

## Government and nepotism in social insects: new dimension provided by an experimental approach

### Непотизм и политика у общественных насекомых: новые горизонты экспериментального подхода

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**Key words:** social hymenopterans, colony structure, castes, conflict of generations, division of labour, polyethism, individuality, flexible behaviour, learning, information transferring.

**Ключевые слова:** общественные перепончатокрылые, структура семьи, касты, конфликт поколений, разделение труда, полиэтизм, персонализация, гибкое поведение, научение, обмен информацией.

**Резюме.** Основная черта общественных насекомых, таких как термиты, муравьи, многие виды пчел и ос — эусоциальность, основанная на совместной заботе о потомстве, перекрывании во времени чередующихся поколений и, самое главное, на разделении функций между репродуктивными членами сообщества и «помощниками», так или иначе лишенными возможности размножаться. Хотя список эусоциальных животных в последние 30 лет дополнился различными организмами (некоторые виды тлей, жуков, креветок) и включает даже позвоночных животных («голые кротовые крысы»), у общественных насекомых представлена самая глубокая дифференциация между сферами размножения и обеспечения в сообществе, а также наиболее жесткое деление семьи на касты и субкасты, связанные с выполнением определенных функций и заданий. У одних видов эта дифференциация закреплена морфологическими различиями, у других она основана на физиологических и поведенческих характеристиках. В большинстве случаев многочисленная каста рабочих обслуживает потребности одной или нескольких размножающихся самок и их потомства.

В 60–е годы Гамильтон предложил элегантное объяснение альтруизму рабочей касты у общественных перепончатокрылых, рассмотрев это явление как частный случай своей теории совокупной приспособленности. Оригинальная система размножения у этих насекомых позволяет анализировать их сообщества как крайний вариант гамильтоновского «альтруизма родственников», когда, отказываясь тем или иным путем от размножения, организм

тем самым способствует выживанию большого числа близких родственников и в итоге его суммарный вклад в генофонд последующих поколений оказывается большим, чем если бы он размножился сам. Для общественных перепончатокрылых характерна гаплодиплоидия: самцы имеют гаплоидный набор хромосом, а самки и рабочие, которые являются неоплодотворенными и не размножающимися самками — диплоидный. Родство рабочих (сестер) между собой составляет 75%, а с самками (матерями) — лишь 50%, поэтому сестрам более выгодно поддерживать воспроизведение себе подобных сестер, чем самок. При этом каждая оплодотворенная самка может держать под контролем десятки тысяч своих «порабощенных» дочерей с помощью физических или феромонных воздействий.

Данная статья посвящена дискуссионному обсуждению двух наиболее важных аспектов функциональной организации семьи общественных перепончатокрылых: «непотизму», то есть борьбе за интересы родственников, которые часто приходят в противоречие с интересами сообщества, и «политике», то есть многообразию форм регулирования отношений при столкновении интересов в различных группировках и между группами. К обсуждению этих вопросов привлечены экспериментальные данные последних лет, в том числе и результаты, полученные автором. В статье намечены пути формирования концепции, которая бы позволила объяснить функциональную структуру семьи общественных насекомых, не прибегая к популярной в последние 150 лет, но уже устаревающей аналогии со сверхорганизмом.

**Непотизм: соотношение полов и интересы родственников.** На современном этапе изучения биологии общественных перепончатокрылых исследователи приходят к выводу о том, что теория Гамильтона без дополнительных объяснений и экспериментов не объясняет баланса интересов в сообществах этих насекомых. Даже в простейшем случае, когда семья основана одной самкой, оплодотворенной одним самцом, у рабочих лишь 25% общих генов с братьями (самцами, которые могут быть произведены данной самкой).

Поэтому они «предпочитают», чтобы 75% потомства составляли бы сестры, тогда как самка «предпочла» бы равное соотношение полов в своем потомстве, будучи на 50% родственной дочерям и на 50% — сыновьям. Такая разница в интересах приводит к типичному конфликту поколений, подробно рассмотренному в теории Трайверса [Trivers, 1974] для разных видов животных. У перепончатокрылых, в силу их гаплодиплоидии, этот конфликт принимает весьма оригинальный характер. Исследования последних лет показали, что у общественных перепончатокрылых самка является не столько «королевой», хотя она воздействует на готовность своих дочерей к размножению с помощью феромонного контроля, сколько жертвой интересов рабочих, которые различными способами (пища, феромоны, дифференцированное отношение к личинкам, физическое воздействие на личинок) формируют соотношение своих братьев и сестер в будущем потомстве матери в соответствии со своими генетическими интересами. При этом простые варианты (в семье одна фертильная самка, оплодотворенная одним самцом) встречаются не так уж часто. Следует учитывать, что неоплодотворенные рабочие при определенных условиях могут продуцировать гаплоидных самцов, что каждая самка может быть оплодотворена несколькими самцами, что основательницами могут выступать многочисленные самки, часть из которых не связана друг с другом родственными связями. Сочетание этих вариантов приводит к драматическим столкновениям генетических интересов различных группировок в семье. Известный исследователь биологии ос Квеллер [Queller et al, 1997] предложил для анализа генетической структуры семьи общественных перепончатокрылых рассматривать основной вопрос, стоящий перед семьей, с «точки зрения» яйца: если наступает время очередному яйцу быть отложенным, и каждая самка (включая неоплодотворенных рабочих) может это сделать, то время каждой из них задаться вопросом: «Почему не я?».

