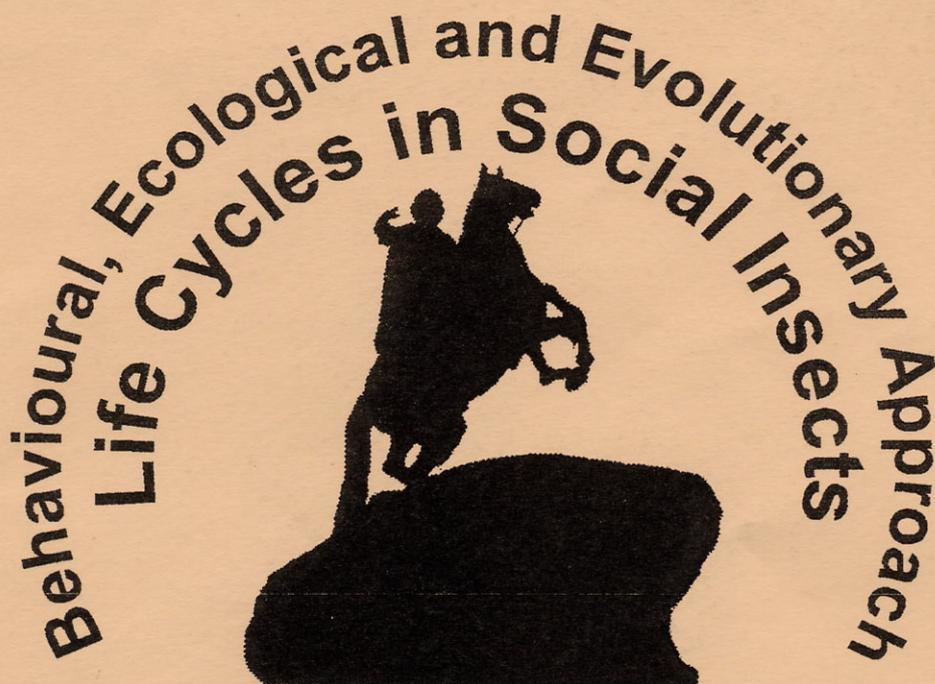


International Symposium
“Life Cycles in Social Insects:
Behavioural, Ecological and Evolutionary
Approach”

St. Petersburg, Russia, 22 – 27 September 2003

PROGRAMME
ABSTRACTS
LIST OF PARTICIPANTS



International Symposium
St. Petersburg, Russia
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International Union for the Study of Social Insects
Russian Language Section

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Edited by
Vladilen E. Kipyatkov

St. Petersburg
2003

INTERNATIONAL SYMPOSIUM
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St. Petersburg State University
The University Conference Centre

PROGRAMME

Monday 22 September

10:00–10:20 **Opening ceremony**

Session 1. Introduction: Two life history issues

Chair: Vladilen Kipyatkov

- 10:20–11:05 *Invited lecture*
Randall Hepburn (South Africa): Absconding, migration and swarming in honeybees: an ecological and evolutionary perspective. p. 27
- 11:10–11:55 *Invited lecture*
Thomas Chapman (Australia): The evolution of defensive behaviour in Australian gall-forming thrips. p. 14
- 12:00–12:15 Discussions & Announcements
- 12:15–12:45 Joint photographing

* The numbers of pages on which the abstracts of invited lectures, talks and posters are printed (see pp. 10–61). The list of poster presentations is on p. 9. The address list of the participants is on pp. 62–64.

** Meals will be served at the restaurant in the University Conference Centre. Breakfasts will be provided each day from 9:00 to 9:45 except on Friday 26 September (see p. 7).

16:10–16:40	Coffee Break
16:40–17:00	Catherine Bridge (UK): Queuing for dominance in a primitively eusocial wasp – <i>Liostenogaster flavolineata</i> ... p. 13
17:05–17:25	Fernando Noll, Sidnei Mateus, Ronaldo Zucchi and John Wenzel (Brazil): Inter caste differences and colony cycle in neotropical swarm-founding wasps (Hymenoptera, Vespidae, Epiponini). p. 45
17:30–17:50	Lidiya Rusina (Ukraine): Colony productivity in <i>Polistes</i> wasps in Kherson region, Southern Ukraine. p. 51
17:50–18:00	Discussions
18:00–19:00	Dinner

Wednesday 24 September

Session 3. Life history evolution in perennial social insects

Chair: Christopher Starr

9:45–10:30	<i>Invited lecture</i> Kazuki Tsuji (Japan): Life history evolution in perennial social insects with special reference to population dynamics and spatial structure. p. 55
10:35–11:20	<i>Invited lecture</i> Jürgen Heinze (Germany): Life in a nutshell – the social structure of <i>Leptothorax</i> ants. p. 26
11:25–12:00	Coffee Break
12:00–12:45	<i>Invited lecture</i> Blaine Cole and Diane Wiernasz (USA): Fitness and selection in the life cycle of the western harvester ant <i>Pogonomyrmex occidentalis</i> p. 15
12:50–13:00	Discussions
13:00–14:30	Lunch

Session 3. (continued) Chair: Graham Elmes

14:30–15:15	<i>Invited lecture</i> Robert Jeanne and Andrew Bouwma (USA): Life history issues in social wasps, particularly the swarm founders. p. 31
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15:20–15:40	Yves Roisin (Belgium): How can split sex ratios evolve in monogynous, monoandrous, worker-sterile ants? p. 50
15:45–16:20	Coffee Break
16:20–16:40	Diane Wiernasz and Blaine Cole (USA): The ontogeny of reproductive allocation. p. 59
16:45–17:00	Discussions
17:00–18:00	Dinner
18:00–23:00	Optional visit to Italian Opera (in Mikhailovsky Theatre) The Theatre of Vincenzo Bellini " <i>Massimo</i> " from Catania, Sicily Vincenzo Bellini " <i>Norma</i> " (1831)

Thursday 25 September

Session 4. Evolution of perennial life cycles in extreme boreal environments

Chair: Jürgen Heinze

9:45–10:30	<i>Invited lecture</i> Vladilen Kipyatkov and Elena Lopatina (Russia): Patterns and constraints in the evolution of seasonal life cycles in boreal ants: ecophysiological and sociobiological approach. p. 34
10:35–11:20	<i>Invited lecture</i> Graham Elmes (UK): Adaptation of the brood cycle by <i>Myrmica</i> ants in order to exploit habitats having cold, fluctuating seasonal climates. p. 17
11:25–12:00	Coffee Break
12:00–12:20	Elena Lopatina and Vladilen Kipyatkov (Russia): Behavioural and physiological control by workers over the development of larvae in the seasonal life cycle of ant colony. p. 40
12:25–12:55	Yaacov Lensky, Sharon Melamed and Itzhak Bilkis (Israel): Alarm pheromone volatile components in honeybee workers (<i>Apis mellifera</i> L. var. <i>ligustica</i> Spin.): chemical characterization and bioassays. p. 39
12:55–13:00	Discussions
13:00–14:15	Lunch

Session 5. Parasitism and life history evolution in social insects

Chair: Vladilen Kipyatkov

- 14:15–15:00 *Invited lecture*
Paul Schmid-Hempel (Switzerland): How parasitism affects life history in social insects. p. 52
- 15:05–15:50 *Invited lecture*
Stefano Turillazzi and Rita Cervo (Italy): Behavioural and physiological adaptations to inquilinism in *Polistes* wasp social parasites. p. 58
- 15:55–16:25** *Coffee Break*
- 16:25–16:45 **Serge Aron** (Belgium): Evolution of miniaturisation in inquiline parasitic ants: timing of male elimination in *Plagiolepis pygmaea* the host of *Plagiolepis xene*, as determined by flow cytometry. p. 11
- 16:50–17:35 *Invited lecture*
Christopher Starr (Trinidad & Tobago): Steps toward a general theory of the colony cycle in social insects. p. 54
- 17:40–18:00 Discussions. Election of the Editorial Board for *Symposium Proceedings*.
- 18:00–19:00** *Dinner*
- 19:00–19:10 Closing of the Symposium
- 19:10** **Farewell Party with Russian beer and soft drinks**

Friday 26 September – Symposium Social Day

- 8:45–9:30** *Breakfast*
- 9:30–12:00 Excursion to St. Isaac Cathedral and looking at the sights of St. Petersburg from the height of cathedral's cupola
- 12:00–13:00** *Lunch*
- 13:00–18:00 A guided bus tour to the suburb town *Pushkin*, the residence of Russian Emperors. An excursion to Catherine Palace with recently restored Amber Room, to Catherine Park and other attractions.
- 18:00–22:00 Symposium Banquet in Russian folk restaurant *Podvorie* (Pavlovsk)
- At 22:00 the bus will depart from the restaurant to transport the participants to the hotels*

Saturday 27 September

Session 7. General session

Chair: Randall Hepburn

- 9:45–10:15 **Yaacov Lensky, Sharon Melamed and Itzhak Bilkis** (Israel): Alarm pheromone volatile components in honeybee workers (*Apis mellifera* L. var. *ligustica* Spin.): chemical characterization and bioassays. p. 39

Session 8. Prospects for the development of life history theory in social insects

Chair: Vladilen Kipyatkov

- 10:20–11:05 *Invited lecture*
Christopher Starr (Trinidad & Tobago): Steps toward a general theory of the colony cycle in social insects. p. 54
- 11:10–11:40 Overall discussion
- 11:40–12:25 Coffee Break**
- 12:25–12:45 Election of the Editorial Board for *Symposium Proceedings*
- 12:45–13:00 Closing of the Symposium
- 13:00–14:30 Lunch**
- 14:30–18:00 The participants are invited to visit famous Russian museums situated nearby the main building of the University, i.e. *Kunstkamera* – the first Russian museum founded by Peter the Great, *Menshikov's Palace* – the first stone building in St. Petersburg constructed by Peter the Great's favourite prince Alexander Menshikov, Zoological Museum, Museum of Anthropology and Ethnography, Museum of Navy (see the map enclosed into the Participant's Bag)
- 17:30–18:30 Dinner**

List of Poster Presentations *

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2. **V. I. Ashcheulov and V. A. Ponomarev** (Russia): Method for diapause termination with the use of water in *Bombus terrestris* queens during laboratory breeding (in Russian). p. 60
3. **John Breen and Audrey O'Grady** (Ireland): Morphometric effects of mermithid parasitism in *Lasius* sexuals (Formicidae). p. 12
4. **Elena Diehl, E. Diehl-Fleig, E. Z. de Albuquerque and M. Bencke** (Brazil): Nesting biology of the fungus grower ant *Mycetophylax simplex*. p. 16
5. **Lesja Firman, Oksana Skorohod, Tanja Pishcheva, Maria Nitochko, Lidiya Rusina** (Ukraine): Queen longevity on nests and seasonal life cycles in *Polistes* wasps (Hymenoptera: Vespidae) in Southern Ukraine. p. 18
6. **Denis Fournier, Laurent Keller and Serge Aron** (Belgium): High reproductive skew and low queen turnover in the facultatively polygynous ant *Pheidole pallidula*. p. 21
7. **Nicola Gammans, Karsten Schonrogge, James Bullock and Michael Fenner** (UK): Does the feeding of *Ulex* elaiosomes to *Myrmica ruginodis* colonies affect the sex ratio of larvae? p. 24
8. **Myriam Harry, Virginie Roy, Evelyne Garnier-Sillam** (France): Trait of life of a soil-feeding termite: evidence of reproductive distortion. p. 25
9. **V. A. Kuryuchkin, V. I. Ashcheulov, V. A. Ponomarev and A. E. Grubova** (Russia): On the structure and asymmetry of ovaries in bumblebees (in Russian). p. 61
10. **Andrei Maysov** (Russia): Geographic variation of the response to photoperiod in the ant *Myrmica ruginodis* (Hymenoptera: Formicidae). p. 43
11. **Emma Napper, Karsten Schönrogge, Jeremy Thomas, John Pickett and Jenny Knapp** (UK): Detection of *Microdon mutabilis* by *Formica lemmani* workers. p. 44
12. **Tatiana Novgorodova** (Russia): Interspecific variation of behavioural models in the ant *Formica cunicularia glauca* Ruzs. in case of trophobiosis. p. 46
13. **Tatiana Novgorodova** (Russia): Size distinctions of *Formica polyctena* and *F. pratensis* trophobionts executing different subtasks in working groups. p. 47

* The numbers of posters correspond to those displayed in the conference hall. The presenting authors are underlined if not the first or the sole. The address list of participants is on pp. 62–64.

** The numbers of pages on which the abstracts of poster presentations are printed.

ABSTRACTS

The annual life cycle of Japanese hornet, *Vespa analis*, colony

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Among seven species of *Vespa* in Japan, *Vespa analis* is undoubtedly the most common, distributed throughout Central Japan. Studies of the insect over the last 20 years have revealed that this species can survive in small areas, one-fortieth the size of its cousin, *Vespa mandarinia*. Nests can be found in fields, woodland or city area, usually 3–4 m from the ground, on tree branches or even in the eaves of homes. The life cycle of *Vespa analis* colony starts in May, when the queen emerges from hibernation and builds a sake bottle-shaped foundation nest, from pulp. Inside in nest she lays her ready-fertilized eggs, which she cares for herself, hunting for insects to feed the growing larvae, until a couple of workers hatch. The workers continue to build the nest expanding it to a multi-layered, ball with a marble design on the surface. Between July and September the colony size increases dramatically to over 100 workers, all continuously feeding larvae, preying for insects and defending the nest from predators. All adult hornets need that the larvae excrete saliva liquid rich in amino acids, which is the primary food supply for the adult workers, giving them energy to fly and all for behavior. The role of saliva creates a social tie between adult hornets and larvae. During one year the numbers of new queens and males increase about 70. In October, mating begins, in a process that results in the death of the male. The female stores the sperm in her body and goes into hibernation for the winter. As the temperature falls, the insect food supply becomes scarce and the hatched adults feed from the honey of autumnal plants and flowers, sometimes leaving yellow pollen stains inside the nest. The larvae begin to starve and stop producing larval saliva, the essential food source of the adult. With suppressed trophallaxis the adult becomes weak and eventually the remaining workers hibernate, but do not have sufficient protection or nutrition to survive the winter. Only the queen wakes up in the spring to continue the life cycle of *V. analis* for another season. This paper will explain the life cycle of the *V. analis* colony in greater detail from the point of view of colony size.

