THE COMPARATIVE STUDY OF SOCIALITY IN THE HIGHER BEES

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Summary

In this paper social systems of the taxonomically related higher bees (carpenter bees, bumblebees, stingless bees and honeybees) are discussed and compared, including a comparison with the kin selection hypothesis. It is concluded that sociality arose and developed as an evolution of competitive interactions within the species and the colony. The significance of kin selection is that it determines the range within which competition could fluctuate, to produce sociality as its evolutionary consequence; kin selection has probably not been a proximate mechanism.

Key-words: Higher Bees, sociality, kin selection, competition.

Résumé: Etude comparative de la socialité chez les Abeilles.

Cet article examine les systèmes sociaux des Abeilles supérieures, taxonomiquement proches (Abeilles charpentières, Bourdons, Abeilles sans dard et Abeilles domestiques), afin de les comparer, dans la perspective de l'hypothèse de la sélection de parentèle. En conclusion, il apparaît que la socialité naît et se développe par le jeu d'une évolution des interactions compétitives entre les espèces et à l'intérieur de la colonie. Le rôle de la sélection de parentèle est de déterminer les limites à l'intérieur desquelles la compétition peut agir, en engendrant ainsi la socialité comme conséquence évolutive; la sélection de parentèle ne serait donc probablement pas un mécanisme premier.

Mots clés: Abeilles, socialité, sélection de parentèle, compétition.

Introduction

Bees and wasps offer unique opportunities to study the evolution of social behaviour, because in these groups all levels of sociality, ranging from solitary ways of life till highly eusocial, occur closely together. Our research group has devoted itself to the study of the higher bees, especially the carpenter bees, the bumblebees, the stingless bees and the honeybees. While the carpenter bees are in the Anthophoridae and the other groups are members of the Apidae, the four groups are closely related, because the carpenter bees can be considered as the Anthophorid sister group of the Apidae (Sakagami & Michener, 1987). Carpenter bee species are, with a few exceptions, solitary; the exceptional species demonstrate facultative and temporal sociality, which is always of a simple form. Bumblebees are primitively eusocial, while the stingless bees and the honeybees are highly eusocial. This group of closely related bees, therefore, offer excellent possibilities to study the various aspects of colony organization, the patterns of interaction between colony members, the resulting division of labour and the physiological differentiations that on the one hand stand at the origin of the diversification, on the other hand are the outcome of the interactions.

Such an approach lays emphasis on the causal mechanisms behind insect sociality. This should be kept separate from functional considerations, such as the kin selection hypothesis (Hamilton, 1964) and predictions on the character of colony organization derived from this hypothesis. Approaches like those by Lin & Michener (1972) on mutualistic interests or by Alexander & Sherman (1977) on parental manipulation, in my view, lead to an understanding of the machinery of social evolution, while Hamilton's hypothesis gives us the abstract laws to which all the machinery has to obey in order that the evolution will reach higher levels, especially the emergence of sterile, yet highly adaptive colony members. These different types of hypotheses belong to different levels of biological research; in the same way neurobiology and architecture are both highly interested in visual perception, but, nevertheless, the two specialisms will never be able to come to a

complete integration. It is the principal difference between a reductionist's approach and a synthetic one.

In the following I intend to discuss colony structure of the four groups of bees in terms of the wheels that keep the colony going, and also in terms of the footpaths or highways present for evolutionary processes. Since evolution is the topic of this paper, the kin selection process will be the guiding line in my discussion.

The carpenter bees

Carpenter bees are generally divided in the small carpenter bees or Ceratinini and the large carpenter bees or Xylocopini. Both groups consist of several hundred of species, and in both groups the step from solitary to social life has been made. Recent studies on the Ceratinini are, among others, those by Maeta et al. (1984, 1985), Sakagami & Maeta (1985), Michener (1985) and Schwarz (1986, 1987). The larger carpenter bee sociality is discussed by Velthuis (1987) and Gerling et al. (1988).