В данном разделе статьи рассматриваются ключевые варианты решения этого вопроса у разных видов и групп видов. Хотя современные данные в целом и не противоречат теории Гамильтона, исключений и вариантов накопилось так много, что актуальными стали поиски иных путей синтеза и формирования представлений о соотношении интересов в семье общественных перепончатокрылых.

Эта задача напрямую связана с функциональной организацией семьи. Если раньше самую многочисленную группировку в семье общественных перепончатокрылых — рабочих — рассматривали исключительно как «сферу обеспечения», в свете последних результатов становится ясно, что рабочие не просто поддерживают процесс размножения собственной матери, но и могут активно «лоббировать» собственные генетические интересы. Этот процесс становится более драматичным в полигинных семьях, где каста рабочих неоднородна по генетическому составу. Для решения этой задачи актуальны вопросы о формах взаимодействия среди группировок рабочих в семьях общественных перепончатокрылых.

**Политика: разделение труда и столкновение интересов.** Одна из наиболее распространенных концепций, объясняющих структуру семьи общественных насекомых — это концепция суперорганизма, дополненная в последние 20 лет концепцией адаптивной демографии. Основная идея данного раздела следующая: поскольку исследования последних двух десятилетий приводят к выводу о том, что каста рабочих имеет реальную возможность воздействия на генетическую структуру семьи, необходимо исследовать баланс конфликтов и кооперации между группировками рабочих особей, что даст возможность объяснить процессы самоорганизации, не прибегая к аналогии с суперорганизмом.

В разделе обсуждаются соотношение таких факторов, воздействующих на разделение труда между рабочими, как возрастной полиэтизм, морфологическая обособленность субкаст, пределы возможностей для переключения рабочих на выполнение различных заданий. Накапливающиеся в последние годы данные о способностях общественных перепончатокрылых к сложным формам научения позволяют перейти от концепции «слепой, ведущий слепого» к концепции, объясняющей распределение заданий между рабочими с точки зрения возможного гибкого поведения индивидуумов.

**Новые горизонты экспериментального подхода: индивидуализированные группы решают сложные задачи.** Основная идея данного раздела основана на экспериментальных результатах автора и может быть сформулирована следующим образом: для того, чтобы выявить наличие индивидуализированных слаженно работающих групп в семье общественных насекомых («команд»), необходимо наблюдение над тем, как семья решает сложные задачи. Это, в частности, достижимо в экспериментах, в которых для получения пищи насекомые должны передавать друг другу достаточно сложно организованную информацию. В опытах с применением нового лабиринта «бинарное дерево» [Reznikova, Ryabko, 1990, 1994] муравьи демонстрировали способность передавать информацию о последовательности поворотов на пути к кормушке, при этом они оказались способными улавливать закономерности

и использовать их для «сжатия» информации при передаче от разведчика к фуражирам. Высказывается предположение о том, что наиболее успешные «команды» рабочих могут способствовать большому успеху в размножении тех самок в семье, с которыми они связаны через процессы ухода за их потомством.

## Introduction

At the beginning of the XX century social insect societies were considered as a model of human society because of their social style of life, their great «houses», division of labour, and other very special and interesting features. The perfect organisation of the honeybee hive becomes the metaphor of social stagnation in human society. Plenty of analogies are reflected in the common language such as ant slavery, army ants, myrmidons, termite royalty, colony territory as an analogy of tribal territory and so on.

Colonies of social insects could be taken as analogies of the perfect welfare state, in which all contribute selflessly to the colony's reproductive interests by caring for the queen and her offspring. For a long time social insects have been used as extreme cases of intraspecific polymorphism and self-sacrificing aid, and to test more general ideas about evolution, as when Darwin noted the special difficulty for his theory to explain trans-generational inheritance of the specialised traits of sterile individuals. As Wilson [1982] has emphasised, social insects achieved full sociality a 100 million years before Homo appeared on the scene, and each of the more than 20000 species of social insects represent an independent evolutionary experiment by which the general theories of socio-biology can be tested and extended.

The main feature of social insects, such as termites, ants and many species of bees and wasps, is eusociality which is defined as that show co-operative brood care, overlap of generations and reproductive cast differentiation. Actually, the first two characteristics have been found in somewhat less social insects and co-operatively breeding birds and mammals which exhibit levels of altruism comparable to that exhibited by many eusocial species of bees and wasps. The most important feature is that in eusocial species their colony life is regulated by the functional division into reproductive and sterile castes. Social insects live in colonies, with most individuals serving as non-reproductive helpers. The reproductive specialisation of social insects have rendered them distinct from most other animals, until Jarvis et al. [1994] discovered nearly the same system in mammals, namely, in mole-rats. A list of eusocial organisms also includes several species of aphids, beetles, thrips and even one species of shrimp. However, in social Hymenoptera and termites a highest degree of difference between reproductive and sterile members of the colony is achieved. The hymenopteran colony is comprised of reproductive male and female and a worker caste of sterile females. The workers may

be differentiated, depending on species, into subcasts, or groups of individuals that perform similar kinds of labour. The individuals within each subcast have similar morphology and are distinct in morphology from members of other casts [Wilson, 1953].

Honeybee (*Apis mellifera* L.) may serve as an example of the most intensively studied among the social insects. A queen lays eggs, but other duties are performed by the workers, which are sterile females. They tend the queen, rear the young, maintain and defend the hive; some of them fly to collect nectar, pollen, propolis, or water according to the immediate needs of the hive. Drones are treated as sex objects, useful only in copulation. After the queen has been fertilised, they are quickly killed or turned adrift by the workers.