Evolution of miniaturisation in inquiline parasitic ants: timing of male elimination in *Plagiolepis pygmaea*, the host of *Plagiolepis xene*, as determined by flow cytometry

Serge Aron

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Sex ratio variations during brood development have important implications for the study of sex allocation in haplodiploid insects. So far, few studies have addressed this question because of the difficulty to determine the sex of the brood. We show that flow cytometry (FCM) can be successfully used in haplodiploid insects to distinguish between male and female brood on the basis of their DNA-content from the very first larval stage. Moreover, FCM was used to determine the timing of male elimination in *Plagiolepis pygmaea*, the host of the inquiline parasitic ant *Plagiolepis xene*. A remarkable feature of inquiline ants is the small size of sexuals, which are of the same size as or smaller than host workers. It has been suggested that miniaturisation evolved by parasites to prevent host workers from discriminating between their own worker brood and the inquiline sexuals, so that male and female inquilines develop even under conditions where the host species does not produce its own sexuals. In line with the miniaturisation hypothesis, workers of the ant *P. pygmaea* cull all the male brood of their own species, whereas at the same time males of their inquiline parasite *P. xene* are reared to adulthood. We tested the miniaturisation hypothesis by determining the timing of male elimination in the ant *P. pygmaea* by flow cytometry. According to the hypothesis, *P. pygmaea* males are predicted to be eliminated after they have reached the size of the largest worker larvae, which is equivalent to the size of the larger sexual larvae of its parasite. Comparison of the sex ratio between different developmental stages shows that males of *P. pygmaea* are selectively eliminated much before reaching the critical size of the largest worker larvae. These results indicate that *P. pygmaea* workers recognize males of their own species on the basis of criteria other than size, and that miniaturisation is not sufficient to explain why inquiline sexuals escape culling by host workers in ants.

Morphometric effects of mermithid parasitism in *Lasius* sexuals (Formicidae)

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Parasitism by mermithid nematodes occurs in the sexuals of some Irish populations of *Lasius*. The parasitized sexuals have extended abdomens and reduced wings and remain in the nest for some time after swarming occurs. The parasite occurs most frequently in *L. flavus* but also occurs in *L. niger*. Both males and queens are parasitized. The parasite is particularly common in the *Lasius* population on the small Clare Island, Western Ireland. Samples were collected during August 2002. The following were investigated: numbers and dimensions of nematodes in males and female ants. The following dimensions were measured on samples of 15 males and 15 females of *L. flavus*, infected with nematodes and uninfected: head and thorax width, femur length, radial cell length and width. Data from two parasitized *L. niger* females are also available. In males there were mostly single nematode parasites, with up to three present. In females, there were up to four present. Mean length of the parasites declined as the number of parasites per individual ant increased. Head width was not affected by the presence of nematodes. The wing measurements showed severe reduction in size in both parasitized females and males. Thorax width, and femur length were significantly reduced in females but not in males. A Principal Components Analysis showed that the morphometric effects of mermithid parasitism were broadly similar in both females and males.

Queuing for dominance in a primitively eusocial wasp – *Liostenogaster flavolineata*

Catherine Bridge

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Liostenogaster flavolineata (Hymenoptera, Stenogastrinae) is a primitively eusocial wasp which exhibits an age-based queue for the inheritance of dominance i.e. the oldest individual upon the nest becomes the reproductive. However, unlike many other social insects, the chance of inheritance in *L. flavolineata* is relatively high because the groups are so small and its aseasonal environment allows for a long-term waiting strategy. While such queuing is a common phenomenon there are a number of reasons why such a system could become unstable. For instance, age-based queuing leads to a negative correlation between group size and a newborn helper's chance of inheritance. In effect, the chances of a newborn inheriting dominance on, for example, a five female nest are small. Such an individual is likely to die before reaching dominance. It seems likely that there would be some pressure for such a low-ranking wasp to 'queue-jump' to dominance. The stability of the queuing strategy in these wasps has never been confirmed. Therefore, I monitored 40 nests, following the progress of 68 known-age individuals. The age-based queue held true for the majority of nests. However, 8 queue jumping individuals were identified upon the nests. In 5 instances, the behaviour of the queue jumper was particularly aggressive compared to its nestmates. This suggests that their queue jumping behaviour may have been challenged. One might also expect size to be a significant factor in the ability of nestmates to jump the queue. However, there was no significant difference in the size of the queue-jumpers compared to fellow nest-mates. Currently, I am performing microsatellite analysis to examine whether the queue-jumpers were aided by their relatedness to nest members. A queue jumper which is closely related to fellow nestmates may be expected to face little opposition in 'jumping over' a less related individual as its role as reproductive will continue to boost the inclusive fitness of its relatives.

The evolution of defensive behaviour in Australian gall-forming thrips

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The gall-inducing thrips on *Acacia* provide a useful taxon for unravelling character states in the early steps leading to the evolution of eusocial organisation. Two distinct adult morphologies are found in some species of gall-inducers. One morph is characterised by reduced antennae and wings and greatly enlarged fore femora, and this form has been referred to as a soldier. This soldier morph is likely to be adapted for gall defence. Studies of these species have revealed considerable variation in life history and form of sociality. For example, the reproductive output of thrips soldiers between species spans the range from equivalent to that of the primary reproductive female to only a few parthenogenetically produced male offspring. Phylogenetic comparative studies enable one to infer ancestral states and test hypothesised patterns of evolutionary change that have led to extant levels of diversity. The utilisation of a well-supported phylogeny for the *Acacia* gall-inducers in combination with genetic and behavioural data has led to the inference that altruistic soldiers appear to have evolved from a non-dispersing, sib-mating, reproductive morph. Furthermore, using independent contrasts, a statistical analysis that incorporates phylogenetic information, a strong, positive, and significant correlation was found between the average volume of gall that a species makes and the number of offspring that soldiers produce. The implication is that as gall volume evolved to be smaller, presumably due to a trade-off between reduced brood size and increased gall survival, the amount of space available for soldier offspring was also reduced. That is, the smaller the gall the greater the reproductive sacrifice a soldier must make when fulfilling the role of gall defender. How were soldiers maintained in lineages where direct fitness was drastically reduced? A comparison of two species suggested that the lowering of direct soldier reproduction was compensated by a corresponding increase in survival of relatives from greater efficacy by soldiers in colony defence. However, a multi-species examination would allow for a more rigorous phylogenetic comparative test of this coevolutionary hypothesis. Using data collected for five species of gall-inducers, a strong but statistically insignificant correlation between soldier ability and reproductive output was found. The power and limitations of a comparative phylogenetic approach to testing evolutionary hypotheses and directing field-based studies will be discussed, particularly, in reference to this interesting group of social insects.

Fitness and selection in the life cycle of the western harvester ant *Pogonomyrmex occidentalis*

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Measuring selection in natural populations of social insects has not been commonly attempted. Part of the difficulty is that selection operates throughout the life cycle of any organism. For long-lived, iteroparous ants, there are few studies where we are able to follow episodes of selection throughout the life cycle. We will argue that considering selection operating on a single stage in the life cycle can lead to misinterpretations of the importance of any particular selective event.

We will discuss the life cycle of *Pogonomyrmex occidentalis* from a long-term study of a population in western Colorado. In this population we have followed demography, growth and reproduction for 12 years. We have collected reproductive data for up to 10 years in a subset of colonies. Using these data we have identified several key selective episodes during the life cycle of the western harvester ant. For males, the major influence on fitness is the number of times that they mate. This is influenced by the size of the males and therefore is related to the pattern of investment in the parental colony. The queens, who can live for as long as 40 years, have a more complicated pattern of selection. During the colony founding stage, larger queens survive better than smaller queens. Again, this is a function of the patterns of investment in the parental colony.

The crucial event that influences survival, growth, reproduction and ultimately colony fitness is the frequency of mating by the queen. Queens of *P. occidentalis* mate large and variable numbers of times (average 6.3, range 2-11). Mating frequency determines the genetic diversity of the colony and therefore a cascading sequence of effects that are related to division of labor. Increased genetic diversity leads to increases in the time that colonies are active. This, in all probability, leads to increased time for foraging. Genetic diversity is also related to increased colony growth rate. Increased colony growth rates lead to increased survival probabilities. Genetic diversity in colonies is therefore related to colony size. Because colony size is related to the output of reproductives, genetic diversity is ultimately related to reproductive output of colonies. It is possible to measure standard quantities such as the selection gradient using these data.

Finally, we consider the fitness benefits to males and females of mating multiply. We will consider how selective events throughout the life cycle of harvester ants select for the promiscuous mating system of this group.

Nesting biology of the fungus grower ant *Mycetophylax simplex*

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The ant genus *Mycetophylax* is commonly found in arid zones of the extra-tropical South America and together with *Mycocepurus* is considered among the Attini as the only genera specialized in arid zones with low plant cover (Mayhé-Nunes 1995).

The study site (29° 20' S, 49° 43' W) of *M. simplex* is a narrow band of coastal sand dunes ca. 300 m far from the shore in Torres, littoral of the Rio Grande do Sul State, southern Brazil. Plant cover is scarce and composed by indigenous grassy.

There is no difference between the color of the sand dunes and the sand deposited by the ants on the soil around the hole. In all nests of *M. simplex* evaluated only one passage hole was present, located on the top of a small sand tower or arranged around the hole like a circle or a semi-circle. Per nest, two to three chambers were found, shaped like a rounded triangle. The depth of the chambers varied from 4.0 cm to 25.0 cm bellow the surface. The last chamber was always greater than the one before and as the depth increased the volume of the chambers increased too. The fungus garden was located above the bottom of the chambers. The workers were distributed through all chambers. Per colony, from 60 to no more than 700 workers were found, variation that could be due to activity period or colony age.

The males and gynes were located in the deepest chambers. In two nests more than one dealate female were found, which could be gynes that had just lost their wings. However, their body dark color indicates they are older, suggesting the occurrence of polygynous colonies in *M. simplex*. New individuals from the reproductive caste were found from December to February indicating that the period of sexual production could be during summer. Comparing the two greatest intra-nest populations (sterile and sexuals), we can see that the nest presenting alates had bigger chambers than the other that presented no alates. This is probably reflecting the increased need for room for males and gynes. So, the period of sexuals production cause some changes in the architecture of the nest.

In all seasons the night seemed to be the period of greater foraging activity, even though some workers were collected during early morning and other periods of the day.

Since a great amount of the studied site are flooded during winter, it was evaluated the number and distribution of the nests during the summer in four plots of 2,500 m² each one. The plots have 20, 209, 284 and 324 nests, respectively 0.01 nest/m², 0.09, 0.11 and 0.13 nest/m². The nest positions showed that the colonies have clumped dispersion.

Financial support: CNPq, FAPERGS, UNISINOS.

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Mayhé-Nunes, AJ (1995) Filogenia de los Attini (Hym., Form.): un aporte al conocimiento de las hormigas fungívoras. Doctoral thesis, Universidad Simón Bolívar, Venezuela.

Adaptation of the brood cycle by *Myrmica* ants in order to exploit habitats having cold, fluctuating seasonal climates

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Ants can adapt in two non-exclusive ways in order to survive in cold environments that have a short summer season: they can either (1) speed-up their brood cycle by evolving a variety of physiological and behavioural adaptations, such as greater metabolic rates so that they grow and develop faster at ambient temperatures or adaptation of nest structure to increase ambient temperatures; (2) adjust their brood cycle so that larvae become long-lived and complete their development over two or more summer seasons. Ants of the genus *Myrmica* can live in the semi-desert steppe zones in southern latitudes and in the northern tundra zone and frequently dominate many of the habitats in between. In this paper I will explore some of the life-cycle adaptations shown by *Myrmica* and discuss how these relate to the ant's social-physiology.

