Sem – VI (UG)

(DSE4T: Unit -5, Insect Society)

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Trophallaxis in Honeybees

Introduction:

Trophallaxis is the exchange of liquid material between individuals, mostly members of the same colony. There are two main kinds of intraspecific liquid food transfer in social insect nests: In the first one, adults exchange liquids with larvae (they imbibe larval saliva from the brood and transfer glandular secretions, honey, and pollen to the larvae). In the second one, the liquid is transferred between two adults. The stomodeal (or oral) trophallaxes are the most common ones. Here, donors regurgitate a drop of food from their crops while one or more receivers drink the liquid. During these mouth-to-mouth contacts, intensive antennation, occasional foreleg movements of both partners or as in stingless bees, the transmission of pulsed vibrations accompany the oral contacts. Adult-adult food sharing also enhance the chance of survival of a colony where unfavourable weather conditions prevent foraging over longer periods of time. During the course of evolution, trophallaxis probably became more important in species for which it considerably improved the efficiency of the performance of vital tasks like food collection or nest construction. The partitioning of tasks is assumed to increase overall colony task performance. Once the material transfer became an important aspect of work organization, it offered an opportunity for both food donors and receivers to acquire information about internal and external environmental parameters via incidental cues, such as searching delays and numbers of receivers and about olfactory as well as gustatory cues contained in the transferred material.

Returning to the nest after Foraging:

In honey bees, young and middle-aged workers perform in-hive duties (e.g., cleaning cells, caring for brood, grooming, receiving and processing of nectar), while older workers forage outside. Nectar foraging in honey bees is a partitioned task: foragers collect nectar in the field and, inside the nest, transfer the food to bees of middle age (often called food processors, receivers or food storers) in the delivery area close to the hive entrance. These bees of middle age are then mainly responsible for processing the nectar into honey and storing it in cells.

Foragers returning from a profitable food source sometimes display dance patterns, which encode the location of a food source. However, the dance display attracts not only potential foragers but also food processor bees which unload the forager. Foragers not only provide information for other individuals, but also receive information during their interactions with hive bees. They seem to use both the time to find a bee for unloading and the number of unloading bees as cues to adjust their dance behaviour after unloading. Thus, social interactions on the delivery area provide the foragers with information that helps them to adjust the dance levels according to the general interest of hive bees in a particular food source and the availability of food processor bees.

The offering behaviour of active foragers:

Foragers often perform several food-offering contacts with a wide range of durations after returning from a nectar source. In general, nectar foragers perform one or two trophallaxes that last for more than 2–3 s per hive stay. During the interactions with a duration of at least 2s, food is effectively transferred between foragers and receivers. Under constant reward conditions, the frequency of food-offering contacts (short and long trophallaxes) is fairly constant between different foraging trips and it is similar for different reward rates offered at the feeder.

In honey bees, short offering contacts can take place before, during, and after dancing, which leads to a rather equal distributing of contacts during hive stays, at least after an increase in food profitability. They play a role in providing information about fluctuating resources, such as the taste and scent of the exploited food source. While the number of short-offering contacts is highly variable, the number of long trophallaxes (longer than 2–3 s) is quite constant and does not seem to depend on the amount of food collected by the forager.

Dynamics of Food Transfer:

Bees modulate their crop-loading behaviour at the feeding place according to the food source profitability. Similarly, they adjust their crop-unloading behaviour during the long trophallaxes according to a food source's profitability. Bees seem to evaluate the profitability of the food source by integrating an overall flow rate throughout the entire visit, instead of measuring only the current flow rate delivered at the feeder. Furthermore, foragers also seem to be able to detect sudden changes in the delivered flow of solution within a single foraging bout (a short period of intense activity of a specified kind), and subsequently adjust the transfer rate within the hive in relation to these changes.