The trade-off between individual sacrifice and colony welfare in social insects can be easily estimated in the cases of colony defence. Thus, in the green tree ant of Australia (*Oecophylla smaragdina*) ageing workers emigrate to special «barrack nests» located at the territorial boundary of the colony. When workers from neighbouring nests or other invaders cross the line, these guards are the first to attack [Hölldobler, 1983]. According to Hölldobler and Wilson [1990], a principal difference between human beings and ants is that whereas we send our young men to war, they send their old ladies.

Hamilton [1964] offered an elegant explanation of how such a system of altruistic behaviour of workers could have arisen in the Hymenoptera. These insects have an unusual system of sex determination, namely haplodiploidy. Males are produced from unfertilised eggs and so they have half the number of chromosomes as the females. The result is that all the sperms from any male possess identical chromosomes since they do not undergo meiosis. Therefore, all the daughters have at least 50% of their genes in common as a result of one parent producing only one type of gamete. Furthermore, on average, the daughters share another 25% of their genes in common from their mother so that the total genetic affinity among daughters is 75%. Therefore, each daughter has only the normal 50% affinity with her mother, so hymenopteran sisters are more strongly related to each other than to their mother and that is more advantageous for each daughter in helping to rear her sisters than for her to have offspring of her own. To make this picture less idyllic, the queen could hold hundreds of thousands of her «enslaved» daughters in check against their interests, either through physical force or pheromone manipulation.

Instead of the term altruism, alternative expressions have been suggested for outwardly selfless behaviour of social insects, such as reciprocation [Trivers, 1971] and nepotism [Alexander, 1974]. In any case, the key question is how natural selection can produce selfish genes that prescribe unselfishness [Hölldobler, Wilson, 1990].

Two myths concerning social life-style in Hymenoptera are becoming categorical.

The first is that eusociality in these insects may be considered as sharp reflection of Hamilton's inclusive fitness theory. Actually, in the case where the queen is the mother of all workers, and she has only mated once, it is easy to explain why individuals might choose to be non-reproductive helpers in colonies rather than nesting alone, and real nepotism may be strongly expected via the 3/4 relatedness. However, numerous recent findings in social Hymenoptera run counter to straightforward expectations of kin selection theory and many investigators show lack of detectable nepotism in hymenopteran colonies.

The second is that distinctive properties and a higher degree of social organisation in social insects are based on rigidly programmed repertoires and very simple rules of self-organisation, so political inter-relations are not to be expected here. However, recently at least several well documented instances exist concerning cognitive capacities and flexible individual behaviour in social Hymenoptera. Essential differences between capabilities of colony members, as well as possible personalised inter-relations, enable us to look for features of politics in a similar sense as in monkeys and apes.

In this paper, against the background of the review of investigations devoted to nepotistic and political inter-relations in social Hymenoptera, new findings of these forms of behavioural patterns in ants are discussed basing on the discovery of individual inter-relations and individual identity in high social ant species. In this context, new data concerning ants capacity to solve problems, transfer symbolic information, discriminate each other and compete and co-operate at the individual level are considered.

#### SEX BIAS AND NEPOTISM

The kin-selection theory does not in itself solve the problem of insect sociality, because another problems remain. Colonies of bees, wasps and ants comprise one to several subgroups, each with distinct genetic interests. Specifically, conflict is expected between the queen and the workers over the two major aspects of reproduction: the relative investment in the sexes and the source of males [Heinze et al., 1994].

Even for the simplest case of a colony headed by a single, once-mated queen [monogyny and monoandry], workers share 75% of their genes by descent with their sisters but only 25% with their brothers. The queen, being equally related to her sons and daughters, prefers that 50% of the colony's reproductive energy be allocated to males, whereas workers prefer to invest 75% of colony's reproductive efforts in the production of sisters and only 25% in raising brothers. Thus, different genetic interests can lead to parent-offspring conflict over allocation to males versus females in the sexual brood [Heinze et al., 1994]. As Boomsma [1996] has noted, the unique opportunity for testing both inclusive fitness theory [Hamilton, 1964a,b] and parent-offspring conflict theory [Trivers, 1974] were presented. Although in a behavioural sense, the queen

«enslaves» her daughters by the power of pheromone control, according to population-level model, in terms of natural selection, queens are considered as victims of the workers controlling sex ratio preferences. The fact is, that for all social Hymenoptera, workers are the most numerous class and might therefore be in a position to exercise collective control being able to control sex ratios against queen interests.

In addition, workers have the option of producing their own sons. Though they typically cannot mate and their ovaries are more or less rudimentary, in many species they are capable of laying unfertilised eggs, which may develop into haploid males. In monogynous and monoandrous colonies, the workers share 50% of their genes with their own sons and 37.5% with their nephews, as compared to 25% shared with their brothers. Selection acting on workers should therefore favour the substitution of sons or nephews for brothers in the reproductive brood. The queen, on the other hand, shares 25% of her genes with her grandson and 50% with her own sons, hence, she should try to prevent workers from laying eggs and rather have them concentrate on her own offspring [Heinze et al., 1994].

As each worker is more related to her own sons than to her nephews, conflicts arise over which of the workers will lay eggs and which continue to take care of the nest. Furthermore, to make matters even more intricate, relatedness among siblings themselves is often not so high because of multiple mating, multiple queens and queen replacement [Crozier, Pamilo, 1996]. The number of males that inseminate queens is a major factor in establishing the kin structure of hymenopteran societies [Page, 1986]. Individual queens may be able to enhance their inclusive fitness by mating with additional males [Francis et al., 1995]; for example, extreme multiple mating occurs in the honey bee, in which queens are able to store a mixture of sperm from 10–20, and even 60, males [Seeley, 1985]; in the case of yellow jacket wasps queens are inseminated by an average 5.5–9.5 males [Ross, Carpenter, 1991]; and in the case of ants the greatest numerical mating frequencies are lower, with a maximum in the range of 5–6 [Page, 1986].