Queen longevity on nests and seasonal life cycles in *Polistes* wasps (Hymenoptera: Vespidae) in Southern Ukraine

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The main factors determining the *Polistes* wasps colony cycle timing in the temperate zone are considered to be queen's activity, age and physiological state of workers (Grechka, Kipyatkov, 1983; Deleurance, 1955). The nest foundation in *Polistes dominulus* on plants takes place usually earlier than in *P. dominulus* in shelter, *P. gallicus*, and *P. nimpha*. The duration of the colony cycle of every species under study is not stable in different years. The same can be said about the separate periods of the colony development (they are (Reeve, 1991): founding phase, worker phase, reproductive phase, intermediate phase). Negative correlation is found between every part of colony cycle. Queen survivorship in colony was very changeable in different years (1995–98, 2002–03). *P. dominulus* queens from haplometrotic colonies on plants demonstrate a tendency for a longer life than those in shelter. When nesting on plants, the *P. dominulus* queen from haplometrotic colonies lived significantly longer in 1997 and 1998 in comparison with 1996 ($p < 0.01$). In *P. dominulus* in shelter queen from haplometrotic colonies disappeared, on the average, earlier in the season than the queens from pleometrotic ones. But valid differences were marked only in 1997. When nesting in shelter, interspecies differences were discovered in 1997. *P. nimpha* queens survived in the colony considerably longer than *P. dominulus* ones. In 1997, survivorship of the queens of *P. gallicus* on plants was considerably longer (61 ± 2.9 days) than of *P. dominulus* (54.1 ± 1.6); it was the other way round in 1998 (23.7 ± 6.9 and 53.8 ± 2.9 respectively). Solitary queens, when nesting on plants, rear more larvae before worker emergence than they do when nesting in shelter. After queen disappearance from the nest, colonies of *P. gallicus* and *P. nimpha* continue their activities more often than colonies of *P. dominulus*.

Defending the fortress: the behavioural ecology of social aphids

William Foster

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Aphids are of exceptional interest to the student of social insects since they include the only eusocial animals that are clonal. Their clonality also makes them intriguing to evolutionary biologists in general, since the emergence of cooperation among clonal individuals lies at the root of the origin of multicellularity, one of the major events in evolutionary history. The social aphids therefore provide a splendid model system in which to examine the issues of cooperation, conflict, and control that underlie the evolution of sociality in general.

The social aphids also provide a compelling range of practical advantages for those interested in the evolution of sociality:

- ✓ they are easy to rear, on either plants or artificial diets
- ✓ they are small enough to be obtained in very large numbers, but large enough to study as individuals
- ✓ the phylogeny of many of the major groups is already known
- ✓ there have been many independent origins of sociality within the aphids, allowing robust comparisons to be made
- ✓ the genetic structure of individual colonies is, in principle, relatively simple.

In this talk I will outline the basic biology of the social aphids; discuss how we may account for the observed distribution of sociality within the aphids, paying particular attention to the importance of life-history; and finally consider possible future developments in the study of sociality in aphids.

The social aphids are rare: only about 1% of the 4500 species have soldiers. They are confined to two subfamilies, the Pemphiginae and the Hormaphidinae, which belong to the same clade within the Aphididae. Sociality has evolved independently at least 17 times within these two subfamilies, and the weapons and behaviour used by the soldiers are impressively diverse. All the aphid species that have soldiers form galls at some stage during their life cycle. The distinctive feature of all social aphids is the occurrence of a soldier caste; these are defensive morphs, usually early instars (firsts or seconds), they may be obligately sterile, they act to defend the clone, and their production imposes a cost on the clone. They engage in a range of altruistic activities, including fighting, gall-cleaning, dispersal and gall repair.

How can we explain the observed distribution of aphid sociality? This can be split in to two parts:

1. Why are all the known social species restricted to the Hormaphidinae and Pemphidinae?
2. Why does only a minority of species within these two subfamilies have soldiers?

The answer to the first question is almost certainly to do with the fact that these two subfamilies are gall-forming. The gall acts as a fortress, which selects for soldierliness both indirectly, by promoting traits to do with fighting for gall-initiation sites and to do with intergall migration, and directly, by promoting traits relating to gall defence and gall cleaning, and by tending to preserve the genetic integrity of the clone.

But gall-living does not provide a complete explanation for the observed distribution of aphid sociality: most of the gall-living species in these and other subfamilies do not have soldiers. The explanation needs to be sought in the application of Hamilton's Rule to a range of species. The genetic preconditions for sociality seem very strong: providing a colony is a pure clone, any helping behaviour that delivers benefits that exceed the costs will be selected for.

There are at least two general reasons that will select against the evolution of soldiers. First, clonal mixing, even within galls, might be quite high. Recent evidence from work by Abbott and co-workers on *Pemphigus obesinymphae* shows that up to 38% of the aphids in galls may be from alien clones. This study also showed that the intruding aphids cheat on the host clone by not helping in gall defence and instead investing in their own growth and reproduction. Second, the ecology of a species, in particular life-history effects, will have a major influence on whether the costs of investment by the clone in soldiers might indeed exceed the defensive benefits the soldiers provide. For example, the duration of the gall, the extent of predation, the growth rate of the colony, and whether the aphids are ant-tended might all influence the selective value to the clone of investing in soldiers. I will discuss these factors, with particular reference to recent work on the genus *Pemphigus*.

Important future developments will include the elucidation of the genetic basis of the soldier polymorphism in the context of aphid polymorphism in general; the detailed understanding of the developmental biology of aphid soldiers; and a description of the genetic structure of the aphid colonies that occur on the secondary host, which are the only social insect colonies that are not protected within some kind of nest or fortress. Social aphids provide biologists with a rich source of evidence about the evolution of sociality, which we are only just beginning to explore.

High reproductive skew and low queen turnover in the facultatively polygynous ant *Pheidole pallidula*

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Reproductive skew – the extent to which reproduction is unevenly shared between individuals in a social group – varies greatly between and within animal species. In this study, we investigated how queens share parentage in polygynous (multiple queen) colonies of the Mediterranean ant *Pheidole pallidula*. We used highly polymorphic microsatellites markers to determine parentage of gynes, males and workers.

The comparison of the genotypes of young and adult workers revealed a very low queen turnover. The main finding of this study was that there was a significant departure from equal contribution of queens to gyne, male and worker production. Reproductive skew was greater for male production than for gyne and worker production. There was no relationship between the magnitude of the reproductive skew and the number of reproductive queens per colony, their relatedness and the overall colony productivity, some of the factors predicted to influence the extent of reproductive skew. Finally, our study revealed for the first time a trade-off in the relative contribution of nestmate queens to gyne and worker production. The mothers contributing more to gyne production contributed significantly less to worker production.

Division of labour and its regulation in a primitively eusocial wasp

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Social insect species that exhibit overlap of generations, cooperative brood care and reproductive caste differentiation have been termed eusocial. Among these, those that also exhibit morphological caste differentiation are termed highly eusocial while those that have morphologically identical queen and worker castes are termed primitively eusocial. Because queens and workers are not morphologically differentiated in primitively eusocial species, caste differentiation is often post-imaginal. The processes by which some individuals succeed in becoming reproductive queens while others end up as sterile workers in primitively eusocial species is of obvious interest. Such post-imaginal reproductive caste differentiation is absent in highly eusocial species because reproductive caste differentiation in these species is usually pre-imaginal. On the other hand, further differentiation of the workers into different kinds of task specialists is a phenomenon that has been extensively studied in highly eusocial species (Wilson, 1971). There has seldom been an opportunity to study both post-imaginal reproductive caste differentiation as well as post-imaginal division of non-reproductive labour in the same species because these two phenomena usually do not occur in the same species.

Ropalidia marginata is an old world tropical primitively eusocial wasp widely distributed in southern India. Although classified as primitively eusocial by the traditional criteria of overlap of generations, cooperative brood care, reproductive caste differentiation and absence of morphological differentiation between queens and workers (Gadagkar, 2001a,b), *R. marginata* appears to have acquired some features resembling highly eusocial species. One such feature concerns the mode of division of non-reproductive labour among the adult wasps. *R. marginata* exhibits a remarkably well-developed honeybee like age polyethism. Workers show a strong tendency to feed larvae, build the nest, forage for pulp and forage for food, in that order, as they age. The frequency and probability of performance of different tasks is strongly influenced by the age of the individual. However, the relative position of a wasp in the age distribution of the colony, rather than her absolute age, is a stronger predictor of her task performance. Soliciting behaviour (a form of trophallaxis) provides a plausible mechanism for the wasps to assess their relative ages (Naug and Gadagkar, 1998a).

Like in the honeybees, age polyethism in *R. marginata* is very flexible and this flexibility comes from the fact that workers are allocated tasks based more on their relative age rather than their absolute age. This can be demonstrated experimentally by creating artificial colonies containing only young individuals (young cohort colonies) or containing only old individuals (old cohort colonies). In young cohort colonies, precocious foragers, i.e., some individuals who begin to forage at an early age when they would not do so in normal colonies, compensate for the absence of older individuals (Naug and Gadagkar, 1998b). In old cohort colonies, hard working nurses, i.e., some individuals who feed larvae at rates higher than they would in normal

colonies, compensate for the absence of younger individuals (Agrahari and Gadagkar, submitted).

Juvenile hormone modulates post-imaginal reproductive division of labor in primitively eusocial species and promotes the production of queens (e.g., *Polistes*) while it modulates age polyethism and promotes the production of foragers in highly eusocial species (e.g., the honeybee). Since *Ropalidia marginata* shows both post-imaginal regulation of reproductive division of labor as well as age polyethism, it is a particularly interesting model system to study the effect of juvenile hormone. A single, topical application of 100 µg of juvenile hormone-III per female wasp accelerates ovarian development of wasps held in isolation. Similar application to wasps released back on to their natal nests has no effect on their rate of behavioral development as witnessed from the age of first performance of feed larva, build, bring pulp and bring food. It appears therefore that in *R. marginata*, juvenile hormone has retained its function of modulating reproductive division of labor and has not acquired the function of modulating age polyethism (Agrahari and Gadagkar, 2003).

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Does the feeding of *Ulex* elaiosomes to *Myrmica ruginodis* colonies affect the sex ratio of larvae?

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Myrmecochorous plants have a mutualistic interaction with ants. Their seeds have elaiosomes: appendages rich in fats, sugars and other nutrients (1). Elaiosomes are attractive to many ant species and are thought to be an adaptation which induces the ant to disperse the seed (2). To date studies have concentrated on how the plant benefits from the mutualism, such as dispersal distance (3), predator avoidance (4), interspecific competition (5) and dispersal to nutrient-enriched sites (6). Few studies have measured the benefit to ants, which is generally assumed to be the nutrient reward from the elaiosome. A previous study has suggested that ant colonies fed with elaiosomes produced more female reproductives than control colonies (7,8). We carried out an experiment to investigate this possibility.

Ulex species have seeds with elaiosomes, which are attractive to *Myrmica ruginodis*. We fed *U. minor* and *U. europaeus* seeds to ten *Myrmica* colonies, while ten received no seeds. Each set of ten colonies comprised five which had one queen and 200 workers (no brood), to investigate how feeding newly-laid larvae with elaiosomes affects the sex ratio produced after one full season. The remaining five colonies had 200 workers and 200 brood to investigate how existing brood are affected by the feeding with elaiosomes.

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Trait of life of a soil-feeding termite: evidence of reproductive distortion

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In tropical ecosystems, termites represent a significant part of the fauna biomass and exhibit four broad trophic groups, soil-feeders, soil/wood interface feeders, wood feeders and litter foragers including fungus-growers. The change from wood to soil-feeding is a major evolutionary shift that has triggered the diversification of the higher termites (Termitidae family). However, very few studies have been devoted to the ecology and genetics of these diploid and social insects, which comprise about 2,600 species. Particularly little attention has been devoted to soil-feeders (60% Termitidae). Ecologically, soil-feeding termites play a major role in tropical ecosystems by dramatically modifying the chemical and physical soil properties resulting in an increased fertility of soils. Our aim was to document a particular trait of life of these insects that is the nest foundation by the study of the population and reproductive structure of the nest.

In an ecological and phylo-geographical study performed in the Lopé forest reserve in Middle Ogooué in central Gabon, we sampled 70 *Cubitermes* nests. Among them, 42 were inhabited by *C. subarquatus* including 11 occupied byinquilines up to 8 different genera. A total of 19 inquilines genera were recorded belonging to various trophic groups. Moreover, on 30 nests examined for reproductives, only 33 % corresponded to the classic scheme of the "royal couple", but 23 % were polygynous and polyandrous, 13.5% strictly polygynous, only 3.5 % strictly polyandrous and 27% were inhabited by a single female without male.

Microsatellites were used in order to test the contribution of the reproductives to the offspring and to assess the genetic structure of the nests. A significant deviation from Hardy-Weinberg equilibrium at most of the loci was recorded. Such variations may be a consequence of the inbreeding, substructuring of the sample (Wahlund effect), or due to the occurrence of an evolutive force susceptible to introduce a sex-ratio distortion or panmixy deviation.

In this respect, we have studied *Cubitermes* individuals coming from 22 different nests to test the presence of *Wolbachia*, an endosymbiotic bacteria, host reproductive manipulative, described to provoke sex-ratio distortion (feminization of genetic males, male killing, parthenogenesis) or cytoplasmic incompatibility which results in partial or complete reproductive failure between individuals differently infected by *Wolbachia*. PCR-amplification of *wsp* gene revealed the occurrence of *Wolbachia* in 77% nests including a total of 83% queens infected and only 26% kings. As no nest with only infected kings was found and the high proportion of females infected, unidirectional cytoplasmic incompatibility is more probably the phenotype induced by the bacteria. Genetic studies are currently undertaken in order to correlate *Wolbachia*'s infection and population structure.

Life in a nutshell – the social structure of *Leptothorax* ants

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Ants are ubiquitous, they play an enormous role in most terrestrial ecosystems and exhibit huge interspecific variation in many fundamental traits of their life histories. For example, colony size at maturity ranges from less than 10 to several 100 Million individuals. The causes underlying this variation are not well understood, and social insects in general are only rarely mentioned in leading textbooks on life history evolution. Obviously, both empirical and theoretical research is needed for a better understanding of life history evolution in social insects.