During the food transfer, the receivers actively heat up their thoraxes. Their heating rate positively correlates with the foragers' thoracic temperatures and with the reward rate experienced by the donor at the feeder. These heating rates also depend on the orientation of the receiver toward the donor. Receivers positioned frontally to the donor forager warm up faster and attain higher proboscis temperatures than those positioned laterally. These differences in proboscis temperature indicate that the unloading bees received different portions of sugar solution.

Receiving bees (mostly food processors) also adjust their nectar processing behaviour in accordance to the profitability of the nectar source. After receiving nectar, food processors perform offering contacts or cell inspections, and often even both behaviours, prior to returning to the delivery area. When performing only one of these tasks, the occurrence of cell inspections increases or, alternatively, the amount of offering contacts decreases when the highest reward rate is offered to the donor forager. Thus, first-order receivers acquire quantitative information about the nectar source exploited by foragers.

Another factor, which correlates with aspects of trophallaxis, is the intensive antennal contacts performed by trophallactic partners during food transfer. In honey bees, the antennal movements of both donor and receiver, which are rapid during the food transfer (mean frequency of 13 Hz), vary according to the reward rate experienced by the food donor and show a positive correlation between both trophallactic partners.

Changing the Trophallactic Role:

After unloading their crop, foragers walk across the delivery area to the hive entrance, thereby often protruding their proboscis and touching the mouthparts of their nest mates. These begging contacts are refuelling events for the forthcoming foraging trip. After leaving the hive, foragers carry more food if they do not know the feeding site well or if they collect far from the nest. This could be explained either by refuelling inside the hive or by unloading only a part of the collected crop. However, begging behaviour can also be observed in foragers that constantly collect food over a longer period of time at a feeder located close to the hive. These begging contacts often last less than 1 s, which indicates that the probability of an actual food transfer is very low. Hence, it is unlikely that foragers are refuelled during these begging interactions.

The distribution of Nectar inside the Hive:

After receiving the nectar from foragers, a majority of processor bees

offer it to other bees, sometimes large parts of their load, on their way to the honey cells. Whereas workers that are not involved in food processing have only 0.25–0.75 trophallactic contacts per 10 minutes, food processor bees perform between 4.3 and 10.5 contacts during the same period of time, which highlights their role in the rapid distribution of the collected food among the hive bees. The workers that receive the food from processors (second-order receivers) are mainly nurse bees, but they can also be foragers and other food processors. These second-order receivers perform about four contacts per 10 min, most of them being offering contacts. As a consequence, the incoming nectar is rapidly distributed among bees of all ages.

Another interesting aspect of trophallaxis in honey bees is the fact that the transfer rates of subsequent trophallaxes are positively correlated. In other words, trophallactic experiences of bees affect their trophallactic behaviour in the immediate future in similar ways as nectar flow rates affect the unloading rate of foragers. Consequently, food receiver bees that are not directly unloading foragers might still be able to acquire information about the colony's foraging situation. Given the extensive sharing of food among bees of all ages, cues present in the collected food that convey information about food source characteristics can reach most hive members in a relatively short time. Information available to most or all individuals of a colony, or "global" information, potentially affects the behaviour of the majority of the nest mates, thereby causing a global response. For example, the sugar concentration of incoming nectar affects the sugar response thresholds (SRTs) of nectar receivers and even of young hive bees, which are not involved in foraging and have little direct contact with engaged foragers.

These results not only indicate a fine-tuning of sensory thresholds in hive bees, but also highlight the role of trophallaxis as a mechanism to transfer gustatory information in honey bees.

Odor learning through Trophallaxis:

Bees are excellent learners and readily establish associations between odors (or other cues) and a reward, such as a sugar solution. During olfactory conditioning the sugar solution functions as an unconditioned stimulus (US), while the odor becomes the conditioned stimulus (CS).

Olfactory learning has a strong effect on foraging decisions. In a series of simple and elegant experiments, von Frisch (1923) showed that bees recruited by a forager showed a strong preference for food with the odor brought back by the recruiting bee. The transferred food samples could function as a reward for learning.