In general, colony kin structure determines the potential opportunities for workers to enhance their inclusive fitness by manipulating colony reproduction. Workers may realise this by causing female-biased sex allocation at low mating frequencies [Pamilo, 1991a], by preventing other workers from producing males at mating frequencies above two [Ratnieks, 1988, Pamilo, 1991b] and by nepotistically rearing full-sister queens at mating frequencies above one [Ratnieks, Reeve, 1991].

All this can lead to within-colony conflicts over resource allocation or over-reproductive opportunities among different queens and different patri- and matrilines [Crozier, 1979; Boomsma, Grafen, 1991]. The agonistic relations and very dramatic conflicts among the queens and egg-laying workers have been observed by many investigators in bumblebee colonies [Doorn,

Heringa, 1986; Duchateau, Velthuis, 1988; Moskalenko, Shalimov, 1997]. In the primitively social carpenter bee, daughters kill their baby sibs after conflict over dominance with mothers [Hogendoorn, 1994]. It is interesting in this context that in many ponerine ants, workers mate and reproduce and may rear no queens at all [Gadagkar, 1994].

Queller et al. [1997] considered the basic question of kin structure in insect societies in terms of a single egg: it is time for the colony's next egg to be laid, and only one individual will lay it; each colony member might well ask «Why not me?»

In general, different families of social Hymenoptera are characterised by different forms of sex bias and of conflicts between colony members. Let us consider several examples.

Paper wasps of the genus *Polistes* possess features of sociality, which may be more easily described in terms of conflicts and co-operations. They were analysed in detail in the experimental work of Queller et al. [1997]. Colonies are begun in the spring by groups of females called foundresses which have usually emerged from the same nest the previous autumn and as a consequence they are close relatives [Peters et al., 1995]. The first several broods of offspring consist mostly of females called workers, but also may include a small number of males. The workers normally act as non-reproductive helpers, but they are not a morphologically distinct caste. If all foundresses die before the end of the season, a worker will mate and become the dominant egg layer [Queller, Strassmann, 1988]. The relatedness estimates of Queller et al. [1997] have shown that the best outcome for most individuals is to be the reproductive egg-layer. Reproductive monopoly stems from the collective preference for non-reproductive specimens, which suppress each other in favour of the queen. After the death of the present queen, the first successor is a subordinate foundress even though workers should generally prefer a worker successor. If all foundresses have died, an older worker succeeds as queen, in spite of the collective worker preference for a young worker. Physical domination by the strongest individual may play some role, but finally age serves as a conventional cue for reducing conflict over queen succession. Older smaller workers succeed before younger larger ones.

Bees of the genus *Apis* are monogynous, i.e. only one queen in a colony may lay eggs. However, as stated above, polyandry is extremely widespread in *Apis*. In evolutionary discussion, recent interest has focused on genetic variance (GV) hypotheses which suggest that queen and colony fitness increased by the greater intro-colonial genetic diversity that is a consequence of polyandry [Pamilo, 1993; Keller, Reeve, 1994]. Oldroyd et al. [1997] divide the GV hypothesis into two categories. The first is based on the hypothesis that genetic diversity within the worker population leads to greater colony fitness because this allows an increased expression of caste and task polymorphism within the colony [Crozier, Page, 1985, Dreller et al.,

1995], helps colonies buffer environmental variance [Page et al., 1995], parasites and pathogens [Sherman et al., 1988]. The second view arise from male haploidy, and relate to the effects of sex determination on brood viability and to conflict between workers and queens over optimal sex ratios [Page, 1980; Ratnieks, Boomsma, 1995].

Bumble bees, *Bombus* spp., are seasonal social insects. Only the fertilised queens over winter to start a new colony in spring. As the colony growth in numbers, tasks such as resource collection are taken over by the workers. At the end of colony cycle, reproduction occurs when sexual females and drones are produced. Before onset of winter, the males die, as does the rest of the colony [Alford, 1975]. Females of several species mate multiply [Hobbs, 1967], and, at least two species, multiple queens are present and can form polygynous colonies [Michener, 1974]. Liersch and Schmid-Hempel [1998] exposed genetically homogeneous and heterogeneous colonies to parasitism under field conditions which was achieved by adding and removing the brood from donor colonies. It turned out that genetically variable colonies were beneficial under parasitism.

It is worthy to note that despite of the haploidy dominance in all Hymenoptera, there are a lot of sub-social and solitary species in wasps and bees. In some subfamilies many kinds of sociality occur; for example, of the currently recognised 10–15 independent evolutionary events of eu-sociality among insects, at least four occurred in lines belonging to a single group of bees, the sweet bee Halictinae. This cosmopolitan subfamily comprises about 4000 described species, many of them solitary, but overall exhibiting a remarkable diversity in social organisation and life history. Various forms of sociality including communal, semi-social, primitively eusocial, and preliminary eusocial have arisen many times among the Halictinae. Likewise, reversals from social to solitary life have evolved repeatedly [Mueller et al., 1994]. Pesenko and Radchenko [1994] analysed features that are necessary prerequisites for the appearance of eusociality, and among them monoandry of females, the ability to control sex of offspring which define fertilised and non-fertilised eggs, and distinguish related and unrelated individuals being temporary helpful to a mother.