Leptothorax are small myrmicine ants that inhabit preformed cavities in the soil, decaying wood, or rock crevices. Average colony size varies little between species, but other important traits, such as average queen number per colony, the degree of reproductive skew, the amount of worker reproduction, and the origin of new colonies, may differ strikingly even among populations within a single species. For example, queens in colonies of *L. muscorum* and *L. canadensis* contribute more or less equally to the colony's offspring (polygyny), nestmate queens of *L. gredleri* and *L. sp.* A form hierarchies, in which the top-ranking queen monopolizes reproduction (functional monogyny). In *L. acervorum*, queen number and the degree of reproductive skew differ between populations, with some populations being almost completely monogynous, others polygynous, and still others facultatively monogynous.

Due to their small colony size, the easiness with which complete colonies can be collected, and the well established protocols for rearing them in the laboratory under near-natural conditions, *Leptothorax* provides a suitable model system to investigate ultimate and proximate aspects of life history variation.

Available information on colony structure in *Leptothorax* match predictions from concession models on optimal skew, according to which reproduction is more unevenly partitioned among queens at higher ecological constraints (Bourke AFG, Heinze J, 1994, Phil Trans R Soc Lond B 345: 359–372). Furthermore, recent investigations suggest that, again as predicted by these models, the presence of subordinate queens in high skew societies somehow increases the reproductive output of the dominant and thus of the colony as a whole. Relatedness, on the other hand, apparently plays only a minor role in the determination of skew, perhaps because in most natural cases queens are on average close relatives.

Absconding, migration and swarming in honeybees: an ecological and evolutionary perspective

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Absconding, migration and swarming among the species of honeybees immediately reflect striking differences as to the extent of resource investment in reproduction and colony mobility. Swarming, absconding and migration are traits correlated with geographic variations in climate and flowering. Adaptations to climatic differences are ubiquitous in honeybees and different constraints operate on open-nesting (*A. florea*, *A. andreniformis*, *A. dorsata* and *A. laboriosa*) and cavity-dwelling (*A. cerana*, *A. koschevnikovi*, *A. nigrocincta*, *A. nuluensis* and *A. mellifera*) species.

The terms "swarming, absconding and migration" are historically conflated for a spectrum of overlapping phenomena. Reproductive swarming is the movement of a queen and part of a honeybee colony from the maternal nest to a new site for colony reproduction. Migration differs from swarming in that neither queens nor drones are produced for the nest is abandoned. Migration is a resource-related, seasonally predictable movement of a whole colony from one region to another; and, a return journey is not an essential requirement. When resources deteriorate, small colonies move. Larger colonies may expand the forage area because small increases in radius result in large area gains for little additional flight costs. In tropical and subtropical areas reproductive swarming varies within species in relation to climatic circumstances and may be continuous throughout the year, occur in a single season like springtime or be biphasic.

Migration is a strategy to maximize the discovery of new sites for colonization. It may serve as a spatial re-fuelling cycle, not necessarily associated with colony reproduction. However reproductive swarming often follows migration in a new location where more favourable conditions exist. Given equitable temperatures for flight and perennial flowering in tropical climates, migration is an evolutionary alternative to massive hoarding characteristic of temperate bees.

Distinctions between migration and absconding were formerly based on the tacit assumption that migration involved very many colonies and absconding but few. Absconding also entails nest abandonment of a whole colony but there are two kinds of absconding: "prepared" and "simple" absconding. The former results from chronic disturbance/predation, declining nest quality, and sustained resource depletion. Like migration, it is predictable because prior to actually absconding, brood, honey and pollen stores all decrease and foraging is reduced. Simple absconding is the response of whole colonies to disasters: fire, floods, and severe predation. Small, newly settled colonies abscond at the least disturbance, larger ones require major interference. Both are less prone to abscond in the ascendant phase of a nectar flow. Migration is essentially synonymous with prepared absconding.

The literature overwhelmingly supports three primary stimuli for prepared absconding or migration: (1) resource depletion – dearth from either extended dry or wet (monsoon) conditions resulting in loss of adequate forage; (2) deterioration of the microclimate of the nest; (3) the persistent infestation and/or disturbance by pests and predators. No specific factor need be unique, nor are multiple stimuli mutually exclusive.

While an absconding or migrating colony could strike out in random directions, essentially leaving their future resource fate to chance, directions of real colony movements to survive dearth periods will likely vary under different types of vegetative resource distributions under different climatic conditions. In tropical areas where resources are patchily distributed but seasonality is low, then a draughts-board solution of colony movement enhances the odds of finding suitable new forage areas. Where vegetative resources occur in larger patches and seasons alternate between wet and dry phases, a direction strategy similar to the tropics is preferred, but distance will be greater. Under temperate conditions with seasonality and a cold winter, prepared absconding or migration are extremely rare.

Desertion of the nest and successful re-establishment elsewhere requires, on a priori grounds, that the bees have sufficient flight fuel and sufficient reserves of energy to construct new combs when they have settled. Absconding colonies typically show a marked increase in the average mass of the honey stomach and engorgement precedes absconding and migration. The amount of wax scales produced in such colonies before moving is twice that of settled colonies. Although a rate mechanism for wax synthesis has not yet been determined, the greater the engorgement of the honey stomach, the greater the wax produced. Thus substantial wax reserves are produced before leaving the old nest.

Small swarms of bees may amalgamate to form polygynous groups. This phenomenon, rarely reported for temperate bees, is commonplace in Asia and Africa and may range from the merger of two queenright swarms to an extraordinary mega-swarm of several hundred queens. These mega-swarms maintain themselves for months by the continual absorption of small absconding or dwindling colonies. These additions replace bees lost in fighting and bring nectar, which they are induced to disgorge. Amalgamation varies in that there is sometimes fighting and sometimes not.

In any event, an almost universal feature of polygynous swarms that eventually settle in a cavity, or are hived, the supernumerary queens are almost always killed, thus restoring monogyny. Amalgamation may occur with or without fighting and conglomerates are unstable until the supernumerary queens are eliminated. Supernumerary queens are eliminated by balling. Amalgamation may favour the genes of a queen whose colony is better at invasion than at stockpiling food or foraging. The possible interplay of pheromones under conditions of amalgamation remain totally enigmatic.

Amalgamation of small swarms (migratory and/or reproductive swarms) into conglomerates provides an immediate solution to building up colony population and reducing *pro rata* costs of survival. Evolutionarily, it also has the effect of directing the energies of non-viable units towards survival of a large social unit. The greater the genetic diversity, the greater the averaging effect on phenotypic behaviour thus effectively enlarging the polyandric mating base, hence patrines, of conglomerates formed by amalgamation.

Once the migrating colony has begun its journey its fate is uncertain, and obstacles to success are evident. The bees must have sufficient fuel, access to flowers along the way, and

the cost of the journey will vary with flying times and speed, distance flown, and ambient temperatures and wind velocities. Calculations provide relevant cost estimates for these journeys. Medium-sized engorged workers carry a maximum sugar fuel load of about 300 J if fully laden. The average worker metabolises about 1 J/h/bee at rest or about 200 J/h/bee for rapid sustained flight. Fuel stores and flowers along the way yield about 30–90 minutes of flying time for a flight range of 15–36 km, distances known for moving swarms.

Protein reserves also come into play. Reduction in egg-laying commonly precedes migration and serves as a protein conservation strategy/mechanism by queens. Likewise, worker bees commonly eat all eggs and most sealed brood before leaving the nest. Thus full preparation for migration includes elevated wax production, increased protein uptake and massive fuel intake.

It is also necessary to consider one of the "grey" areas associated with swarming and supersedure. These are conditions in the colony, which involve polygyny and, ultimately, the elimination of supernumerary queens. In the natural course of swarming in some species the old queen may be present with a new queen for some months and this constitutes failed swarming. In such cases failed swarming becomes successful supersedure. This implies that if the "swarming" event occurs the associated mating flight is taken by the young queen from the natal colony and mating must be successful before either queen departs in a swarm. Failed reproductive events are indicated by the presence of queen cells without continuity in egg-laying (queen was not successfully mated).

Queen replacement based on the eggs of laying workers may arise following queen loss during mating or in supersedure but is relatively rare. Nonetheless, this thelytokous parthenogenetic trait remains entrenched in the gene pool and, given the appropriate colony conditions (supersedure or queen loss), is readily expressed in one species. In genetic models of this trait the thelytoky gene persists even though only a small percentage of colonies produce queens in this way. The gene frequency for thelytoky may be remarkably high and exist in a stable, polymorphic equilibrium supported by unusually high multiple matings. Alternatively, it could be argued that such allelic differences could be rapidly selected against unless their effects on the overall phenotype were small.

Life history transitions in social wasp evolution

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Changes in life history parameters mark major milestones along the route to sociality in vespid wasps. In an idiobiont parasitoid lineage, the ancestral proto-vespid evolved nesting behavior, central place foraging, and oviposition into an empty nest cell. Simultaneous progressive provisioning of differently aged larvae set the stage for sociality. Inter-individual variation in development, due in part to differences in larval provisioning, then yielded first brood offspring workers like those that characterize *Polistes*-grade sociality. Precursors of many of the key components of *Polistes* life history can be seen among Stenogastrinae. Evolution of workers precipitated a major shift in demography. Whereas solitary wasps have high probability of low fitness, *Polistes* wasps have low probability of high fitness. These different life histories have corresponding differences in strength of selection on life history traits. Strong selection on proto-*Polistes* wasps could have led quickly to traits such as protogyny (enabled by haplodiploidy), pleometrosis, and some specific behaviors associated with larva-adult trophallaxis. Evolution of Vespine-grade sociality from *Polistes*-grade sociality reflects emphatic selection favoring workers as first brood offspring and underscores the adaptiveness of *Polistes*-grade sociality. A second major life history transition was the evolution of swarm founding, which occurred independently several times in vespids. It marks transition to a life history characterized by few propagules but high probability of persistence of individual colonies (although not necessarily nests). Thus the first major life history transition in vespid social evolution, from solitary to social, has great disparity in reproductive success among independent foundresses as one of the most salient features. The second major life history transition, from independent to swarm founding, has colony persistence among wasps that were already social as its most salient feature. Multiple analogies can be drawn between the evolution of sociality in insects and the evolution of multicellular individuality in eukaryotes.

Life history issues in social wasps, particularly the swarm founders

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In 1964 Charles Michener published a paper entitled 'Reproductive efficiency in relation to colony size in hymenopterous societies.' Using data on a variety of bees, wasps, and ants from the published literature, he plotted colony productivity, measured as number of immatures in the nest, as a function of colony size, in numbers of females. For most species, the larger the colony the lower the productivity per female. This relationship is sometimes referred to as "Michener's paradox" because, other things being equal, it should select for smaller, more efficient, colony size. In spite of the fact that little effort has been made to corroborate Michener's pattern since it was first proposed, it has hardly been questioned. Michener recognized that colony size is closely correlated with the stage of colony development. Therefore, in selecting published data to include in his analysis he was careful to control for ontogenetic effects on size by including in his survey only colonies collected within narrow seasonal limits. When it came to his analysis of the tropical swarm-founding social wasps, however, this criterion failed, because colony cycles of these wasps are not seasonally synchronized. Thus, the ontogeny effect was not controlled for, and in fact colony stage varied widely among colonies in the datasets he used. We show for two species of swarm-founding wasps that when stage of colony development is held constant per-capita productivity is independent of colony size. We conclude that the pattern Michener reported for these wasps was due largely to ontogenetic effects and to differences among species, rather than to decreasing 'efficiency' with increasing group size.

Reproductive strategies in termites: sociobiology versus ecology

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The theoretical background for the study on reproductive conflict in social insects relies on the haplo-diploid genetic system of Hymenoptera, primarily of ants. This genetic structure results in a relatedness asymmetry among nestmates: relatedness within the unisexual progeny of the reproductives is higher than between the generations (Hamilton 1964, *J Theor Biol* 7, 1–52). High relatedness – a key parameter in insect societies – gives rise to co-operation over conflict, especially in colonies with only one reproducing female (queen, monogynous) and one reproducing male (king). In contrast to ants, however, all termite species are diplo-diploid and develop steriles of either sex. In addition, polygyny is rather frequent: several reproducing females (nestmate queens) co-exist in a colony (polygyny). Hence and in contrast to Hymenoptera, a priori relatedness asymmetry should not be found in termites and the mean relatedness might be low among nestmates. Nevertheless, all living termite taxa are eusocial. To apply the hypotheses developed for social Hymenoptera to the termites it has been suggested that inbreeding cycles within a termite colony would result in homozygosity and thus relatedness asymmetry would develop in colonies founded by unrelated but homozygous alates (Bartz 1979, *Proc. Natl. Acad. Sci. USA* 76, 5764–5768). Furthermore, for polygynous termite colonies it has been postulated that nestmate queens are related as co-operation is predicted to be more likely among relatives compared to non-sibs. In contrast to Hymenoptera, so far little is known about reproductive conflicts and the genetic background of termite colonies, in particular in polygynous ones. Hence, in our studies we compare in termites the within-colony genetic structure, and the origin and consequences of polygyny. We focus on two distant termite taxa living in contrasting environmental conditions. Relationship, ecological factors, and the occurrence of polygyny in termites will be assessed.

