rotting wood, young individuals get these symbionts through anal trophallaxis. Bee conony consists of three castes: queen, workers and drones. Workers (females) are steriles, while drones (males) and queen are reproductive. Sometimes reversal from eusociality to solitary life cycle may also see in Halictids and Xylocopins. Some eusocial insects cross the evolutionary point of no return. Eusociality is sometimes managed by a set of pheromones that alter the behavior of castes in the colony.

Results and Discussion

Hymenoptera have a haplodiploid sex determination system

(Arrhenotoky), where unfertilized haploid eggs give only males progeny and fertilized diploid eggs gives only females progeny. This is a type of kin selection, which promotes altruistic behavior among them. Honeybees are most studied eusocial insect. Honeybees have three castes: queens, drones and workers. Drones mate with queen after which they die. Female larvae fed 'royal jelly' emerges as queens. Royal jelly contains a specific protein called 'royalactin', which increase body size, promote ovary development and shortens developmental time period. After mating, young queen takes a bunch of workers with her and set up a new colony. Female larvae do not fed the royal jelly emerges as workers. Workers perform a variety of jobs in the hive. Some are hive cleaners, some are nurses, some are chaperons, some are guards, some are foragers *etc*. There is a pattern of behavioral development among them is called 'age polyethism', in which workers rotate their jobs with age. They all start by doing generalized jobs like hive-cleaning. Then they progress towards more specialized jobs like nursing and chaperoning. Later they become guards and in the end, when they are older, they become foragers. This behavioral development is accompanied by changes in neurochemistry and pattern of gene expression [1, 16].

By mapping phylogenies Bryan (2002), showed that eusociality has arisen only three times within Halictid bees in contrary to the earlier estimates of six or more times. Reversal from eusocial to solitary behavior have occurred as many as 12 times, indicating that social reversals are common in the earliest stages of eusocial evolution [2]. In contrary to this Sara and Robert (2014) no reversal to a solitary life cycle from eusocial is observed till among honeybees and stingless bees. This suggests that these species may have crossed an evolutionary 'point of no return' which forced the workers to loss their reproductive potential. Eusociality appears to have arisen four times independently (twice in Apidae and twice in Halictidae) with many subsequent modifications. The evolution of complex eusocial behavior occurred twice in the Corbuculates and once in Allodapini [3]. Daniel *et al*. (2013) compared the genomes of seven ants, the honeybee and various solitary insects to examine whether eusocial lineages share distinct features of genomic organization. Each ant lineage contains approximately 4000 novel genes, but only 64 of these genes are conserved among all seven ants. Correspondingly ant genomes show divergence of non-coding regulatory genes. They proposed that changes in gene regulation played a key role in the evolution of insect eusociality, whereas changes in gene composition were more relevant to lineage specific eusocial adaptations [4].

Sandra and Amy (2015) review the molecular evolution of sociality. They try to assess that whether transitions from solitary to primitive sociality to advanced sociality represent incremental changes. Currently there are many hypotheses related to the evolution of eusociality in insects. Gene expression based hypotheses includes 'the ovarian ground plan hypotheses, 'the maternal heterochrony hypotheses and 'the genetic toolkit hypotheses. Genome sequence based hypotheses includes 'the novel genes hypothesis' the protein evolution hypothesis' and 'the conserved regulation hypothesis'. Hypotheses focusing on the earliest origin of sociality predict that transitions from solitary to incipiently social societies involves changes in the timing of gene expression and all individuals remain totipotent into adulthood and throughout most of their lives and are capable of performing reproductive and foraging tasks. Intermediate stages of social evolution from incipiently to primitively social roles become less flexible and more fixed genomic changes. Transcriptome studies suggest that wasps are the oldest eusocial groups, while bees and ants branched from the wasp lineage around 145 mya in Cretaceous period [5], [6]. Social insects use variety of olfactory, tactile, visual and vibrational messages in their communication. However most communications is done by chemical called pheromones. Pheromones are generally produced by exocrine glands and released into the environmental and show certain degree of species specifity. These pheromones can induce changes in the hormones or in nervous system finally resulting in a modified behavior [7]. Individuals that make a social insect colony are often referred as single super organism. It is obvious that eusociality is recently evolved trait as compared to evolution of insect brain. Individual cognition is required for foraging, finding or construction shelter, confronting predators, finding mating partners' *etc*. collective cognition of colony increase the potential of these tasks [8]. Social insects share information among colony members and get benefited. With increasing social complexity, social insects need greater diversity of messages for communication and coordination. Best example of communication in social insects is dance languages of honeybees. Intra specific communication among social insects can either be mutually beneficial or beneficial for one and neutral for others [9].