While the bees and wasps offer a graded series of living species that range from completely solitary to completely eusocial, the ants are all highly eusocial and lack species that display a solitary lifestyle. In many ant species, polygyny, i.e. the occurrence of multiple functional queens in the colony, is common, with pleometrosis (foundress associations) and secondary polygyny (the addition of queens to a colony) as the major types. All these variants temper the interpretation of worker altruism as the dominant mode of ant life. Hölldobler and Wilson [1990] have analysed tides in kin selection theory applying to ants.

Recent findings in ants have added new paradoxes for a kin selection paradigm. De Heer and Ross [1998]

investigated the paradox for kin selection theory being presented by multiple-queen (polygyne) colonies of the introduced fire ant *Solenopsis invicta*. Egg-laying queens within these societies are, on average, unrelated to one another, and the numbers of queens per colony are high, so that workers appear to raise new specimens that are no more closely related to them than are random individuals in the population.

J.M. Herbers and R.J. Stuart [1998] tested the hypothesis [Trivers, Hare, 1976] that sex ratio in slave-making ant species should reflect the queen's interests whereas sex ratios in free-living host ants should reflect the workers interests. These authors investigated patterns of allocations to males versus females, as well as allocation to growth versus reproduction for slave-making ants in the tribe Formicoxenini. They found little support for the hypothesis of exclusive queen control; instead, their results implicated queen-worker conflict, both over male-allocation ratios and over allocation to growth versus reproduction.

Finally, an essential difficulty for the kin selection paradigm concerns the ability of hymenopterans to distinguish their kins. Actually, when considering the kin structure of a hymenopteran colony, nepotistic behaviour should be based on the capacities of nest mates to discriminate their colleagues belonging to the same or to different matriline and patriline. Anyhow several studies have found evidence for kin discrimination within honey bee colonies [Page et al., 1984, 1989; Vischer, 1986], but it remains unclear whether worker honey bees discriminate between sisters in their own and in different patrilines in a natural context [Moritz, 1991]. Recent careful studies on ants and social wasps failed to find any evidence for nepotism [Queller et al., 1990; Carlin et al., 1993]. Multiple-queen colonies of the introduced fire ant may provide a more clear-cut case of nepotism: queens in these colonies are on average unrelated to one another and singly mated [Ross, 1993]. De Heer and Ross [1997] suggested that in such selectively important contexts as tending egg-laying queens and feeding maturing winged queens, workers should discriminate between related and unrelated nestmates, but they failed to find this. Moreover, they found that ants did not behave nepotistically when deciding which female larvae to rear as new queens.

At the same time, much evidence has been assembled to scheme that social hymenopterans use olfactory and other cues for nestmate discrimination and they can easily distinguish alien individuals [Wilson, 1971; Hölldobler, Wilson, 1990]. This has also been demonstrated for one Argentine ant, *Linepithema humile* [Keller, Passera, 1993] in that females (and/or males) prefer to mate with unrelated over related individuals. To conclude, these insects undoubtedly have the neurosensory capabilities to discriminate among nestmates of varying degree of relatedness, but they rarely use them.

These and other results do not argue against kin selection theory in general, but a great deal of exceptions have been found presenting a challenge to look for other ways to explain social lifestyle in hymenopterans.

#### DIVISION OF LABOUR AND EXPECTATIONS FOR GOVERNMENT

The extraordinary complexity in eusocial colonies, and similarities between the rules and algorithms of morphogenesis in the development of a multicellular organism and of sociogenesis in the ontogeny of the insect society, enable many investigators to treat the colony as a functional unit termed «superorganism» rather than as a group of individuals [Wheeler, 1928; Wilson, 1982]. Furthermore, the insect colony maintains a constant ratio of different worker subcaste and age classes and thus may show an adaptive demography [Hölldobler, Wilson, 1990].

Other analogies come from scientists who deal with human societies. Thus, Johnson [1995] argued with Tiger and Fox [1971] who missed the existence of politics in ant colonies. This author considers societies of social Hymenoptera as a remarkable example of those systems in nature in which conflicts of interest exist among co-operating social colleagues, so government could be found here.

The almost all researches of social insects are now in accordance, non-reproductive members of the colony have the power to influence reproductive processes, and it would be possible to look for complex behavioural processes for maintaining an equilibrium between conflict and co-operation among workers themselves. However, nowadays most of the models of social life in insects seem not to provide room for political inter-relations among workers, as they based on tough programmed behavioural characters. At the same time, there are some limited, yet well documented, evidence of the extraordinary learning capability of individuals and flexible behaviour and inter-relations between them. The aim of this issue is to review these data in respect of models of social lifestyle.

As almost all models of the division of labour in social Hymenopterans are based on inherited properties, they are closely connected with view of selective advantages of multiple mating or of multiple queens. A general example is that the resulting increase in genetic variation could allow the establishment of a more efficient division of labour due to better matched individual work profiles.

In the most species of social Hymenoptera division of labour is based on the two main vectors: morphological caste differentiation and temporal division of labour, often called age polytheism when worker behaviour changes systematically with age. It is now believed that the organisation of social insects is more a kin to a distributed process rather than to tough accordance between implementing to a definite caste and task performance. An individual does not perform a single task, but can perform any of a number of tasks. The process by which an ant colony assesses its current needs and «assigns» a certain number of members to perform a task is known as task allocation [Gordon, 1995].