Schedorhinotermes lamanianus (Rhinotermitidae) is abundant in humid lowland forests in Africa. It is a subterranean species feeding on wood. In its habitat wood is a permanently available and almost unlimited food source. Colonies can be easily spotted due to their foraging galleries on trees. Young colonies are strictly monogynous with an unrelated pair of sexuals. During maturation the colonies become polycalic with numerous secondary queens in subsidiary nests. Polygyny apparently develops when the primary queen loses physiological control of the entire wide-spread colony. Despite of the termites' ability to recognize kin (Kaib *et al.* 1996, *Proc Roy Soc London B*, 263, 1527–1532) we have strong evidence that among nestmate queens no reproductive dominance develops – all nestmate queens are functional. Nestmate queens in polygynous colonies are daughters of the colony founding queen and king (Husseneder *et al.* 1999, *Behaviour* 136, 1052–1063). Thus, we do not find evidence for high levels of inbreeding, which eventually could lead to homozygosity in alates and thus relatedness

asymmetry in newly founded colonies. Hence, relatedness asymmetry does not develop in *S. lamanianus* colonies.

Macrotermes michaelseni (Termitidae) is a fungus growing termite abundant in semi-arid savannahs of eastern Africa. It feeds on dry grass, an over time strongly fluctuating food source. Neighbouring colonies compete for food (Kaib *et al.* 1997, *Mitt. Dtsch. Ges. allg. angew. Entomol.* 11, 189–192). In newly founded *Macrotermes* colonies, polygyny is frequent (Darlington 1985, In: *Caste differentiation in social insects* (JAL Watson, BM Okot-Kotber, C Noirot, eds), Pergamon Press, Oxford. pp 187–200; Korb, pers. comm.). Queens in polygynous colonies are typically primary, unrelated and of about the same age, which provides strong evidence that polygyny is based on pleometrosis. During early colony development, the frequency of polygyny becomes reduced. Compared to queens in mature monogynous colonies the queens in mature polygynous colonies show a higher level of mutilation, and we suggest that in young colonies the reduction in the number of queens is the result of within-colony conflict and thus is moulded by sociobiological processes. Hence, polygyny may be correlated with factors related to early colony age.

In mature *M. michaelseni* colonies, the number of eggs laid per queen is proportional to her body weight. In polygynous colonies, all nestmate queens are functional but there is evidence for conflict. When monogynous and polygynous colonies of equal age are compared, queens in a polygynous colony have lower body weight. Hence, an individual queen in a polygynous colony lays less eggs and thus loses reproductive potential. However, on the colony level, the overall reproduction in polygynous colonies is higher compared to that of monogynous colonies (Kaib *et al.* 2001, *Insectes Soc* 48, 231–237). Polygyny increases the competitive power and the work force of a colony, which may result in a differential and higher survival rate of polygynous colonies compared with monogynous colonies.

The percentage of polygynous *M. michaelseni* colonies in a population varies also across time and space. In semi-arid savannah ecosystems ecological conditions strongly fluctuate as primary production depends on rainfall. *Macrotermes* species utilise dry grass which grew during previous wet seasons. The frequency of polygynous colonies is negatively correlated with the annual rainfall, and hence with the fluctuating availability of food. Furthermore, polygyny increases towards the species' distributional borders where the environmental conditions become harsher (Brandl *et al.* 2001, *Insectes Soc* 48, 134–137). There is evidence that in mature colonies adverse environmental conditions force unrelated queens to co-operate. However, when environmental conditions improve, within-colony conflicts may dominate over co-operation and may lead to an elimination of queens. Hence, the resource availability seems to mould the level of conflict within polygynous colonies.

In conclusion, we suggest that in young colonies sociobiological processes and in mature colonies physiological and ecological factors control conflict and co-operation in termite colonies. Furthermore, we conclude that in termites ecological rather than genetic factors favour sociality.

Patterns and constraints in the evolution of seasonal life cycles in boreal ants: ecophysiological and sociobiological approach

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In a pioneering study of life history evolution in social insects Oster and Wilson (1978) primarily concentrated on the scale and timing of the allocation of resources between worker and sexual production. For perennial species, such as ants, they predicted so-called "*bang-bang*" strategy which maximizes colony's fitness (i.e. sexual production) by alternation ergonomic and reproductive phases within each year. The ergonomic phase within a season should be as long as possible so that more workers are available to raise the largest number of sexuals during the second part of the year. Since then little attention has been paid to the role of seasonality in life history evolution in ants (e.g., Bourke & Franks, 1995).

Our field and experimental data on more than 70 ant species belonging to 21 genera and 4 subfamilies collected during many years and the thorough analysis of literature allowed us (Kipyatkov, 1993, 1996, 2001) to conclude that most temperate ants evidently differ in seasonal timing of worker and sexual production from the predictions of Oster and Wilson. *First*, most species raise their alate reproductives not in late summer after the worker brood is already produced, but quite the reverse – just after the overwintering. *Second*, the production of sexuals is always accompanied by rearing of workers which can emerge even in greater numbers than winged reproductives, i.e. a complete switch from worker to alate production does not in fact occur.

Thus, most temperate ants use *the strategy of preceding production of sexuals* in their annual cycle (Kipyatkov, 1996, 2001), which means that the colony's annual cycle should be organized in a way to maximize the quantity of diapause larvae and new workers produced by the end of each brood-rearing season. These workers will facilitate colony's winter survival and will rear alates next spring. For this purpose the brood-rearing should start in spring as early as possible and continue as long as possible. At the same time the brood stages and adults present in a colony by the end of warm season should be able to survive during long and cold winter. This is why most temperate ants have evolved appropriate forms of winter dormancy and efficient mechanisms controlling the onset and completion of diapause at the proper time (Kipyatkov, 1993, 2001).

Temperate ants use two main *seasonal strategies of brood-rearing* (Kipyatkov, 1996). The most widespread is *the strategy of prolonged brood-rearing* distinguished by delaying development of a large proportion of larvae (so-called *slow brood*) which continue to grow in autumn, overwinter in diapause and pupate during the next summer yielding alates and workers. Only some larvae develop from egg to pupa within the same summer season without overwintering (so-called *rapid brood* that yields only workers). This strategy has evident

advantages important for adaptation to temperate and boreal climates (Kipyatkov, 1993, 1996): (1) the larvae can be reared from early spring up to late autumn thus utilizing the whole warm period of a year; (2) the quantity of rapid brood can be changed to adapt to long-term and short-term climatic variations and to the duration of the warm season.

The strategy of concentrated brood-rearing is employed mostly by species of the tribe Formicini. The development of all brood stages is restricted to the warm season in these ants. Only queens and workers are able to diapause. Larvae have no dormancy and all finish their development during the summer, all sexuals and new workers emerge from pupae until autumn cold weather and colonies overwinter without brood. Evidently, this is only appropriate for temperate and boreal ants in combination with very fast brood development, allowing them to rear sexuals and new workers from eggs during a short warm season. In fact among temperate ants *Formica* species have the shortest developmental times and their development is more temperature dependent, which allows *Formica* workers to rear the brood much faster at higher temperatures (Kipyatkov & Lopatina, in prep.).

Although ants are rather thermophilic insects many of them have successfully populated boreal regions and some species are even abundant in the forest-tundra zone. It is worth looking thoroughly into the evolution of seasonal life cycles in ants as they advance to the North. What are the main modes of their adaptation to the environments with extremely short and cold summers? What factors may constrain this adaptation and prevent ants from penetrating farther to the North? We will consider these factors at length and show that they might be not only of ecophysiological but also of social origin.

The analysis of a simple dynamic model of an ant colony demonstrates that as the species proceeds to the North the total seasonal brood production per queen (or per monogynous colony) should decline. Other circumstances being equal, this should result in smaller colony size in more northern populations. Our preliminary data show that seasonal brood production, number of overwintered larvae and number of workers per colony actually decline on the average from St. Petersburg (60°N) to Murmansk (69°N) in *Myrmica ruginodis*.

The second prediction from the model is that natural selection should increase the rate of brood growth and development in more northern populations because this would allow colonies to produce more brood per season. In other words, northern ants should rear their brood more intensively as far as this is permitted by their physiology and ecology.

Our experimental work on the intraspecific latitudinal variation of ecophysiology in three *Myrmica* species, done in part jointly with G. W. Elmes (UK) and M. G. Nielsen (Denmark), have confirmed this prediction. We found that: (1) The eggs, larvae and pupae from northern populations develop faster at temperatures above 16–18°C in comparison with the same brood stages from southern populations. Brood development in northern populations is usually more temperature dependent (higher slopes of regression lines of developmental rate on temperature), and characterised by higher temperature thresholds (Kipyatkov & Lopatina, 2002; Lopatina *et al.*, 2002). (2) Northern workers rear larvae more quickly than southern workers regardless of the origin of larvae under common-garden conditions (Elmes *et al.*, 1999). (3) The differences between colonies kept at low (14–18°C) and high (20–25°C) temperatures in brood rearing efficiency appear much more pronounced in ants from northern populations. In other words northern colonies produce eggs and pupae under lower temperatures evidently worse in comparison with colonies from southern regions. (4) *Myrmica* populations from higher latitudes

have higher Q10s and, thus, their respiration metabolism is more intensive than that of southern populations at higher temperatures but less intensive at lower temperatures. Consequently, the individual metabolism in northern populations appears more temperature dependent allowing them "to live faster" and to respond more quickly to changing temperatures (Nielsen, *et al.*, 1999).

From all this we concluded ((Kipyatkov & Lopatina, 2002) that the thermal reaction norm of *Myrmica* colonies changes to adapt brood rearing to boreal and subarctic climates in such a way that brood growth and development become more temperature dependent in environments with colder and shorter summers. Consequently *Myrmica* colonies from northern populations need on the average higher temperatures in their nests for successful production of new adults as compared to southern ants. Our data on nest microclimate show that northern colonies rear their brood even at higher average temperatures than southern ants owing to the adaptive changes in habitat preferences and the improvements of the nest structure.

What are the factors that put the limit for an ant species expansion to the North? For species using the strategy of concentrated brood-rearing this simply might be so short and/or cold summer season that ant colony can't rear enough new adults to maintain a minimum size necessary for successful survival during the winter. Ants employing the strategy of prolonged brood-rearing are presumably able to extend the development of their larvae over three or even more summer seasons and adapt to high-latitude habitats in that way. It is well-known that the prolongation of larval development for several years is an adaptive strategy of most non-social arthropods in tundra and high Arctic (Danks, 1981). We will argue, however, that social factors prevent ants from evolving this adaptation.

The analysis of the dynamic model of an ant colony using the strategy of prolonged brood-rearing demonstrates that as the species expands to the North the quantity of rapid brood should diminish until it disappears entirely at some latitude. Now all the larvae overwinter and pupate during the next summer. Each summer a colony must grow up the brood in a quantity sufficient to replace the loss of workers and to produce sexuals. The natural selection apparently leads to the situation when the workers rear as much brood as they can to ensure colony survival, growth and reproduction. In this situation the extension of development of some proportion of larvae to the third summer season might be possible only if the mean total quantity of brood available in colony at each time is augmented by the same factor because colony still needs to produce as many new adults each summer as before. Such an increase is, however, infeasible since the workers already rear as many larvae as they are able to handle with. Thus, the social mode of life and the dependence of brood on the worker care hinder the extension of development of considerable proportion of larvae to the third year.

Our field studies revealed the absence of rapid brood in *M. ruginodis* colonies in the Polar Circle region. All or nearly all overwintered larvae pupate, however, during the summer and only a few may hibernate once more. Thus, these data confirm the predictions of the model developed above. One can conclude, therefore, that the northern border of species range in ants using the strategy of prolonged brood-rearing is primarily determined by the minimum duration of the summer season allowing the majority of larvae to finish development during the second summer of their life. The selection for faster brood development discussed above may advance this border even a bit more to the North. But the magnitude of possible increase of the development rate is evidently also constrained by physiological factors of still unknown nature.

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Changes in the life cycle of the honeybee in small babynuc colonies at unusual temperature regimes of overwintering

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In the regions with temperate climate honey bees usually overwinter in large colonies with 15–30 thousands of workers. They form winter cluster at the temperatures $<14^{\circ}\text{C}$ with 10° at the surface of cluster and 30° in its centre. Colonies with less than 10,000 bees cannot survive in nature, but can survive in special conditions, i.e. in wintering building with the constant temperatures of $4\text{--}8^{\circ}$, in special hives with two or four colonies, where they form the common winter cluster near the partitions or in the styrofoam hives of special geometry (Komissar, 2002). But the minimal quantity of bees in a colony is 5,000 for these methods of overwintering.

Tiny babynuc colonies with 500–1000 bees are used in summer for queen mating. Usual practice is to liquidate them in August after the end of the queen rearing season. There exists the practical need to store these tiny colonies with the aim of reserve queens storage. Komissar (1994) has proposed a new temperature regime named High Temperature Wintering (HTW) for their overwintering. A hive is kept under $10\text{--}20^{\circ}$, but its volume is connected with the outside space by a tunnel where low temperature serves as the cold lock for the active bees.

The behaviour of bees in the tiny colonies appeared the same as in usual colonies in autumn. They stopped to use new combs for brood rearing in August and ceased brood rearing at all in September. The shortening of the day length is the signal for reproductive diapause onset. In winter the bees don't form the high density cluster and increase RH and CO_2 concentrations in the hive. The absence of cluster and drying effect of system "cold outside – tunnel – warm hive" are two reasons of the dehydration of bees at HTW. In our experiments the quantity of water in the bee body at HTW fell to level of 65 mg per bee (67% of water) and this value was 80–85 mg (70–72%) per bee from the winter cluster. The water supply is obligatory at HTW and colonies died without it.