Trophallaxis in Termites

Introduction:

There are two types of trophalaxes, named stomodeal (mouth-to-mouth) and proctodeal (anus-to-mouth), which are seen among social insects. In termites, mainly proctodeal trophalaxis is seen for transfer of specially microbial symbionts, with other nutritional and social cues.

The ancestor vertically transmits gut symbionts to neonates:

The gut symbionts inherited from a common ancestor require vertical intergenerational transmission. The digestive tract of neonates is free of microbes, and establishment of the full complement of mutualists is an extended and sequential process; it varies in length between species, but typically is not complete until the third instar. Bacteria are established first, followed by the smaller flagellates, and finally, the large flagellate genera that not only phagocytose host-ingested wood particles, but also are host to nitrogen-fixing bacteria that densely cover their surface. Young instars initially have a 'completely dependent nutrition' but progressively become competent feeders. Until then, they rely on repeated trophallactic transfer of gut fluids from an adult for gut symbionts, as well as for energy and nutrients ultimately derived from the wood diet and symbionts of the parents.

Interdependence of life history characters:

The life history characters shared by termites are homologous and should be considered a feature of their common ancestor. Most notably, the ancestor had obligate biparental subsociality, inextricably linked to host dependence on gut symbionts, the need to transfer those symbionts between generations, nutritional dependence and vulnerability of neonates, and consequently, costly parental care.

These constitute an integrated, covariant character set, one in which individual components cannot respond to selection without changing another trait that also contributes to fitness. As such, they are expected to respond to selection pressures.

Trophallaxis integrates the microbial, social and nutritional environments:

Like coprophagy, proctodeal trophallaxis spans the microbial, nutritional and social environments but with broader scope and deeper impact. First, unlike coprophagy, proctodeal trophallaxis requires physical contact and behavioural interaction. Second, the behaviour allows for inter-individual transfer of materials that would otherwise degrade in the outside environment. This includes the

trophic stages of gut protists and hormones, enzymes, metabolites, and other chemicals that may serve as physiological or behavioural signals. Third, it is impossible to separate symbiont transfer from nutrient transfer during proctodeal trophallaxis because the symbionts themselves also serve directly as food. Both gut flagellates damaged by the proventriculus and bacteria lysed in the foregut of termites are utilised as nutrients by the recipients of proctodeal fluids.

Trophallaxis, revamped:

All trophallactic exchanges are evolutionarily rooted in unidirectional parent-to-offspring brood care. Subsociality and parent-to-offspring trophallaxis co-evolved in the ancestor. Eusociality and colony-wide trophallaxis co-evolved in the descendents, simultaneously providing infrastructure for building an information network and circulation system for the superorganism. In addition to reciprocal transfer of microbial mutualists, trophallaxis in termites allows for the rapid tracking of colony status, inter-individual communication, recognition of colony members, efficient use of moisture and the distribution of factors associated with caste differentiation. The behaviour also mediates the re-ingestion, re-digestion and redistribution of gut contents among individuals according to the ontogenetic and seasonal needs of the colony. It is the multitude of host-microbial units that serve as the bioconversion machine, and trophallaxis that acts as the circulatory system. It is in this last capacity that alloparental (parental care provided by an individual towards a non-descendant young) trophallaxis may have had its greatest impact during the early stages of termite eusociality, because it allowed for recalibration of the nitrogen allocation system in a family living out its life within a single log. The limited nitrogen available could be shunted not only from one biochemical process to another, or from one cell to another, but from one insect to another, allowing prioritisation of the classes of recipients and thus differential fecundity and development within the group. The nitrogen demand for increased reproduction by the mother was met by redirecting available reserves and by lowering nitrogen expenditures elsewhere in the family. Evolutionary trade-offs are magnified when limited nutrients provide their material underpinnings, particularly when nitrogen, a key building block in nucleic acids and proteins.