Of the Hymenoptera, the ants have the greatest differentiation among the workers. Although workers of most species of ants are monomorphic, some species

have two or three morphological subcastes [Oster, Wilson, 1978]; for example, in a colony of green tree ants *Oecophylla smaragdina* there are workers with large or small heads called majors or minors respectively which perform different tasks [Wilson, 1971]. In the leaf-cutting ants of the genus *Atta*, workers have wide size variation, but the variation is continuous. Although there are no discrete size classes of workers, ants of different sizes fall into four partially discrete physical subcastes, are based on body size, called role clusters. Different size classes of workers are tailored to the special needs of harvesting, retrieving and processing the leaves on which fungus is cultured. In sum, ants that garden and nurse tend to be small bodied while the foragers or excavators are the largest ants of the colony. In contrast, in most species of the genus *Formica*, workers are monomorphic and are not considered to have physical subcastes [Wilson, 1980].

In the case of bees, workers are generally characterised as monomorphic, but variation in body size differs among species. Primitive eusocial bees, such as bumble bees and sweet bees (Halictidae) have high within-colony size variation, whereas the highly eusocial honey bees and stingless bees (Heliponinae) have low size variation [Michener, 1974]. Waddington [1987] researched in detail the effects of body size on behaviour of individual honey bees and on social interactions between bees. It turned out that age of first foraging, frequency of foraging, and distance flown from the hive to flowers are affected by body size.

Both in the bees and the ants, workers perform a sequence of different tasks as they age; for example, in the red wood ant *Formica polyctena*, young workers stay inside the nest and spend time tending brood, caring for other workers and the queen, and cleaning the nest, and older workers forage and construct the nest [Otto, 1958]. As Zakharov [1980] demonstrated, the oldest workers become patrollers and spend time at the peak of a nest mound. In the bees, workers of different ages perform different roles such as cell cleaners, nest brooders, food accumulators and foragers [Lindauer, 1952; Seeley, 1982].

In their experimental work, Calderone and Page [1996] supported the developmental-programmed model of temporal polyethism and behavioural canalisation in the honey bee. They introduced to a colony four groups of workers, emerging at 6-days intervals, with some of them, deprived in an incubator, lacking pre-foraging experience. Foraging activities were quantified for two sets of workers from strains of bees selected for high and low pollen hoarding. The results suggested that a forager's task selection is primarily determined by her genotype and immediate environment. High-strain workers collected pollen more often than low-strain workers, regardless of their pre-foraging environments. Differences between deprived and non-deprived groups of the same strain and age were rare.

Most models of social organisation in hymenoptera are based on those view that these organisms are literally the blind leading the blind [Franks et al., 1992];

namely that the theory of self-organisation is based on stochastic processes which may be described by simple mathematical models [Deneubourg et al., 1987]: individual randomness and competition between different pieces of information are the factors that generate individual behavioural patterns and society organisation. Thus, in certain species of army ants, hundreds of thousands of workers are able to create raid structures with a beautiful «fractal» organisation [Deneubourg et al., 1989].

Recently a number of studies on social insects have shown how self-organisation is involved in collective pattern formation; for example, Camazine [1990] has demonstrated how honeybees use simple rules to create patterns in their usage of the comb for rearing larvae or storing pollen on honey.

Franks et al. [1992] described the sophisticated building by blind bull-doing in the ant, *Leptothorax tubero-interruptus*. The central question of their paper was «how do social insects collectively build complex nests in the apparent absence of central planners, architects, blueprints or quality control overseers?». Of particular interest is the fact that the species investigated naturally use flat crevices in rock, so they do not have to construct the roof and floor of their nests. The ants simply build a perimeter wall around their colony. Such building is essentially two-dimensional. The ants apparently use very simple rules both to make their nest to an appropriate size for their colony and to co-ordinate their building activities. Laboratory experimentation and a computer-stimulation model have shown how the ants could use a simple self-organising procedure. Each builder, by pushing its building block into others, adds its work to existing structures. Building workers do not communicate directly, but can communicate efficiently via the products of their successful labours.

Gordon [1989, 1995a,b] considers the ant colony as analogous to systems that are not commonly thought of as societies. She has found that neural network models may help to explain how a single set of rules at the level of the individual can generate a variety of behaviour of an entire colony as the colony faces different circumstances. Most remarkable, it seems to her that ant colonies refine their responses as they age, in a process perhaps similar to the way higher organisms learn as they mature.

Studying the processes of task allocation in ants, Gordon [1995a] asked a basic question about the dynamics of colony behaviour: does the number of individuals engaged in one task influence the number engaged in another? The author compared this with a similar question about a human city: is the number of people in cars on the highways a function of the number of people in the city's office buildings? If the public transport system is interrupted, will it affect the number of people in restaurants? To us it is obvious that different human tasks are independent, but in ants, several results support the notion that an individual uses both environmental information and social interactions in

its decision whether to be active and which task to perform. However, no ant is keeping track of the big picture.

Solé and Delgado [1996] introduced analogies between neural sets and insect colonies, in a new class of models, the so called fluid neural networks. They have shown that collective logical gates can be built in such a way that complex computation is possible by means of the interplay between local interactions and the collective creation of a global field.

All of the reviewed models of social life-style consider cognitive processes and individualised interactions for social insects as redundant. To summarise, the collective capabilities of social insects are based on non-linear co-operative processes: robustness of behavioural patterns against noise, collective decision making and emergent computation. Individuals display a limited repertoire of activity patterns, gathering information from the environment as well as from their nestmates before a collective decision is adopted. It could be said that politics within the insect colony are much the same as political inter-relations within a human brain.

However, another set of arguments come from data concerning excellent learning capabilities of social insects. Symbolically, that one of symposia held at the 12th Congress of the International Union for the Study of Social Insects (Paris, 1994), organised by C. Masson and M. Lehrer, was named «Learning and Memory: Cognition in Social Insects?» Masson and Lehrer [1994] noted that although many kinds of activities are innate to the social insects, at the level of the individual animal, it is mainly the foraging task that requires a flexible behavioural repertoire, and thus an excellent learning capacity. To optimise its foraging success, the insect must remember the route to a foraging site, as well as the route back to the nest, and the question remains, whether or not cognitive processes are involved in some of the performances observed.