In the naturally overwintered colonies the start of brood rearing is in the early February and the hypothesis exists that the surplus of water in bees is the main reason of this phenomenon (Omholt, 1987; Möbus, 1998). Shortage of water at HTW of small colonies leads to the absence of brood rearing up to the first cleansing flight (the end of March in Northern Ukraine), but after it their activity and water consumption are increased essentially and queens start eggs laying.

Our results support the hypothesis about the important role of quantity of water in the bee's body for the start of brood rearing.

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Alarm pheromone volatile components in honeybee workers (*Apis mellifera* L. var. *ligustica* Spin.): chemical characterization and bioassays

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Until recently, most chemical characterizations of honeybee worker alarm pheromone components were based on their extraction from the sting apparatus with organic solvents. Thus, over 40 compounds were characterized as alarm pheromone components, even though some of them are integument-specific ones. The present work is aimed at: (I) a chemical characterization of organic compounds in headspace of intact sting apparatus, Koschewnikow glands, sting sheath glands, and setaceous membrane, (ii) a study of specific behavioral responses of guardian bees to each of the identified components and to their mixtures.

The headspace analysis was performed as follows. Purified air was pumped through the samples across a glass column filled with an absorption matrix. Trapped volatiles were eluted with methanol and analyzed by GC coupled with MS or FID detectors. At least 25 different compounds were detected in the headspace of intact sting apparatuses. We identified them using the NIST library of Mass-Spectra and the Internal Standards. We used the obtained data as a basis for compound identification whenever analyzing headspace samples by GC-FID approach. We found in the sting apparatus the following eleven major components: Isopropyl acetate (1), n-Butanol (2), Isoamyl alcohol (3), sec-Butyl acetate (4), n-Butyl acetate (5), Isoamyl acetate (6), 2-Heptanol (7), n-Hexyl acetate (8), Benzyl alcohol (9), 1-Octanol (10) and 2-Nonanol (11). The headspace samples of homogenized Koschewnikow glands, sting sheath glands and setaceous membrane were separated into 14, 13 and 13 major peaks, respectively. Out of these we identified nine (1–6, 9–11), eleven (1–11) and eleven (1–11) peaks, respectively.

We examined the behavioral response of guardians to: (I) headspaces of entire sting apparatus, (ii) their components (sting glands and setaceous membrane), and (iii) identified organic compounds or their mixtures. Guardians displayed alarm response to all of the 11 above-mentioned compounds. Their response to each compound applied separately was weaker than that displayed to their mixtures, or to headspace of intact sting apparatuses. However, when the compounds mixture was prepared according to the quantitative chemical analysis, and the guardians were exposed to the headspace, their response was similar to what we previously observed using a headspace of intact sting apparatuses. Thus, the volatile organic compounds identified in the present study are volatile components of alarm pheromone that are produced and secreted by Koschewnikow glands and sting sheath glands.

Keywords: Apis mellifera; Sting apparatus; Alarm pheromones; Volatiles identification; GLC-MS

Behavioural and physiological control by workers over the development of larvae in the seasonal life cycle of ant colony

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It is well known that ant workers can control the egg-laying by queens and the development of larvae. Brian (1955) showed that autumn (i.e. diapause) workers of *Myrmica rubra* were unable to cause larval pupation whereas spring (i.e. non-diapause) workers forced larvae to grow and pupate. Later the workers of the same species have been found to control effectively larval development and queen oviposition during the photoperiodic induction and termination of their diapause (Kipyatkov, 1974, 1976).

During last years we studied the phenomenon of worker social control over larval development and diapause in several ant species, e.g. *Camponotus herculeanus*, *C. japonicus*, *Lasius niger*, *Leptothorax acervorum*, *Myrmica rubra*, *M. ruginodis*, *M. lobicornis*. The cross replicated experiments in which diapause or non-diapause larvae were given to groups of diapause or non-diapause workers were carried out (Kipyatkov *et al.*, 1996, 1997; Kipyatkov & Lopatina, 1999).

We discovered that the level of worker influence on larval development widely varied among species from a nearly full control in *Camponotus* to a rather slight regulation in *L. acervorum* and *M. lobicornis*. In *Camponotus* species the overwintered (i.e. non-diapause) workers forced all the diapause larvae to grow and pupate. At the same time the workers that have not spent several weeks in the cold (i.e. still in diapause) totally prevented normally overwintered larvae from growth and development. On the other hand in *L. acervorum* and *M. lobicornis* diapause workers had no influence on the growth of overwintered larvae and could not prevent them from development. In *L. niger*, *M. rubra* and *M. ruginodis* we observed an intermediate situation: some overwintered larvae still managed to pupate even when fed by autumn workers and only a portion of diapause larvae were forced to develop and pupate by spring overwintered workers.

Consequently, quite similar seasonal life cycles of temperate ants, which all include winter larval diapause, could be controlled by rather different physiological mechanisms of diapause induction and termination.

Brian (1975) has first demonstrated that in the presence of a queen *Myrmica rubra* nurse workers changed the quantity and quality of food given to larvae. These results allowed us to expect that trophic factors could participate in the process of larval diapause induction and termination in this species. We studied, therefore, in detail the behaviour of nurse workers in *M. rubra* during photoperiodic induction and termination of diapause.

It turned out that physiologically active (i.e. non-diapause) workers fed diapause larvae nearly 10 times more frequently and gave them about 2 times more food per unit time compared to the same larvae fed by physiologically inactive (i.e. diapause) workers (Kipyatkov & Lopatina,

1988). Thus the frequency of feeding and the amount of food may represent the elements of worker control over the process of diapause induction and termination in larvae.

We have then supposed that nurse workers could affect larvae via tactile stimulation. To investigate this question we began from the analysis of the flow diagram of behavioural acts of nurse workers during their manipulations with larvae, which has been derived from the results of several hours of observations (Kipyatkov & Lopatina, 1989). The sequences of behavioural acts that end up with the feeding of a larva most often consist of palpation or licking of the body forepart and the mouth of a larva. These behavioural acts serve as signals for larva to know that the worker is ready to feed it. Feeding usually starts after a motor reaction of larva in response to tactile stimulation by a worker. Palpation and especially licking of the larval body forepart and mouth are also used by nurses to stimulate larvae to ingest more food.

Then possible role of tactile stimulation of larvae by nurse workers in induction and termination of diapause was evaluated (Kipyatkov & Lopatina, 1990) in cross replicated experiments with diapause and non-diapause larvae and workers (see above). The behavioural interactions between nurses and larvae were observed and quantified. It was found that physiologically active (i.e. non-diapause) workers made much more attempts to feed larvae, stimulated them by tactile signals more intensively and responded (by feeding a larva) to larval motor reactions more frequently than did diapause workers. The developing (non-diapause) larvae responded to the nurse workers' food offer more frequently compared with diapause larvae. Diapause larvae were less responsive, but their reactions were more adequate and were more frequently observed just after specific worker stimuli (palpating and licking the forepart of the body and mouth of a larva). As a result, the intensity of tactile stimulation of larvae by nurse workers was the greatest when physiologically active workers cared for diapause larvae, i.e. during the termination of their diapause. The stimulation was the least when diapause workers cared for developing larvae, i.e. during diapause induction in larvae. The mean duration of worker-larva interaction (measured as a number of behavioural acts per interaction), the mean number of feedings per interaction and the occurrence frequency of feedings and stimulating behavioural acts (especially of mouth licking) rose with the increase of workers stimulating activity.

It is noteworthy that the differences in tactile stimulation level and in feeding frequency became evident immediately at the start of worker-larva interaction in these experiments. If some chemical substance received by larvae from workers or the food itself were the cause of termination or induction of diapause then the differences in nurse worker behaviour would be observed only after some period needed for the effect of chemical or trophic stimulus become apparent. We concluded that tactile stimulation of larvae by nurse workers could also be an element of worker control over the development and diapause of larvae. Tactile stimulation may have direct influence on the receptors of larvae and affect their development through nervous and endocrine system.

It has been recently demonstrated that northern *M. ruginodis* workers rear larvae more quickly than southern workers regardless of the origin of larvae under common-garden conditions (Elmes *et al.*, 1999). We suppose that northern nurse workers may force larvae to develop faster by means of tactile stimulation as well as by feeding them more frequently and giving them more food per unit time.

It is worthy to study the role of worker control over the development of larvae in the seasonal colony cycle of other ant species.

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Geographic variation of the response to photoperiod in the ant *Myrmica ruginodis* (Hymenoptera: Formicidae)

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We studied the differences in photoperiodic response and their relevance to seasonal cycle control in *Myrmica ruginodis* colonies from three geographic latitudes. The study was conducted at the Laboratory of Entomology of Biological Research Institute in Peterhof in 1998-1999.

In 1998 we kept ant cultures from Kiev, 50°N, Vladimir, 56°N, and St. Petersburg, 60°N, under long days at 12-hours daily thermoperiod (15/25°C) and then distributed them to several categories of day-lengths: long day, intermediate and short day (17.5, 16 and 15 h for Kiev, 22, 17.5, 16 and 15 h for Vladimir and SPb, respectively). A category termed "control" (12 h for all) was used to make the study comparable to earlier ones. We determined the timing of larval diapause onset (after which a culture gives no new pupae), by weekly removal of newly produced pupae, and crudely estimated the timing of diapause onset in queens (when they stop egg-laying) by the absence of eggs. In 1999 we used ant cultures from Belgorod, 50°N, and Peterhof, 60°N, to get better estimates for the time of queen diapause onset: after keeping the ants under long day at constant optimal temperature (22 ± 1°C), we transferred them to long-day, intermediate, short-day, autumnal (17, 16, 15, 14 h for Belgorod and 20, 18, 16, 15 h for Peterhof, respectively) and "control" conditions (13 h for both) and then weekly removed newly laid eggs.

In 1998, the time of larval diapause onset in cultures from Vladimir and SPb did not differ significantly among the photoperiods or the populations and was close to the natural time of the event at 56–60°N (early August). Ants from Kiev showed quantitative response: earlier larval diapause onset under shorter day-lengths; the time of the event was close to natural one (late August) even under 16-h day-length, observed in early August at 50°N. Eggs disappeared from all cultures under 12 h; under other day-lengths a few cultures of all the populations contained eggs till the last census (22 November). In 1999 all queens of the both populations stopped egg-laying under 13–15 h, earlier than, or close to natural timings, whereas under day-lengths 16 h and longer several queens oviposited until the last check (12 October). Overall, queens of all the latitudes responded similarly; day-lengths below 16 h had strong diapause-inducing effect, except 15 h on Kiev population in 1998 (due to thermoperiod stimulation?).

Thus, the study suggests that in *M. ruginodis* photoperiod controls the diapause onset in larvae (and queens?) at 50°N, but intracolony factors take over in more northern areas. For queens at 56–60°N photoperiod is not relevant, because in nature they enter diapause in late August, when the daylength there is still 16 h. Their inadaptive response to the daylength supports the idea of southern origin of northern populations.

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Detection of *Microdon mutabilis* by *Formica lemani* workers

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The hoverfly *Microdon mutabilis* is an obligate predator of *Formica lemani* and a UK Red Data Book species. *M. mutabilis* females lay eggs at the entrance to *F. lemani* colonies. After seven days the larvae hatch and move into the brood chambers, where they develop for up to two years feeding on the ant brood. *F. lemani* appear to be able to detect the eggs of *M. mutabilis*, however the eggs are not always destroyed (Elmes *et al.*, 1999). It has been suggested that *M. mutabilis* eggs may chemically mimic the cuticular hydrocarbons of *F. lemani* eggs and brood and even mimic individual colonies thus gaining protection from ant attack.

We carried out chemical analyses of the *M. mutabilis* egg surface and *F. lemani* workers and brood. In addition, bioassays were used to assess the behaviour of *F. lemani* workers toward *M. mutabilis* eggs and other stimuli (*F. lemani* eggs, non-conspecific eggs and inert Teflon "dummies"). Results showed that *M. mutabilis* eggs do not mimic the cuticular hydrocarbons of *F. lemani* workers or brood. Bioassays showed a significant difference between the treatment of *F. lemani* eggs and *M. mutabilis* eggs but no difference between non-conspecific eggs or dummies.

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Inter caste differences and colony cycle in neotropical swarm-founding wasps (Hymenoptera, Vespidae, Epiponini)

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The Epiponini belong to the swarm-founding polistines. Neotropical, polygynic, and abundant, these wasps represent the greatest species radiation of social Vespidae. Morphological caste differences are absent or not clear in some species, but some of them present conspicuous morphological differences. Size difference between castes increase as colony cycle proceeds in some species, in other species this difference is fixed or caste differences are absent throughout the colony cycle. Such patterns allied to the usual occurrence of non-inseminated females in several taxa give support for both pre-imaginal and post-imaginal caste determination in epiponines stressing the existence of various types of social regulation. These types are: 1 – Absence of morphological differences between queens and workers in the whole colony cycle (post-imaginal). 2 – Absence of morphological differences between castes, but young females can develop ovaries only in some phases of the colony cycle (post-imaginal). 3 – Morphological discontinuities between castes varying according to colony cycle, and non-inseminated laying females always present (pre-imaginal). 4 – Caste differences increase according to the colony cycle and non-inseminated laying females appear only in some phases (pre-imaginal). 5 – Queens are always distinct from workers, and no variation in this pattern occurs during the colony cycle (pre-imaginal).