In our studies we concentrate on two Israeli species, Xylocopa sulcatipes and X. pubescens. The first one is a desert specialist while the second one inhabits characteristically the more vegetated habitats, but together they can be found in natural oases and in the more recent human desert settlements. Our study area is the Field Study School in Hatzeva, located in the Rift Valley, some 30 km south of the Dead Sea.

Xylocopa sulcatipes characteristically nests in canes, flower stalks or thin branches that are already hollow or contain a soft pith, or burrows itself a tunnel in soft wood. Nests are always of a linear arrangement. At the bottom of the nest the first cell is made; it contains the bee bread, a mixture of pollen and nectar, on top of which an egg is laid. The cell is closed by a cell partition made from shavings obtained from the tunnel wall, and glued together. New cells are always in front of the older, and this limits the time a mother can continue to construct new cells, for the first young will destroy younger cells when it emerges. We may suppose, therefore, the existence of a selective pressure leading to a rapid production of as many cells as possible in the short time span available.

In the desert environment two factors limit the populations of this bee: the shortage of suitable material to nest in, and the problems related to food collection from a vegetation that is scarce and often unpredictable in its productivity. Shortage of nesting material leads to an often strong competition for nests, and shortage of nearby flowering plants gives rise to bees that find it more economic to rob other's nests from their provisions. A breeding female, therefore, finds herself trapped between two selective pressures, one leading to high levels of foraging activity, and another leading to efficient nest defense. It is in this dilemma that the presence of two females in a single nest becomes attractive: one to stay home while the other forages.

Groups of bees in one nest are the result of incomplete dispersal, being the young from the parental nest or being the bees from a winter cluster,probably consisting of in part unrelated bees, or a group can be the result of a successful attempt to intrude in the nest of a solitary female. Almost always a social nest contains two well-developed females, or it contains a mother with her emerged, but still incompletely developed

offspring. In both species a frequent food exchange between the foraging mother and her young bees and the consumption of an astonishing large amount of pollen, collected by the mother and eaten by her offspring, indicate the existence of a form of brood care unprecedented among solitary bees. This care for the brood takes about two weeks, and can develop into a dominance hierarchy consisting of an active mother and the last remaining, inactive daughter.

In X. pubescens the nest is most frequently of a branched type, constructed by a female in dead branches or trunks of trees, or, as in our field station, in boards specially provided for them. The nest starts with a solitary female, but once offspring emerges, the mother may combine feeding these adults with the continued preparation of new brood cells in one of the tunnels of the branched nest. Daughters and sons position themselves in front of the nest while the mother is out, and the one that is the first to meet the returning mother will obtain the major part of the nectar collected (Velthuis & Gerling, 1983).

In the large carpenter bees division of labour is of this, most primitive nature; an active bee forages and reproduces, while an inactive bee stays behind in the nest. The advantages to the active bee of having a guard are understandable, but why should the other one remain inactive? We observed a frequent trophallactic contact between the two females, and also observed the inactive bee to take from the pollen carried to the nest. This indicates that she obtains her nourishment easily. Another aspect is, that she may inherit the nest in case the active bee falls victim to a predator or other casualty when out. In that case she may take over activity immediately, like any solitary female, or she could await the emergence of the immatures of her former partner and could attempt to dominate them. And finally, there is the option to contest the dominance relationship within the nest and to force the partner to continue as a guard or to leave. All these kinds of changes have been observed, and are not influenced by the degree of relatedness between the adults (van der Blom, 1989; van der Blom & Velthuis, 1989).

Since the environmental conditions that make it profitable to nest together may change during the season, from year to year and from place to place, there is no constant selection for either becoming social or for remaining solitary, and this explains the facultative nature of this kind of sociality. To my opinion it does not make much sense to distinguish various levels of sociality, for even if we can distinguish moments of eusociality and of semisociality, there is not a distinctive climax in the development of the nest. It might also be clear, that although these bees have a sex determination mechanism of the haplo-diploid type, they do not exploit it in terms of inclusive fitness. Daughters may successfully contest the dominance of their mothers at times when these mothers are still fully capable of making a nest elsewhere.

