PREFACE

Social insects are among the most diverse and ecologically important organisms on Earth. This book presents current research in the study of social insects, including food storage behavior in social Hymenoptera; the global empire of an invasive ant; asymmetric trophallaxis between workers of the stingless bee; termite breeding strategies; as well asbiogenic amines and division of reproduction in social insects.

Chapter 1 - Social insect colonies have been traditionally divided in to primitive (less social) and highly eusocial colonies. A trait used to distinguish these two categories in Hymenoptera is the perennial or annual existence of the colony. One aspect that differs between an annual and perennial colony is the flow of nutrients into a colony and the level of food storage. This chapter reviews food storage behavior in social Hymenoptera. It then discusses how this behavior ties in with nutrient flow, recruitment behavior and the evolution of perennial life histories. Four traits energy storage, nitrogen (protein) storage, the presence of a food-receiving caste, and directed recruitment (the ability to relay location information to recruits) are examined in their relative importance to the transition from an annual to a perennial life history in both fluctuating climates (climates that alternate between favorable and harsh conditions) and non-fluctuating environments. Of the four traits, only energy storage and the food-receiving caste are universal among all perennial colonies thus are probably essential for the maintenance of a perennial life history. Nitrogen storage and directed recruitment appear to only be essential for perennial colonies in fluctuating environments.

Chapter 2 - This paper discusses methodological and theoretical issues associated with proboscis conditioning in neglected pollinators. The case is made that the search for learning curves similar to those found in *Apis* is hindered by several factors. Among the most important are the lack of consensus on what is classical conditioning and the allure of cognitive explanations of insect learning. However, the problem is fueled by few examples of individual data and no generally accepted learning taxonomies. On the other hand, the possibility exists that the proboscis learning found in *Apis* is overestimated as a research methodology. The few cases of proboscis conditioning in pollinators not generally used as model systems (not *Apis* or *Bombus*) are compared to results found with honey bees. Although generally conditioning is less complete, what is also noteworthy is the spotty occurrence of cases across the pollinator taxa. Finally, suggestions are provided on the type of training variables that should be manipulated in an effort to find learning curves similar to those found in *Apis*.

Chapter 3 - In Hymenoptera, sex of an egg is determined by egg fertilizations on a haplodiploidy sex determination system. Female reproductive organs in eusocial species have unique functions to regulate ovarian development and control the sex of an egg. Egg fertilizations could be controlled by muscle activities of the spermathecal pump and/or secretion of the spermathecal glands. Activities of the spermathecal pump are regulated by neuronal systems and may inhibit release of sperm for unfertilized male eggs. Secretions of the spermathecal glands could activate spermatozoa from the spermathecal receptacle and therefore, lack of spermathecal gland secretions may cause unfertilization of eggs. In highly eusocial species, especially honeybees, queens can control the egg fertilization in response to comb cell types for oviposition. They can make a choice of the cell types and behaviorally control the egg sex ratios in the colonies. Workers in honeybees can develop reproductive organs in the absence of a queen and lay only unfertilized eggs. They select preferentially male comb cells for the oviposition to produce larger males for mating competition between males. I introduce general structure and function of female reproductive organs for controlling egg fertilizations, physiological processes for regulating reproductive states and behavioral controls of the egg sex ratio in colonies in Hynemoptera.

Chapter 4 - Social insects have obtained their prosperity by cooperation among individuals. This can be applied particularly to the success of invasive ants, which form unusual social structure called supercolonies, within which individuals can move freely among physically separated nests, and thereby gain high population densities to dominate indigenous ants. Native to South America, the Argentine ant *Linepithema humile* has been unintentionally introduced into many parts of the world during the last 150 years. Although it is well known that the introduced Argentine ant populations form much larger and fewer supercolonies than the native populations, the relationship among beyond-ocean populations has been poorly understood. Recent studies, however, are uncovering the behavioral, chemical and genetic relationships among introduced Argentine ant populations worldwide. Individuals from the dominant supercolonies around the world have very similar cuticular hydrocarbon profiles (nestmate recognition cue), and do not show aggressive behavior toward each other, when artificially put into contact. The supercolonies constitute the largest cooperative unit ever known. Their genetic closeness suggests a common introduction pathway. Considering historical records, descendants of the most ancient introduced population have spread to many parts of the world, without losing memory of their roots. In this chapter, we introduce the nestmate recognition system and mechanism of supercolony expansion in invasive ants, with the global empire of Argentine ants as an example.