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Interspecific variation of behavioural models in the ant *Formica cunicularia glauca* Ruzs. in case of trophobiosis

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Long termed investigations have shown that ants of different species use specific schemes of interaction with aphids: from non-coordinated work of singly foraging trophobionts to professional specialization (Novgorodova, Reznikova, 1996; Reznikova, Novgorodova, 1998). According to flexibility of territorial and foraging behaviour of ants it is possible to expect some plasticity in organization of trophobionts work. Factor initiating changing of trophobionts behaviour can be, in particular, deficit of carbohydrate food. This situation appears either while decreasing of available food resources or when the family's needs change as a result of growing of the family's number.

The aim of the work is to investigate interspecies variety of interaction schemes of the ants *F. cunicularia glauca* with aphids-symbionts by comparative analysis of organization of trophobionts work in families with different number and in conditions of different accessibility of food resources. Investigations were carried out in the forest-park zone of Novosibirsk scientific center in 1994–2000. Six families with section-nests (numbered about 800–1200 individuals) and 4 – with capsules- nests (2500–3500 individuals) were explored in the field. Deficit of food was modeled in laboratory conditions by changing number of aphid colonies available to the ants (about 600 individuals).

Observations were accompanied by group and individual marking and by testing the aggressiveness of ants. In total, 230 ants in the field and 256 – in laboratory were marked. Ethograms have been got for 67 and 47 individuals correspondingly. Observational time is about 350 hours. It turned out that insufficient ensuring of a family by the carbohydrate food, both in conditions of deficit of food resources, and as a result of the growing of the family's number, brings to considerable re-organisation of trophobionts work. Schemes of ant-aphid interaction become more complicated changing from a non-co-ordinated work of singly foraging trophobionts up to the development of professional specialization in small groups servicing separate aphids colonies. It is possible to expect that schemes of interaction with aphids in ant species possessing plastic territorial and foraging behaviour consist of a small row of variants altered in difficulty and can change in accordance with family's needs.

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Size distinctions of *Formica polyctena* and *F. pratensis* trophobionts executing different subtasks in working groups

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Recent field observations (Novgorodova, Reznikova, 1996; Reznikova, Novgorodova, 1998) have shown that ants use different schemes of interaction with aphids: from non-coordinated work of singly foraging trophobionts to professional specialization in working groups with clear division of two main functions (honeydew collecting and colony defence). The most complex scheme of ant-aphid interaction – professional specialization – is characteristic of the dominant ant species with large families: *F. polyctena* and *F. aquilonia* – in forest and *F. pratensis* – in steppe associations. The aim of the work is to find out if there are any size distinctions between trophobionts executing different subtasks in working groups of *F. polyctena* and *F. pratensis*.

Investigations were carried out in the forest-park zone of Novosibirsk scientific centre in 2001. Size of *F. polyctena* and *F. pratensis* trophobionts was estimated by measuring of the widest place of the ants' head (in mm). Earlier we have shown that working groups of *F. polyctena* trophobionts consist from ants with different functions: "shepherds" collect honeydew droplets, "guards" protect colony, "carriers" transport honeydew to the nest, and "scouts" search for new aphid colonies. Unlike *F. polyctena* we revealed only two "professional" groups in *F. pratensis*: "shepherds" and "guards". They carry honeydew to the nest themselves, as "carriers" are absent in groups. "Guards" probably execute functions of "scouts".

It is stated that ants with different professions are significantly differ according to their size (t-test; $p < 0.05$): *F. polyctena* – "shepherds" (1.36 ± 0.27 ; $n=100$), "guards" (1.45 ± 0.24 ; $n=100$), "carriers" (1.69 ± 0.31 ; $n=100$), "scouts" (1.04 ± 0.09 ; $n=30$); *F. pratensis* – "shepherds" (1.87 ± 0.24 ; $n=100$), "guards" (2.03 ± 0.14 ; $n=100$). Scouts' functions were found to be executed by the smallest individuals in red wood ants, which is consistent with data of laboratory investigations where only small insects executed the scouts' functions in working groups while transmitting information about food (Reznikova, Novgorodova, 1998).

The study was done under the supervision of Zh. I. Reznikova and was supported by grants of the RFBR (02-04-48386 and 03-04-06030).

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Life history strategies and caste evolution in termites

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Life history parameters of termite colonies have seldom been the subject of specific investigations, but a relationship between life histories and caste patterns has long been pointed out. Termite taxa have been arranged along a continuum between two extreme conditions of colony size, longevity and social complexity. At one end, small, relatively short-lived colonies, devoid of a true worker caste, live in a single piece of wood that serves at the same time as food and nesting site. At the other end, large, long-lived colonies, with a complex caste system including sterile workers, build elaborate nest structures which they leave to forage for a variety of food sources. Species with an intermediate biology nest in logs but exploit other wood items through a network of subterranean galleries. Besides the onset of sociality itself, the most critical step in this evolution is the emergence of a caste of permanent workers. Several hypotheses have been proposed to account for these events. Analogies were sought among social Hymenoptera (relatedness patterns and various aspects of social life), among other wood-dwelling insects (onset of gregariousness and sociality), among other "fortress defenders" (origin of soldier caste), and among cooperatively breeding vertebrates (evolution of helping behaviour). The resulting situation is a rather confuse picture of caste evolution and related selective pressures in termites. I will first redefine the options open to individual immature termites and recalculate the associated genetic payoff, taking care to use a common currency for all options. Because all termite species known so far must, at some point of their life cycle, go through a phase of alate dispersal, I will argue that the genetic payoff to a termite individual can, and should, ultimately be expressed at the number of copies of its genome this individual manages to squeeze into alate dispersers of its home colony. On this basis, I will then critically examine previously proposed evolutionary relationships, (1) between inheritance opportunities, delayed dispersal and helping, (2) between available food resources, dispersal risks, and developmental decisions, (3) between foraging behaviour and the emergence of a true worker caste. Without denying the importance of home breeding (usually through neoteny) in the life cycle of many termite species, I will show that this phenomenon is unlikely to have favoured the evolution of sociality and sterile castes. The main difficulty is to explain why individuals that refrain from dispersing actually postpone breeding. It appears more parsimonious to consider that helping *per se* provides enough inclusive fitness benefits to justify delaying dispersal. I will also argue that dispersal risks, however high, should be considered as constant and thus of little bearing on developmental and behavioural decisions. By contrast, opportunities for future benefits offered within the home colony are of higher interest. The link between developmental decisions and resource availability in termite colonies has long been suggested, but only recently been put to test. I will then present ways to investigate the events that allowed termites to overcome the problem of resource exhaustion within their home piece of wood. Of particular

interest are cases where the correspondence between confinement to a single piece of wood and absence of workers is not fulfilled. Preliminary studies in the genus *Prorethra* will be presented, which show that these basal Rhinotermitidae, without workers, have developed a complex foraging behaviour allowing them to locate and exploit external sources of wood. I conclude that the notion of "ecological constraints on dispersal", widely applied in evolutionary studies of other social insects and vertebrates, needs to be used with caution whenever termites are involved. It often appears more judicious to focus on opportunities offered through the home colony. Because of the consistent presence of a dispersing alate phase in termite life cycles, it is appropriate to focus on this phase to evaluate reproductive payoff or fitness estimates. One should consider that the driving selective pressure on any individual termite's behaviour and development is the need to increase the representation of its genes into the ultimate alate output of the colony—including the possibility of being itself part of this alate output. This attitude should provide a common frame for studying the evolution of helping and that of sterile castes in termites.

How can split sex ratios evolve in monogynous, monoandrous, worker-sterile ants?

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Split sex ratios, with some colonies producing predominantly or exclusively gynes while others specialize in males, are a common feature of ant populations. Up to now, only one model can unequivocally predict such a specialization (Boomsma and Grafen, 1991). This model assumes that relatedness asymmetries due to haplodiploidy (worker-gyne vs worker-male) vary between colonies, e.g. because some queens may have mated more than once. This hypothesis has proved successful in some instances, but several examples are now known in which it cannot hold. For instance, in the monogyne form of the fire ant, *Solenopsis invicta*, a split sex ratio is observed with constant relatedness asymmetries. I will present here a simple model providing an alternative hypothesis for the evolution of split sex ratios. We consider monogynous, monoandrous, worker-sterile, and perennial colonies, without restrictions to dispersal. The key assumption is that the queen has complete control on diploid egg production, whereas workers have complete control on brood development: they may eliminate eggs or larvae of either sex and determine the caste of the female brood. Therefore, the question is: considering that the workers will do what is best for themselves with the available eggs, should the queen lay diploid eggs *ad libitum*, letting workers bias the sex allocation towards gynes, or alternatively, should she limit their number to favour the production of males? If the genetic payoff to the queen is plotted against the number of diploid eggs she lays, two relative maxima are observed. One is a peak obtained for a given, limited number of eggs, for which workers should raise all diploid eggs as workers to enhance colony productivity, and release only male sexuals. The other maximum is actually a plateau corresponding to unlimited eggs, from which workers raise as gynes the maximum investment in sexuals that the colony can sustain. Which maximum is higher, the peak (limited eggs, all-male sexuals) or the plateau (unlimited eggs, all-female sexuals), depends on the sex investment ratio at the population level. There is an equilibrium value of this ratio (somewhere between 1:1 and 3:1 gyne-biassed) for which both strategies yield an equal payoff, and which corresponds to equal numbers of male- and gyne-producing colonies. This "mixed evolutionary stable strategy" model fits rather well the monogyne populations of *Solenopsis invicta* (Roisin and Aron, 2003).

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Colony productivity in *Polistes* wasps in Kherson region, Southern Ukraine

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Basing on our present data of the inter- and intraspecific variation in the population structure of three *Polistes* wasp species, their colony organisations and colony productivity in different years, we discuss some possible regulation mechanisms in *Polistes dominulus*, *P. nimpha*, and *P. gallicus* in Kherson region of Southern Ukraine. Population systems of the species under study are characterised by differences in semisocial group forming, renesting ability, differentiation in the colonies' producing off-spring. Birds, grasshoppers, ants and a parasite wasp *Latibulus argiolus* regulate *Polistes* wasp density and its population structure. It was found that every species has its specific seasonal development and the date of nest founding, worker and reproductive emergence. For different species, similar changes in colony parameters (queen productivity of different species, queen longevity on nest, the worker number and similar cells reuse for brood rearing) are marked in different years. In our opinion, it points to the impact of climatic factors on the process indicated.

Nest dispersion in populations, queens' shifts among nests, usurpation rate can be connected with population number. Density depending factors influence pleometrotic and obligatory haplometrotic species in some other way.

How parasitism affects life history in social insects

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Parasites extract a part of an individual host's resources and therefore affect the ergonomic profile of a colony. Such parasite-induced effects are expected to change the life history of a colony. Changes can be passive, that is, when the colony only suffers from damage, or it could reflect the strategies of the host colony or the parasite. Little is known about these questions in social insects. Here, some expectations are formulated and reference is made to other (non-social animals). Empirical evidence from social insects is added and a few recent experimental findings as well as conceptual insights are presented.

Phylogenetic analyses of life history traits in allodapine bees and their implications for social evolution

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Allodapine bees provide enormous material for comparative approaches to social evolution. Sociality varies widely among both genera and species. Some of this variation appears to be associated with ecological features, but some variation appears to show signs of strong phylogenetic constraint. Importantly, several key life history traits also vary widely among allodapines and these have the potential to strongly influence the kinds of sociality that can evolve. DNA sequence data accumulated over the last few years now allow us to begin exploring transitions in key life history and social traits from a phylogenetic perspective. One major finding from sequence based analyses overturns the prior hypotheses that the evolution of progressive provisioning of brood, and the origin of sociality, occurred within lineages leading to the extant taxa. Instead, both sociality and progressive provisioning are plesiomorphic for the tribe. Mass provisioning and solitary behaviour in the genus *Halterapis*, which was previously regarded as the most basal allodapine clade, is apomorphic. Although allodapines have traditionally been regarded as displaying recent origins of sociality and that this might provide insights into early stages in social evolution, it appears that social behaviour in this group has an ancient origin, and that extant forms of social organization result from selection operating on forms of alloparental care that evolved at least 30 mya. However, allodapines do provide extensive material for investigating both the elaboration and loss of social organization. Cofounding has arisen only once, but size related reproductive castes have evolved at least several times. Voltinism, egg-laying schedules, patterns of brood rearing, and colony phenology show strong phylogenetic patterns, and in at least some circumstances major transitions in these traits seem to have evolved very rapidly and correspond to generic-level divergences. However, current data do not suggest that any particular life history or ecological factors are critical to the evolution of eusociality, or its loss. This could mean that we are yet to identify key factors underlying complex sociality, but it could also mean that for this tribe at least, evolutionary transitions in social organization are capricious.

Steps toward a general theory of the colony cycle in social insects

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The fundamental nature of the colony cycle in social insects has long been recognized, and the basic pattern for most major groups has been known for roughly a century. Nonetheless, there has been little attempt to lay the theoretical groundwork to understand how colony cycles are shaped by natural selection.

It is proposed to initiate this process by taking advantage of a) the structural resemblance between colony cycles and the life cycles of individual organisms (superorganism concept), and b) the substantial existing body of theory concerning life cycles (life-history theory).

A review of the basic parameters of life cycles shows that most of these are readily applicable to colony cycles. The main exception appears to be sex ratio, which has no evident meaning at the colony level.

Some basic ideas in life-history theory are reviewed, with a view to illustrating the kinds of testable hypotheses about colony cycles that these can suggest by analogy.

Finally, an appeal is made for the establishment of a permanent central database of social-insect colonies, partly in the service of a general theory of colony cycles.