This is one of vividly discussible issue. Thus, several authors suppose that the honey bees possess a geometric representation of space in form of a cognitive map based on latent learning [see Gould, 1986], and others conclude that the multiple set of orientation mechanisms is sufficient to explain goal-oriented behaviour in the bee without the necessity to assume cognitive maps [Wehner, Menzel, 1990; Dyer, 1991; Geiger et al., 1994].

Mazokhin-Porshnyakov's [1969, 1989] experiments demonstrated that the honey bees and social wasps are capable of abstraction, extrapolation and solving rather complicated tasks at a level of vertebrates, such as dogs and monkeys.

From early experiments of Schneirla [1946] it was known that some ants perform almost as well as rats in simple maze-learning tasks. Udalova and Karas [1993] have demonstrated, with the use of a symmetrical multi-choice maze, the ability of ants to analyse the axial symmetry of the maze and to formulate a generalised scheme of space. The capacity of ants for solving logi-

cal problems and for transmitting complicated information by means of a distant homing system has been shown in experiments [Reznikova, 1979, 1982, 1983]. Dlussky [1981] has demonstrated that ants are able to switch over different ways of communication depending on environmental conditions.

Rosengren and Fortelius [1987] provided evidence of extremely long-lasting storage of spatial information in red wood ant foragers, even through several months of winter dormancy. They consider as misleading the popular metaphor that ants live in a miniature world, where grass stems are as big as trees, and prefer holistic pattern which is based, at least partly, on canopy orientation.

To summarise, authors characterise red wood ants as «replete ants» storing, not lipids in their fat-bodies, but habitat information in their brains.

Even tool use is known (although discussible) for several ant species which is based on not hardened, but quite flexible behavioural patterns: ants use bits of dry soil or grass in order to facilitate transport prey issues [Fellers, Fellers, 1976; Paiva et al., 1995].

#### NEW DIMENSION FOR GOVERNMENT AND POSSIBLE NEPOTISM IN SOCIAL INSECTS: COMPLEX TASKS AND INDIVIDUAL IDENTITY

Another way to construct analogies of government and nepotism in insect societies based on individual inter-relations and individual identity is presented. The current study is believed to be one of the first demonstrations of its kind. As it can be seen from the above review, only a few studies have been devoted to the capacities of social insects to solve rather complex problems. Meanwhile, there is some evidence that in top social species of ants and bees, «gifted» individuals differ a great deal from others and are able to cope with rather complex tasks. Naturally for ants it is far more complex to find a new aphid colony within a huge three-dimensioned tree crown and attract foragers there than to find a bit of dry stem on a soil surface and bring it to a mound.

In his remarkable experiments (in which this author used to take part as a student), Mazokhin-Porshnyakov [1974] showed that nearly all foragers from a hive coped with a task of discriminating figures of different sizes from their shapes; for example, the individual bees had been trained to choose the biggest figure from three rounds, then from three squares and so on. The task was to choose the biggest figure of any shape. The bees never failed to choose the right figure when, for example, three triangles of different sizes were demonstrated to them. However, another task proved far more difficult. Two chains were shown to the individual bee, which were composed from 8 small figures (rounds, rhombuses). In one chain figures was disposed by pairs (two rounds, two squares), while in another they were disposed randomly. The next time the same bee was shown two chains, but composed from other components. The bee had to grasp that the right choice is the



chain composed of coupled figures. Only 5 bees from 100 who were able to solve this problem. In experiments on ants, nearly the same correlation has been revealed in foragers which had to find food items inside mazes of different degrees of complexity [Reznikova, 1975, 1983].

Until recently, existence of personalised «bands» («cliques», «teams») within insects colonies, which may be based on individual identity and individual interrelations, was unknown. According to Hölldobler and Wilson [1990], the relation of the members of an ant society to one another can be characterised as one of impersonal intimacy. Ants do not appear to recognise one another as individuals. Their classificatory ability is limited to the recognition of nestmates, different castes such as majors and minors, the various growth stage among immature nestmates, and also possibly kin groups within the colony.

There are, however, several findings in literature that would suggest that the existence of teams within colonies consist of members of different castes that come together for highly co-ordinated activity in the performance of a particular task. Thus, Waddington [1988] has described the so-called «dance-groups» in honey bee colonies, grouping around a scout bee when she dances.

Another description of team organisation, cited by Hölldobler and Wilson [1990] as exceptional, refers to Franks [1986]: in the swarm-raiding army ants *Eciton burchelli*, large prey items are transported by structured teams, which include members of different castes.

In addition, Robson and Traniello [1994] examined the organisation of foraging in the group retrieving ant *Formica schaufussi* with a protocol that emphasises the description of both individual and group behaviour; they found a major difference between mass-recruitment species that are characterised by the collective action of simple individuals, and the group retrieving ones. In the latter case, a colony design is based on «complexity rather than simplicity». It is especially interesting result in that the removal of the discovering ant during the process of recruitment leads to the dissolution of the retrieval group.