Chapter 5 - Two kinds of parasites, i.e., a strepsipteron, possibly *Xenos myrapetrus* (Trois) and an undescribed gregarine were recognized in the neotropical swarm-founding wasp, *Polybia occidentalis* (Olivier). Although the proportions of workers that were infected by these parasites varied greatly among colonies, a prevalence of infected workers was recognized. Five external characteristics and the number of hamuli were measured and compared among uninfected workers, stylopized (i.e., infected by Strepsiptera) workers and workers infected by gregarines. Stylopized workers were significantly smaller than uninfected workers, while workers infected by gregarines were significantly larger than uninfected workers. Moreover, number of hamuli in workers infected by gregarines tended to be greater than that in uninfected workers. In one of our colonies, in which a large number of workers had been stylopized, the number of strepsipteran larvae per host tended to be negatively correlated with mean body length of strepsipteran larvae, indicating that the greater the number of strepsipteran larvae, the smaller the mean body length was. These findings were consistent with those of our previous study conducted in a consubgeneric wasp, *P. paulista*. Since the nutrients of stylopized workers may be plundered during their growth period, their body size may be consequently reduced. On the contrary, gregarines may manipulate host larvae to solicit more food from adults or increase the development time of larvae longer, and therefore produce more parasites from a larger host.

Chapter 6 - In several species of social insects, there is a positive relationship between the food exchange that occurs during trophallaxis and the ovarian development of workers, indicating that food transfers are important for the establishment of reproductive hierarchies between the colony members. In this chapter, we tested if such correlations also occur between workers of the stingless bee *Melipona quadrifasciata anthidioides*. Due to the difficulty to follow the totality of worker behavior inside the nest, we housed six newly-emerged workers in confined conditions, away from the mother colony and older workers, with pollen and honey *ad libitum* and under stable conditions of temperature and illumination. We measured their trophallactic behavior until the moment the first worker died; after that all workers from the group were dissected for the measure of their ovarian development. We found significant differences in the individual trophallactic behavior exhibited by workers, since some workers were mainly food donors whereas others were mainly receivers, and all contacts were initiated by the soliciting bee. Moreover, only 15% of the trophallactic contacts were longer than one second, and thus, possibly resulted in an effective food exchange. However, there was no correlation between the ovarian development and the trophallactic behavior of workers, which might be caused by the experimental conditions the workers were kept, and the small age they died, which was five days after the start of the experiment. However, considering that *Melipona* workers from different species highly vary in their ovarian development and egg-laying capacities, and that individual workers exhibit significant differences in their trophallactic behavior, it is reasonable to presume that under natural conditions trophallaxis might have a relevant role in their ovarian development, but this possibility yet remains to be tested in regular colonies.

Chapter 7 - Social insects are an interesting model to neurobiological studies due to the simplicity of its brain commanding the complex behaviors demanded by eusocial relationships and its capacity of learning and memorizing. In their social structure, usually have differentiated sex and caste, where individuals have different morphology, physiology and behavioral patterns correlated with their functions in the society and represented by some brain polymorphism. They have a rich behavioral repertoire and perform various tasks throughout their lives that involve a complex and diverse system of learning. The brain is the main center of association of the insect. Receives sensory impulses coming from the sense organs of the head and from the ventral ganglia nerve chain, through ascending interneurons. Orders emanating from the brain to the antennae muscles and the posterior part of the body, passing through the descending pathways, pre-motor, going to the ganglia of the ventral nerve chain. In addition, the brain is the center of the integration of activities, which produce organized patterns of long-term behavior driving their changes by learning. In general, the brain of insects is divided into three regions: the protocerebrum, deuterocerebrum and tritocerebrum. The protocerebrum is the largest fraction of the brain, including the optical lobes, a pair of lateral-dorsal mushroom bodies, the cerebral bridge and the central body; the deuterocerebrum is part of the brain containing the olfactory antennal centers, and the cell bodies of motor nerves of the antennae muscles and usually form a pair of lateral lobes distinct. The tritocerebrum is very small in insects, consisting of two small lobes after the deuterocerebrum connected by circum-esophageal commissures to the subesofagean ganglia. Forward, this region connects through nerves, with the oral region and the ganglia of estomogastric nervous system. Despite this apparent simplicity, have systems of spatial orientation and communication very complex and studies have shown that neurotransmitters and receptors are common to those found in vertebrates. According to the developmental stage and the activity performed, the pattern of protein expression is different, reflecting differential gene expression in neurons according to environmental and / or physiological stimuli received, many of these genes similar to those expressed in neurons of vertebrates. This ability to respond physiologically to the varied stimulus, turn on or turn off some genes, stimulating or blocking specific neuronal receptors, makes these insects can be used as models in studies of new drugs possibly neuroactive and also to analyze the effects of neurotoxic substances, as some studies have shown.