The bumblebees

Bumblebees are primitively eusocial. Primitive means that the queen starts a nest solitarily, and therefore she is equipped with all the capabilities also encountered in the workers. Eusocial means that the climax of the

colony is the society of an egg-laying mother queen assisted by her daughters, who perform the worker duties. These workers, however, have ovaries, and at the end of the colony cycle they use these ovaries to produce eggs, from which males can be reared. Like in the honeybees the bumblebee queen possesses pheromonal means for preventing the workers to start laying these eggs to soon. Van Honk et al. (1980) demonstrated the mandibular glands to be a source of such pheromones, and Röseler et al.(1981) showed these pheromones to be involved in the regulation of the activity of the corpora allata of the workers. Van Honk & Hogeweg (1981) analyzed the dominance relationships among the colony members and described how the most prominent workers, called "elite" workers, can be distinguished long before they will take part in the egg-laying in the colony. A mathematical model of the emergence of this dominance structure has been proposed by Hogeweg & Hesper (1983).

Van Doorn & Heringa (1986) greatly improved our understanding of the origin of the "elite" workers. They belong to the oldest group of house bees, joined by some of the younger house bees, but if it takes to long to reach the moment on which eggs by workers can be laid, these older workers may be replaced by younger sisters. There is a lot of dynamics in the hierarchical structures among the workers. Van Doorn (1987) also investigated the physiological background of dominance relationships. The workers' flexibility with respect to tasks performed decreases with their age and with the number of workers present. Foragers easily return to house duties, but house bees are very reluctant to fill vacancies in the forager force.

The division of labour is not affected by juvenile hormone applied to some of the workers. The influence of JH on worker dominance, evident in small, queenless groups, is easily overridden by factors acting inside the colony. Workers that were allowed to develop their ovaries outside the colony return to their original social position and reduce their ovary activity conform that position when placed back in their colony. If workers are deprived of their ovaries they may become "elite" workers and then will perform all the activities of laying workers, except for constructing the waxen egg cell and, of course, those behaviours that are closely related to oviposition. In distinction to the colonies of the carpenter bees, a bumble-bee colony is a stable, well-regulated structure, in which the colony needs and the dominance of the queen regulate the activities of its members.

In the life cycle of a bumble-bee colony different phases can be discerned: the solitary phase, during which the queen raises her first group of workers, the stable social phase, and the final phase characterized by much aggression, worker oviposition and oophagy. Duchateau & Velthuis (1988) investigated the timing of these phases and the factors leading to the next phase.

Most important is the intermediate phase, where workers assist their queen in raising offspring. The duration of this phase is about 31 days; in agreement with Pomeroy & Plowright (1982) we could find no demographic reason why this period should shift into the competitive last phase of the colony cycle. There are neither behavioural characteristics of any of the workers or of the colony as a whole that could predict this final shift (Duchateau, 1989). It is of interest, that the queen anticipates the beginning of egg laying by her workers by switching from the laying of fertilized eggs to the laying of unfertilized ones. Queens differ with regard to the moment of this

switch: part of them do it well before the onset of worker egg laying, with the consequence that there is still a long time to go and, therefore, that many males will be produced, while another part shifts relatively late. This has as a consequence the build-up of a larger worker force. These two moments for this shift, however, have in common a relatively low ratio of larvae/workers, a colony character that fluctuates in a very characteristic way. At the onset of the emergence of the first workers this ratio is rather high, decreases till a minimum and, due to a temporary standstill in the emergence of the workers, increases again. Once further workers emerge, the ratio goes down again and continues to do so. Those colonies that are characterized by an early switch to male production have their switch in the first minimum of the larvae/worker ratio. Since for rearing a queen from a diploid egg a large amount of larval food is necessary, these colonies hardly produce any queens. Late switching colonies, however, may start rearing queens before the queen limits this production by providing only haploid eggs. It is most intriguing that the average biomass investment in the sexual forms of the two types of colonies is the same.