The question of constant membership and individual recognition has been so far obscure. Only one paper in which individual ranking as well as individual recognition among ants within small working groups has been described [Zakharov, 1980]. The work of Reznikova and Ryabko has showed that personalised teams in ants are connected with the discovery of the existence of the complex communicative system in top social ant species which requires the existence of individuals with different levels of learning capacities. These long term experiments have revealed a developed symbolic «language» in three ant species, which is probably even more intricate than in honeybee [Reznikova, Ryabko, 1990, 1994, 1996; Ryabko, Reznikova, 1996]. This communicative system is based on the existence of small bands within the ant colony which are composed of a discovering ant (a «scout») and 5–8 recruits. Ants

of the highly social species *Formica polyctena*, *F. sanguinea* and *Camponotus saxatilis* (800–2000 specimens each) were kept in transparent nests in laboratory areas. Each worker was labelled with an individual colour mark. The composition of ant's groups were revealed during preliminary stages of the experiments.

The main point of this approach is that the experiments provide a situation in which ants have to transmit quantitative information to the experimentalist in order to obtain food. This information concerns the sequence of turns towards the trough. A new laboratory system called «binary tree», where each «leaf» of the «tree» ends with an empty trough versus one filled with syrup, was used. The simplest design was a tree with two leaves and two troughs with syrup in one of them. In this situation an ant scout transmit one bit of information to foragers: to go to the right or to the left. In other experiments, the number of forks in one branch increased to six. To prevent access to food in a straight line, the set-up was placed in a water bath, and the ants reached the initial point of the tree by going over a bridge.

To start the experiment, an ant scout was placed at the trough containing food. When it returned to the foragers in the nest, it started to contact them. After the scout made one or more trips, foragers began to follow her towards the maze, but as soon as they started moving, the scout was removed from the arena with tweezers. So the foraging team had to reach a goal without their guide. To avoid odour tracks, the original maze was replaced by an identical one.

In total, more than 300 teams of three ant species were used in these experiments with binary tree and several other variants of mazes. It is important to note that not all of the scouts managed to memorise the way toward the maze; moreover, the number of such scouts dropped with the complication of the task, e.g. in the case of two forks, all active scouts and their groups were working, while in the case of six forks, only one or two were working. The second important thing is that every scout invests its efforts only in its own small group and its prosperity depends on the scout's ability to transfer them the information about the food source.

Contrary to most previous opinions, special mechanisms of individual identity in ants have been displayed. Behavioural patterns of group identity have been based on grooming, antennae contact and food exchange, while ranking have been based on begging.

Constancy of membership were examined in two colonies of *F. sanguinea* and *F. polyctena*, seized all team members from 9 scouts. 3 scouts appeared to mobilise their previous acquaintances and attract new foragers, 4 scouts were working solely, and 2 ceased to appear on the arenas. During another experiment, scouts were seized from 5 *F. polyctena*'s teams. It was possible to see foragers from those groups on the arenas, without their scouts. 15 times different foragers were placed on the trough with the food, but after their return to the nest, they contacted other ants rather rarely and occasionally.

To summarise, searching and other out-nest work in the colony are carried out by compact work groups based on long-term individual contacts and exchange of information. Possibilities to redistribute work between individuals are related to the complexity of the problem. Scouting ants and foragers cannot exchange their roles, and foragers cannot transmit information. Individual abilities of scouting ants define the activity of the whole ant team.

Recent field observations [Reznikova, Novgorodova, 1998] have shown that in nature, small work teams solve problems of the family, such as honeydew collection. Groups of *F. polyctena* ants servicing separate aphid colonies are very permanent and consist of individuals of different professional orientation. «Shepherds» collect honeydew droplets, and «guards» are more aggressive, they scaring away predators and alien ants and protecting aphids from rain. These two groups are interchangeable, but activity of «shepherds» in the exchange is more successful. «Carriers» carry honeydew to the nest and are unable to fulfil other functions. Most interestingly some scout ants have been shown to search for new aphid colonies and attract foragers to them. These ants are most successful in the exchange of functions as they are able to cope with many tasks. This would suggest that laboratory experiments reflect a real natural situation for highly social ant species.

All these results would suggest that «political life» in ant societies is largely governed by scouts. However, this concerns only those «ant primates» which possess huge colonies of about one million nest-mates and great domes. There are only several top social species among thousands. In experiments I compared «language» behaviour and corresponding colony structuring high and low social ant species. Patterns of individual inter-relations are significantly different in species with large or small colonies, such as species of the subgenus *Serviformica* and of the genus *Myrmica*. The most important difference is that in species with small colonies, social life is based on anonymous contacts, i.e. these ants do not identify each other individually. The distinction between individualised and anonymous inter-relations in ants is comparable with Eibl-Eibesfeldt's [1989] distinction between individualised and anonymous human societies.

For the data obtained, it would appear that, at least in some species of social insects, features of a developed governmental life peculiar to systems of a definite size-similar, for example, to certain features peculiar to thermo-stable organisms.

Speculation about nepotism in ants is that, within the ant colony each cluster of bands is connected with one queen by continuing processes of grooming and food exchange. I have been unable to measure in this study if queens and associated workers are more closely related genetically. However, based on as yet limited data, it can be predicted that successful scouts and their cliques are able to promote their inclusive fitness by more successfully rearing the queen which is more closely related to them. Under conditions of food short-

age and in other complex situations, small bands within the ant family compete for different resources. It was observed that in such situations of competition those bands succeed which are connected with more agile scouts.

In this way, nepotism could operate at the level of individual inter-relations among workers within the ant colony in polygynous species with the highest level of social organisation.

### Acknowledgements

Supported by Russian Fund for Basic Research (grant 02-04-48386). I express my gratitude to Dr Frank Salter (Humanethologie und Humanwissenschaftliches Zentrum der Ludwig-Maximilians-Universität, München) for the scientific and financial support.

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