Chapter 8 - The purpose of this chapter is to exhibit research developed about morphological studies in honeybee organs and others social insects, specifically in midgut and Malpighian tubules. The chapter will include a review of relevant articles about structure and function of these organs to provide knowledge of social insect biology with emphasis in larvae and adults of bees, as in *Apis mellifera* as in Meliponini. This section of the chapter will discuss the basic tissue architecture of midgut and Malpighian tubules and some differences according species and groups. Since the histology and ultra-morphology of midgut and Malpighian tubules are well characterized, any modification in their structure and function or in the physiological process of programmed cell death, induced by xenobiotics, can be diagnosed. The midgut and Malpighin tubules of larvae and adults of bees are involved in the absorption an excretion of chemical compounds, respectively, an assessment of their morphology can reveal ultrastructural alterations induced by environmental stressors such as pesticides. Then, in a second section of this article, the subject is to report on the advances of the morphological studies of honeybee organs in response to pesticide exposure, which will contribute to data acquisition for building shared knowledge on bee biology and toxicology, providing arguments for effective policy marking in this field of research.

Chapter 9 - Since the middle of the 20th century, improvements in analytical technologies have permitted the identification of cuticular hydrocarbons present on the cuticle of almost all insects.

Concomitantly, a great deal of attention has been paid to the determination of their role at the individual, colonial, and populational level. Many studies pointed to the importance of the surface lipids which cover the insects' cuticle. They are important for the survival of individuals and at a higher level, to maintain colony integrity and species survival. The lipid layer is responsible for the water-repellent character of the cuticle which is its primary function. It reduces surface transpiration and protects terrestrial insects from desiccation. Furthermore, it creates a barrier against micro-organisms and inorganic chemical components. More recently, bioassays have shown that surface hydrocarbons are important tools for recognition systems for solitary insects but above all, for social insects where the chemical communications between individuals are complex. Cuticular hydrocarbons serve as contact pheromones when insects encounter each other. They permit insects to identify « friends » from « foes », nestmates from non-nestmates. They constitute a true chemical signature. They also maintain the social structure of insect colonies by separating individuals according to their functions within the colony, according to their physiological states and their hierarchical rank. They constitute a fertility signal for the queen which indicates its presence for the workers which retain their reproduction. Furthermore, cuticular hydrocarbons can play a major role in sexual behavior as an attractant or repellent. They can also be involved in courtship behavior. These are kairomones or allomones in host-parasite and prey-predator relationships, and contribute to mutualistic relations between insects.

Nowadays, the identification of all these functions allows biologists to use cuticular hydrocarbons as tools to conduct eco-ethological studies. For example, it is possible to use hydrocarbon composition as taxonomic character to identify cryptic species which are morphologically close. This could be useful in conservation planning. These components should equally allow a better understanding of ant colonies structure, for instance, the boundaries of polydomous colonies or especially in the context of an invasion when ants form super-colonies.

Chapter 10 - Division of reproduction in social insects is a behavioral specialization to enhance the efficiency of individual behaviors, and the growth and reproductive success of the colony. Queens engage directly in reproduction, whereas workers perform other tasks including taking care of the queen and broods, guarding the nest and foraging. Workers can change their reproductive states and lay eggs under certain conditions such as in the absence of a queen. During the transition of reproductive states, a brain specialized to worker's behaviors can be reconstructed to a queen's type morphologically and physiologically. Physiological processes of the transition for reproduction in social insects are recently elucidated. Biogenic amines are key substances for behavioral and physiological changes during the transition. They have roles as neurotransmitters, neuromodulators and neurohormones in the peripheral and central nervous systems by acting on target cells through binding to receptors in insects. Dopamine and tyramine may play regulatory roles in the transition of the reproductive individuals from normal workers in honeybees. The differences of brain dopamine levels between reproductive and non-reproductive individuals in several species of social hymenopteran may contribute to caste–specific behavioral expression. These biogenic amines may interact with other hormones regulating the physiological states for reproduction. A part of the physiological processes is confirmed by molecular biological experiments detecting the gene.