Once the workers start preparing for their own reproduction, by eating eggs from the queen, making their own egg cell and laying their eggs in it, the efficiency of the colony drops to low levels. Many eggs and young larvae produced in that period are destroyed, and it is mainly the immature offspring of the queen, produced before the onset of this reproductive competition, that succeeds to complete development into the adult stage.

If we compare this pattern to the general predictions of the kin selection theory, taking into account that our bumble-bee queens mate with only a single drone, we may note that, with respect to the parent-offspring conflict concerning the production of males, the bumblebee situation is more advanced than the theory predicts. In the theory, first developed by Trivers & Hare (1976), it is demonstrated that, because workers are more related to their sons than to their brothers, the workers should compete with the queen when it comes to the production of the males. Since workers sharing the same father are more related to the sons of their sister than to the sons of their mother, theory predicts that those workers that are unable to reproduce themselves, such like the foragers, should support their egg-laying sisters. A general revolt of the workers can be expected.

Bumblebees deviate from this general prediction in two ways: the queen, by anticipating egg laying by the workers, is able to produce the great majority of the eggs that give rise to the males of the colony. The causal machinery is more refined that the theorists anticipated. The second remarkable observation is that workers do not join their efforts once the opportunity for worker egg laying arises. They compete strongly and destroy most of what could be gained in terms of direct and inclusive fitness. Here the causal machinery is apparently less developed than the theoretical approach could lead us to expect.

A further remarkable observation is that apparently a number of colonies, by having an early switch to male production, thereby largely by-passing the production of queens, depend for their reproductive success on the queens produced by other colonies. Males are about half the weight of a young queen; by investing the same amount of biomass in males only, these colonies produce three males where the other colonies produce a queen and one male per unit biomass. Three sexuals, compared to two in the

other colonies, could mean a better transfer of genes to the next generation of colonies, as long as this exclusive-male strategy is a rare one. The total number of queens in the local population determines the number of males that will mate, and this determines how many males are produced in vain. If producing males early in the season is an advantage in terms of the mating biology of the species (time to become sexually mature; the establishment of a best territory, etc) an early shift to male production is already selected for. In that case the two reproductive strategies, represented by the two moments for the shift in queen behaviour with regard to fertilizing/not fertilizing the eggs, become equally rewarding if the two strategies occur in the same frequency. It is of interest, that in our sample of colonies the two types of colonies did occur in the ratio 10:11, and that the populational sex ratio that should result from such a ratio, 4 males to 1 queen, has been observed for some Canadian bumblebees as well (Owen & Plowright, 1982).

A final remark on the bumblebees concerns the parasitic character of producing males only. This strategy reduces the fitness of queen-producing colonies, for their males are supposed to be produced in vain. And, the male that inseminated the early-switching queen, did so also in vain, at least in terms of maintaining being represented in the population. His daughters were all workers, and hardly any of them can be expected to raise a successful son.

The stingless bees

Stingless bees, like the honeybees, are highly eusocial. As a consequence there are no solitary stages in colony development; colony multiplication is by swarming. In distinction to the honeybees a large number of Meliponine species are known, and, more important for a comparative study, these species are rather diverse in many aspects of their biology. Pioneer studies on this diversity are the papers by Sakagami, Zucchi, and several others on Brazilian species, reviewed by Sakagami (1982) and Sakagami & Zucchi (1974).