Michael *et al*. (2012) reviewed the cleptobiosis in social insects. Cleptobiosis is the stealing of food or nesting material or other valuable items either from member of same or a different species. Cleptobiosis is done either by deception or by force. Best reported examples of cleptobiosis among insects are *Ectatomma ruidum* (ectatommine ant), *Messor capitatus* (harvester ant) and *Lestrimellita limao* (stingless bee). Cleptobiosis reduce the time and effort of foraging and save energy but sometimes it can also increase the risk of disease and parasite among group members [10]. Susan and Amy (2012) review the role of epigenetics and phenotypic plasticity in eusociality. Phenotypic plasticity includes transcriptional regulation, post transcriptional modification, alternative splicing and epigenetic modification of DNA such as DNA methylation. Phenotypic plasticity helps organisms with same genotype to adapt variable environments. Honeybee genome possesses a complete set of DNA methyl transferases and DNA methylation has been experimentally verified in several studies. Differential methylation has been demonstrated to be involved in caste determination in honeybee. Caste determination in honeybee is also controlled by environmental factors, especially larval nutrition which further affects hormonal signaling, gene expression and developmental fate. The royalactin in royal jelly may stimulate growth factor signaling pathways, leading to queen development [11].

Noa (2012) describes personality in social insects. They show that social insects have two levels of organization: individuals and colonies. Both individuals and colonies have their own personalities. Because colony is made up of individuals, their personality affects colony personality. Because natural selection acts on colonies, behavioral variation at the colony level will determine which colony will survive and reproduce in given population. The personality of a individual can be determined during its development by many factors such as type of food, temperature *etc*. Even colony personality may change over time due to environmental factors [12]. Qian Sun and Xuguo Zhou (2012) discussed the corpse management among social insects. Corpse management is critical for colony hygiene. Many solution of corpse management such as corpse removal, burial, avoidance and cannibalism have independently co evolved with eusociality. Social organisms regularly face death of their colony members. Exposure to corpses makes them vulnerable to contagious pathogens and parasites. To maintain healthy colonies eusocial Hymenoptera and Isoptera evolved innate behavior of corpse management both at individual and colony level. Avoidance is common in solitary or gregarious insects. The term 'necromone' used to describe death recognition chemicals. Honeybees, ants and termites recognize dead by chemical cues but the specific chemical signal is unclear. Two hypotheses *viz*. 'fatty acid death cue' and 'chemical vital sign' are proposed for induction of undertaking response of death recognition. Once death cues are recognized, social insects respond to it differently. Necrophoresis (corpse removal) is common in honeybees and ants. Covering the dead (burial) and intraspecific necrophagy (cannibalism) is also seen in ants and termites [13].