Stingless bees are mass-provisioners of the brood cells; once the construction of a cell or a series of cells is completed, the queen initiates a state of arousal in the workers, who gather in the vicinity of such cells, running in an 'agitated' manner on the comb, occasionally diving into the U-shaped cell. Then the queen positions herself close to a cell, the 'cell fixation' phase, and probably releases a pheromone which induces the workers to discharge food into the cell and the other empty cells if present. Worker after worker dive in the same cell, until the liquid food reaches a certain level. The queen, inspecting the cell once in a while, upon discovering that the proper amount has been deposited, lays an egg on top of the food and moves away from the cell, to other provisioned cells if present, or to a remote place in the colony. A worker positions herself on the oviposited cell, the tip of the abdomen in the opening, and by pressing the cell rim inward this bee closes the cell.

An interesting feature of the stingless bees is the occurrence of worker egg laying. In some species, like Scaptotrigona postica, workers produce the majority of the males (Beig, 1972). In that case they deposit their egg into the cell after the queen did so; the male larva hatches before the

female larva and is able to destroy its competitor for the food. In other species the worker egg is deposited before the queen oviposits, and is usually devoured by the queen. Often such an egg is not deposited properly onto the food, but on the cell rim, a type of worker behaviour that guarantees the unsuccessful development. However, there are more indications that such eggs serve another function than reproduction, such as insufficient development of the egg envelope, leading to a different shape of the functional and the trophic egg. In Scaptotrigona both types of worker eggs occur, and this is an indication that variation in the behaviour received from nestmates superimposes on the physiological processes of oogenesis. In Plebeia remota worker eggs are deposited somewhere on the comb surface or are produced when a worker encounters the queen. Such worker-queen interaction involves antennation, darting movements by the queen and rapid retreat by the worker. While retreating, the worker may 'forget' her abdomen, stumbles over it and while the tip of the abdomen is pointing towards the queen the egg is produced and generally taken by the queen (van Benthem, 1987). In still other species worker ovaries are never activated in colonies having a queen, but only in orphaned colonies. And then there are species where even in that situation worker ovaries remain inactive.

This variety of situations indicates the various levels at which the queen may control worker reproduction: by reducing or prohibiting the physiology of oogenesis, by behavioural means in that the workers do not oviposit, by oophagy, by modifying the moment on which the egg will be deposited, so that unripe eggs appear. And, at the same time, it may happen that worker oogenesis leads to real reproduction. The worker-queen conflict of the theoretical approach apparently unifies a wealth of causal mechanisms.

In our department detailed studies have been made by Sommeijer and collaborators, using mainly Melipona favosa. This bee has colonies of only a few hundred individuals, which makes it possible to mark bees individually and to study the various aspects of the division of labour. It was found that several tasks related to reproduction are performed by the same individuals, such as cell building and the provisioning of these cells. This task is characteristically performed by bees of 8-12 days old. Although several individuals are involved in the construction of a single cell, there is always only one bee at a time working at that cell. Some of the constructors are more active than others. Those that are the most active at a given cell, are also the most active in provisioning that cell. Eggs are laid by workers of 9-27 days old. From these data (Sommeijer, 1984) we get the impression that the behaviour of the individual is like that of a solitary bee, the social aspect being that several workers work at and provision the same cell. The queen interferes by laying the egg before any of the workers is ready to do so.

How does the queen know about the progress of cell building, enabling her to arrive at the cell at the time it has been completed? Sommeijer & de Bruijn (1984) discovered that building workers frequently leave the building area and pay a visit to the queen, who is at a remote place in the colony, where they participate in court formation. The activities of the court bees contain information about the progress of the cell building, because the antennations of the queen's body by the workers increases in frequency; simultaneously the frequency by which the queen grasps the head of the worker increases. In the last phase of the extra-oviposition period

this leads to infrequent food transfers from the workers to the queen. From the studies reviewed by Sakagami & Zucchi (1974) and Sakagami (1982) it is clear that court behaviour of the workers contains many elements that suggest an aggressive origin of this behaviour, modified, so to say, into a ritualized form.