Group selection is the strong binding force in eusocial evolution. Group selection with addition of cooperative behavior becomes colony selection and is the result of the interaction of all members with their environments. Harmony among group members and genetic fitness of the group is important for colony making. Kin selection is also important in social interactions of the colony members. Only communal behavior is not sufficient for the transition to eusociality, it may be pre adaptation to eusociality [14]. Martin *et al*. (2010) discussed the evolution of eusociality in 'Nature' journal. They tell that altruism in which individuals reduce their own reproductive fitness to raise the other's offspring is the most advanced form of eusociality. Kin selection theory based on concept of inclusive fitness is the most plausible explanation for the evolution of eusociality. They also highlight the limitations of this theory and show that natural selection theory may provide simpler and superior explanation. Altruism is the antithesis behavior arises by natural selection of colony over individuals. Even Darwin considered this as paradox. Darwin considered queen caste as plant and worker caste as vegetables. It means saving plant is more important than vegetables. The concept of inclusive fitness was first proposed by J.B.S. Haldane in 1955 and full theory was given by W.D. Hamilton in 1964. Hamilton gives mathematical expression of degree of cooperation (altruism) as $R>c/b$ (Hamilton rule). It means cooperation is favored by natural selection if relation coefficient is greater than the cost to benefit ratio. Relation coefficient (R) is the fraction of genes shared between altruist and the recipient. If benefit to a brother or sister is greater, than the two times ($R=1/2$), or benefit to a parent is four times ($R=1/4$), or benefit to a first cousin is eight times ($R=1/8$), then altruism will be favored over selfishness through natural selection. Haplodiploidy mechanism in which fertilized eggs become females and unfertilized eggs become males, sisters are more closely related to each other's ($R=3/4$) than daughters to mothers ($R=1/2$). As we know haplodiploidy is common among Hymenoptera (ants, bees and wasps), so these colonies evolve more frequently in Hymenoptera due to kin selection. But Isopteran are diplodiploid and even all haplodiploid hymenopteran species are not eusocial [15].

Conclusions

One man can't build a city but a group of men can. Eusociality gives confidence to organisms living in colony. I think eusociality evolved independently in different groups of insects over time. Eusociality also depends on ability of mimicry. We have to keep in mind that Isopterans are hemimetabolous and Hymenopterans are holometabolous. Both have different time of origin and evolution, so the same pattern of eusociality among them is can only be possible due to convergent evolution of eusociality. Because of same needs and same environments (niches) all eusocial groups got similar pattern of eusociality due to presence of same types of genes. It is possible that they got same genetic expression due to similar environment. Most eusocial insects are small in size as compared to their predators and food sources, so they might evolve gregariousness first and when gregariousness got naturally selected and increase their chances of survival and reproduction, they might increase the cooperation gradually during evolutionary time and evolved with refined eusociality.

Communication in eusocial insects can be compared to orchestra, where all musicians follow the principal who leads the group. It can also be compared to parade, where parades follow instruction of marshal. Eusociality also reduce the intraspecific competitions. I think insects brain are not so developed to understand the concept of family, so altruism and kin selection might free from the biases of family. The evolution of all three basic characters of eusociality (cooperative brood care, reproductive division of labor and overlapping generations) can be explained by different methods. Benefit of overlapping generation can be explained by differential genetic programming. It means different genes switch on and off at different time of life cycle. Overlapping generations provide a better chance of survival and reproduction by availability of all gene expressions simultaneously in a colony. Cooperative brood care helps in conditions like predator threat, food unavailability, proper utilization of available resources, adverse climate *etc*. Reproductive division of labor is useful for haplodiploid eusocial organism due to absence of major variations among them. Haplodiploidy (Arrhenotoky) is only possible because haplodiploid organisms are able to survive with single copy of their genes. This ability is absent in diplodiploid organisms. So I think haplodiploidy is the method of parthenogenesis and we know that parthenotes are like clones and they reproduce many progeny simultaneously so gregariousness among them is obvious. Due to haplodiploidy, they are with little variations due to absence of crossing over. Due to these little variations they can't easily adapt to new environments. We also know that parthenogenetic species not last long, but eusociality helps haplodiploid eusocial organisms (Hymenoptera) to survive. In case of diplodiploid eusocial organisms (Isopterans), individual reproduction and survival might not benefitting them so they choose to help Queen and King as long term survival strategy of species. I think that individuals are not fit to survive with some particular genes in particular environment (like type of diet), but if they care for King and Queen (making appropriate environment), it will help them to survive with activations of particular genes. Overall genes of eusocial organisms are less fit for survival and reproduction in solitary conditions but when they alter genes by their cooperative effort (like fed with royal jelly) they become greater fit for survival and reproduction. We must not compare eusociality of insects to the sociality of mankind because sociality among mankind is due to more complex and developed nervous system (protein regulated), but eusociality among insects is more instinctive (genetically regulated).

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