Aggressiveness is even more pronounced in colonies lacking their queen and in which worker egg laying serves the production of sons rather than providing nourishment to the queen. Once the cell is completed one or several of the workers apparently use an ability that under queenright condition was restricted to the queen, that is causing excitement. This is probably related to the accumulation in a number of workers of the food that will be discharged into the cell. The same worker produces the signal leading to the deposition of that food, and than the workers that carry a ripe egg compete strongly for that cell. One after the other mounts the cell, pushes the egg-layer away from the cell, eats the egg if there is one already, until the eggs inside these workers are depleted or until one worker proves to be strong enough to complete the whole process of egg laying and cell closure. Quite often the cell is opened again by another laying worker (Velthuis, 1976; Sommeijer & Velthuis, 1977).

In conclusion we may say that such observations reveal a very important competitive background of the high level of sociality attained in these bees.

As far as real reproduction by workers is concerned it appears as if the maturity of the worker egg (Sommeijer et al., 1984) is a function of colony size, of colony condition and of environmental factors. We do know very little about mating frequency in the various stingless bee species, but what is known points to a singly-inseminated queen. This makes the tremendous variation in the use of the worker ovary in this group of bees rather intriguing.

The honeybees

In comparison to the preceding groups of bees this one is only small, only 5 species have been distinguished and they probably do not vary very much with respect to what will be discussed here. I will restrict myself to the European honeybee, Apis mellifera.

Dominance mechanisms based on queen pheromones have been studied for over 35 years (cf. Velthuis, 1985). At least three glandular systems are involved, producing a whole array of components. It is also clear that these components do not serve a rather specific function each, but that the complex of substances enables the workers to recognize the queen as such. All their responses to being with a queen are to be considered as adaptations to the specific environmental conditions, and they register these conditions through their sensory apparatus. The distinction between primer pheromones and releaser pheromones is inappropriate. At the most we can distinguish between primer and releaser effects, but I consider this not very elucidating.

It is known that worker honeybees are able to lay eggs; they do so almost exclusively under queenless conditions, but when a colony is preparing to swarm a high percentage of workers may have activated ovaries (Verheijen-Voogd, 1959). Rarely will they lay in the presence of the queen

(Page and Erickson, 1988). Like in the bumblebees and the stingless bees, only a minority of the workers will lay when orphaned; there are dominance structures in a queenless colony deciding about reproductivity.

A very special aspect of honeybees is the fact that queens mate with many drones, ranging from 8-18. Sociobiological theory predicts that if workers are able to distinguish their patrilineal origin, subgroups of workers could exist that will compete for the possibilities to produce the male offspring. In the same way as indicated for the bumblebees, within each subgroup the workers should cooperate, should select their best reproductive workers and should support them, but should compete with the other subgroups and with the queen. Their relatedness with the various males that could be produced is: 0.5 with their own sons; 0.375 with the sons of their full sisters; 0.25 with the sons of their mother and 0.125 with the sons of their half sisters. The sequence also gives the priorities for every worker if she would have the ability to make the appropriate discriminations.

The question whether worker honeybees are able to recognize patrilineal relatedness got much attention. A number of authors indicated the existence of such abilities; however, I am intrigued why this does not lead to regular drone production by workers in queenright colonies. In the concept of competition being the driving force behind social evolution it is not in the interest of a queen that her workers take part of the reproductive output of the colony, and already at the level of the bumblebees we find the ways in which queens escape from this reduction of their fitness. It is therefore, that we (Breed et al., 1984; Hogendoorn & Velthuis, 1988) studied the problem under conditions where the normally present regulating factors can act. Most of the studies in which patrilineal recognition mechanisms were revealed are with queens that are inseminated with the semen from two drones only. In our last study we inseminated a queen with the semen of either two or of eight males, one of them being from A.m. ligustica origin, the others from A.m.mellifera origin. The daughters of these drones can be distinguished by the colour of their integument. In queenright colonies having two patrilines workers show a slight tendency to discriminate between full and half sisters with respect to their food donations to nestmates, while this was not found when eight patrilines were present. If the colonies were deprived of their queens in both colonies food was given preferentially to full sisters; in the two-male colony this tendency was lower than when queenright, in the eight-male colony this was higher than when queenright. In the orphaned colony fathered by two drones aggressiveness was significantly directed towards half sisters, but in the eight-male colony aggression was considered to be randomly directed.

Some concluding remarks

We found in the honeybee that if a queen is present she may annihilate the effects of patrilineal recognition cues in two ways. One is by distributing so much of her pheromones that worker kin recognition disappears in the background noise of the complex signalling, the other is the evolutionary step of mating with several drones. Drones from the same population cannot be expected to be completely different in the discriminators they transmit to their daughters, and many drones represented

in one spermatheca necessarily leads to significant overlap. In addition the queen herself transmits discriminators which, due to the reduction division, also has important consequences for the acuity of the discrimination mechanism. Once the patrilineal distinction is obscured the best a worker can do is supporting the queen in the production of males, for the average relatedness to a laying worker approaches 0.25. A laying worker, therefore, should find herself opposed by everybody else in the colony. And, indeed, in the honeybee drones originate from the queen.

In this picture, based on the continuing evolution of causal mechanisms that are instrumental in intra colonial competition, we have to fit the fact that worker honeybees do possess ovaries, although they can hardly be expected to make a proper use of them. I suppose the ontogeny of the worker, including all its physiological aspects, to be a continuing modification of a solitary bees' construction. The raison d'être of a solitary bee is its reproduction, and if during development conditions are sub-optimal, an adult will emerge that saved on all kinds of properties, but the last it will hand in is its potential to reproduce. The presence of ovaries in a worker, even if they are never functional, seems therefore less astonishing than the complete absence. It has to be said, however, that in a few representatives of the ants workers are without ovaries.

Evolution of sociality can be considered as an arms race. Workers are the losers in the classical sense of evolution, but due to their relatedness to the individuals they help to raise, their genes survive in the population. As long as their relatedness to the offspring of the colony is greater than that of the egg layer, the alleles that characterize worker properties increase in frequency relative to the alleles characterizing the queen. Caste dimorphism develops only in matrifilial societies and is probably linked to females being singly inseminated. Semisocial colonies consist of principally identical individuals, and it could be doubted whether such forms of sociality depend on haplo-diploidy to evolve.

If evolution of sociality is a kind of arms race between queen and worker, we can also understand why occasionally a worker may lay an egg. Mechanisms to suppress worker egg laying evolve as long as a further reduction can be achieved. But selective pressure to continue the further refinement of such mechanisms cease to occur, once worker egg-laying became a rare event. A rare occasion is what is left, as a proof of a long evolutionary fight won by the queen. In the honeybee the activation of the ovary of the worker is under control by the queen, and if she fails, workers take their chance. In several stingless bees the mechanism is in the eating of the eggs and in the usurpation of the cells prepared for egg laying. But if the queen reaches her limit of egg production, possibly in large colonies, workers may produce males.

Sociality, characterized by competition between individuals, is also characterized by cooperation and efficiency at the colony level. Cooperation, as the outcome of intra specific competition, seems possible only if the participants of the interaction differ in their capabilities and their needs, either temporarily or permanently. If it is only temporarily, the system could do without relatedness of the partners, and indeed, in the carpenter bees, relatedness does not seem to affect their interactions. Permanent differences occur only where we find morphological castes, and these are restricted to matrifilial societies.

In my view, evolution of sociality is based on the modification of the causal mechanisms involved in intra specific competition. Kin selection and its inclusive fitness components has not been a driving force behind social evolution, but it determines the range within which the competition could fluctuate to produce sociality; it unites all the mechanisms, and, historically, it brought about the aspects of convergency so prominent among social insects.

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