Life history evolution in perennial social insects with special reference to population dynamics and spatial structure

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Ants, termites and swarm-reproducing bees and wasps have a perennial life, which leads to overlapping generations and age structures of populations. In such a situation theory of life history evolution (Stearns 1992, Charlesworth 1994) contends that fitness of an allele may not simply be measured by the average lifetime reproductive success of the allele's bearers. The average lifetime reproductive success can be an estimate of fitness when the population size is constant over time, regulated by a density dependent process under overlapping generations. While when the population is not regulated by a density dependent process and regularly experiences an increasing phase, the intrinsic rate of natural growth (r) can be an appropriate measure of fitness, by which one can more precisely predict the change in the allele-frequency over time. In other words, the growth rate of the population that exclusively consists of the allele's bearers can be a measure of fitness of the allele. Importantly, in an increasing population, r can be enhanced by an earlier reproduction, and this "timing effect" on fitness is often stronger than the effect of over-production of offspring. However, most sociobiological models for social insects ignore this and implicitly assume a stable population with a constant population size, because they use inclusive fitness that is in principle a product of the number of reproductive offspring (lifetime reproductive success) and relatedness.

Social insects, especially ants, are dominant in various types of landscapes, therefore I believe that without empirical evidence one cannot assume that all ant populations are stable, regulated by a density dependent process. Previously we tried to explain polygyny (coexistence of multiple reproductive queens in a colony) in ants, which is often regarded as a challenge to kin selection theory, by developing a life history evolution model that takes population dynamics into account (Tsuji and Tsuji 1996). Generation time is short in polygynous ants (which often are fission reproducers) that makes a high potential r , as compared which monogynous ants that are often independent colony founders. Therefore, in environments where ant populations are subject to frequent density-independent fluctuations, polygyny is favored by natural selection and/or advantageous in interspecific competition. The above discussion is supported by empirical data in Okinawa (Tsuji and Tsuji 1996) showing that polygynous ants are more predominant in open habitats with frequent disturbance by human activities than in forests with little human disturbance.

In this paper, I discuss mainly two issues. First, I argue that the pattern observed in Okinawa, i.e. polygynous ants are more dominant in open lands than in forests, is a general phenomenon at least in relatively humid warm regions of east Asia. Second, we address a more general theoretical question on the relationship between habitat disturbance and the evolution of dispersal behavior, on the basis of ant life histories.

Tsuji and Tsuji's life history model ignored spatial structure (as did in most inclusive fitness models). However, the dispersal distance should differ between the fission and the independent founders, and the former can migrate only to short distances. Therefore, spatial and temporal distribution patterns of habitats are likely to influence the consequences. Furthermore, Tsuji and Tsuji's conclusions are counter intuitive in a general ecological sense, because they predict that in disturbed habitats (that are subject to density independent population fluctuations) dependent founders, i.e. short-distance dispersers, are more advantageous. Whereas in general migration is believed to be adaptive when environmental disturbance occurs in an unpredictable way (Roff, 1994).

In order to take spatial structures into account, we introduced the Coupled Map Lattice Model (M. Nakamaru, Y. Beppu, K. Tsuji, in prep). In this model an ant colony can occupy a site in the two-dimensional lattice of which size is $N \times N$ sites. It has vacant sites and sites occupied by ant colonies. We assume two clonal strategies, the independent founder and the fission founder. Each fission founder-colony, after reaching a threshold colony size, divides the colony into two equally sized offspring colonies. One will migrate to one of 8 neighbour sites, the other remaining in the original site. While independent founder-colonies produce dispersers that migrate randomly into a vacant site in the entire lattice, when they reach a threshold colony size. Each colony shows a logistic growth in each. Then we introduced a random disturbance by which some sites are "cleaned" (all colonies die in the disturbed sites). We let p be the probability that disturbance take places at a site (occurrence-probability). We also let q be the probability that the disturbance spreads to the one of the nearest neighbour sites of a disturbed site (spreading-probability). We assume that disturbance spreads with this probability instantaneously. When p is low and q is high, the lattice has a small number of large disturbances. When p is high and q is low, the lattice has a lot of small disturbances. When both p and q are high, there are a lot of large disturbance in the lattice. We have obtained remarkable results of the model: When both p and q are high all ants go extinct regardless of the strategy, whereas fission founders tended to win under high p and low q . Independent founders win only when both p and q are low.

This implies that frequent local disturbances can favor fission reproduction in ants. In other words, long-distance migration by alate queens is not advantageous when local habitats are frequently disturbed. In more general sense, our model predicts that organisms (super organisms in social insects) which can perform a kind of "vegetative propagation", like fission of ant colonies, will become predominant in environments where frequent disturbances occurs locally.

The above discussion is an extension of classic theories of life history evolution, however, has not attracted much attention of sociobiologists studying social insects. One possible reason for this is that the models do not deal with intracolony conflict, which is a main issue of the Hamiltonian inclusive fitness paradigm. In my view, however, kin selection is an important but only a part of a more comprehensive theory of life history evolution. Hence assumptions, for example a stable population, as we have pointed out, are required in order to hold the Hamilton's rule true, inclusive fitness theory is not almighty.

I believe that some issues are not well understood by kin selection theories, because the phenomena include situations where assumptions (which are not usually explicit) of usual kin-selection models do not hold. Polygyny in ants including the uniclonality should be one of such

issues. Finally, we need a theoretical approach with combine theories of life history strategy and kin conflict.

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Behavioural and physiological adaptations to inquilinism in *Polistes* wasp social parasites

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There are three species of *Polistes* wasp inquilines living in the Mediterranean area: *Polistes sulcifer*, *P. semenowi* and *P. atrimandibularis*. The first two species parasitise one (*P. dominulus*) or two (*P. dominulus* and *P. nimphus*) host species, respectively, while the third is much more generalist. We have found it on the nests of four species living in the plains (*P. dominulus*, *P. gallicus*, *P. nimphus*, *P. associus*) and one species in mountain areas (*P. biglumis*). Our group has conducted research on all the species, especially on their behaviour, chemical ecology, mating systems, etc.

Polistes wasp social parasites present various morphological, behavioural and physiological adaptations to the parasitic life which distinguish them from their hosts. These adaptations involve all the developmental stages.

Usurping females of *P. sulcifer* and *P. semenowi* attack the host nest and defeat the dominant individuals by cutting their legs with powerful, oversized mandibles. Other body parts of the parasites are adapted for fighting. The conquest of the nest is completed by the submission of the subordinate females. *P. atrimandibularis* use their weapons to prey on accessory nests of the host species when larvae in the main nest require more food.

Colony control is achieved via chemical mimicry, i.e. the parasites adjust their cuticular hydrocarbons to those of the host colony. In this way the parasites obtain the collaboration of host workers in the rearing of their larvae.

We found that parasite eggs and larvae develop in less time than the host larvae and they are nourished significantly more by the host workers. Evidently the parasite larvae can attract the attention of the tenders; yet we recently observed that they deliver less saliva to the tenders when solicited.

Shortly after emergence, the young male and female parasites abandon the host colonies and migrate to the mountains where they mate in lek systems maintained by territorial males. After mating, the females search for a hibernation site, usually under stones or in rock crevices. Altitudinal migrations are one of the puzzling aspects of their life cycle discussed in this lecture.

The ontogeny of reproductive allocation

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Sex allocation in social insects has been framed by two perspectives – genetic relatedness and resource availability. Although genetic relatedness makes predictions about how a colony should divide reproductive effort between males and queens, these decisions are not expected to change over the lifetime of a colony. Theories of sex allocation based on resource availability predict that colonies will divide reproductive effort between the sexes based on their cost of production in the context of food availability or predictability. Resource availability may vary as a function of colony age, colony size, or location. Most sex allocation theory assumes that the fitness gains from males and queens do not vary among individuals or colonies, however, differences in sizes of males and females may influence fitness and this can also contribute to allocation decisions. We will discuss the relative importance of genetic relatedness, resource availability, and colony size/age in shaping patterns of reproductive allocation in the harvester ant *Pogonomyrmex occidentalis*, using quantitative data from 200 colonies studied from 1994–2003.

Способ преодоления диапаузы при помощи воды у маток шмелей *Bombus terrestris* при лабораторном разведении

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Широко известен способ искусственного преодоления диапаузы у шмелей при наркозе CO_2 . Этот способ преодоления диапаузы используется при массовом разведении шмелей в лабораторных условиях. Но при разведении шмелей возникает ряд трудностей связанных с применением CO_2 . Во-первых, из-за плохого качества CO_2 может происходить гибель шмелей. Во-вторых, многие авторы указывают на вредное воздействие наносимое шмелям при передозировках CO_2 . Негативное влияние наркоза CO_2 может выражаться в появлении бесплодия или отрутневения маток шмелей, в нарушении функций иммунной системы насекомого.

Альтернативным способом преодоления диапаузы является преодоление диапаузы при использовании дистиллированной воды. Шмелиные матки, прошедшие спаривание и выгул помещаются в дистиллированную воду комнатной температуры. Время пребывания в воде было увеличено до 30 минут, затем 2-2,5 часа перерыв и еще 30 минут снова в воде. Отсчет времени пребывания в воде начинается при полном обездвиживании насекомого. За время перерыва (2-2,5 часа) шмелиные матки постепенно начинают двигаться, затем активно летают по вольере для выгула. При меньшем пребывании шмелиных маток в воде не накапливается достаточного количества CO_2 и не происходит перестройки организма как после диапаузы. При более длительном сроке пребывания маток в воде резко увеличивается отход насекомых. Длительное пребывание в воде вызывает гибель шмелиных маток.

Возможно, при помещении маток шмелей в воду происходит "закупорка" трахей водой и идет накопление CO_2 , который вырабатывается организмом. Повышение концентрации CO_2 в организме шмелиной матки способствует необходимым перестройкам физиологических процессов, которые вызывают преодоление диапаузы и в дальнейшем способность откладки оплодотворенных яиц. При способе преодоления диапаузы с помощью воды не происходит передозировки CO_2 в отличие от прямой наркотизации CO_2 .

Проведенные исследования позволили достичь положительного эффекта, который выражается в том, что стало возможно преодолевать диапаузу у шмелиных маток без использования CO_2 . Преодоление диапаузы при помощи воды позволяет приблизить разведение шмелей в лабораторных условиях к естественному ходу развития шмелей в природе, т.к. при диапаузе в природе возможно кратковременное затопление водой.

Эксперименты проведенные в лаборатории шмелеводства ФГУП "Совхоз "Тепличный" г. Иваново позволили с помощью данного способа преодоления диапаузы осуществить получение шмелиных семей, которые показали отличные летные и опылительные качества в теплицах хозяйства.

Особенности строения и асимметрия яичников шмелей

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Половая система самок шмелей включает парные яичники, парные яйцеводы, непарный яйцевод, на дорсальной стороне которого имеется семяприемник. Непарный яйцевод открывается половым отверстием около основания жалоносного аппарата. Яичники шмелей состоят из четырех яйцевых трубочек (овариол) каждый в отличие от яичников медоносных пчел, у которых число овариол в яичниках может достигать 300-350, а иногда и 400 (Шванвич, 1949; Папичев, 2000).

Собственно яйцевая трубочка разделяется на передний отдел – гермарий и задний – вителлярий. Гермарий заключает внутри большое количество первичных половых клеток (оогониев), из которых в результате дифференцировки образуются яйцеклетки (ооциты) и питательные клетки (трофоциты). Образовавшись в гермарии, яйцевая клетка передвигается в вителлярий, где окружается слоем клеток фолликулярного эпителия, имеющими питательное значение для ооцита. По характеру поступления питательных веществ в созревающую яйцеклетку, яичники шмелей, как и других представителей перепончатокрылых, относят к политрофическому типу (Шванвич, 1949; Яковлев, 1974; Росс, 1985). Овариолы яичников такого типа отличаются наличием в каждой фолликуле обособленной группы питательных клеток, расположенной со стороны гермария. Яйцевая трубочка оканчивается овариальной ножкой. В энтомологии по количеству яйцевых трубочек принято оценивать потенциальную плодовитость (Дербенева, Ухова, 1974). Однако этот вопрос в отношении шмелей практически не ставился. В 2002–2003 гг. нами проведено изучение яичников шмелей *Bombus hypnorum* (14 экз.), *B. lapidarius* (13), *B. hortorum* (8) отловленных в природе и *B. terrestris* (60 экз.) из лабораторных линий.

У 5,26% рабочих особей шмелей отмечено полное отсутствие правого яичника. Асимметрия в количестве яйцевых трубочек в правом и левом яичниках отмечена у 6,3% особей: их число колебалось как 3–4, 4–5 и 5–6. Среднее число фолликулов в яичниках шмелей составило у *B. hypnorum* – 25,8; *B. lapidarius* – 40,0; *B. hortorum* – 28,8 и *B. terrestris* – лабораторная линия (11 поколение), полученная из Голландии – 44,8; гибридная линия ивановско-голландская (9 поколение) – 78,5, т.е. гибриды могут быть потенциально более плодовиты.

Таким образом, асимметрия в числе яйцевых трубочек наблюдается как у диких, так и у лабораторных шмелей. С помощью корреляционного анализа установлен характер связи между массой тела и потенциальной плодовитостью. Связь положительная, слабая, достоверная. При возрастании массы тела потенциальная плодовитость шмелей увеличивается незначительно.

В ходе исследований было впервые установлено, что, в яичниках шмелей может встречаться не только 8 трубочек, т.е. в двух яичниках по 4, а по 10 (по 5 в каждом яичнике), или наблюдаться асимметрия (4 и 5 трубочек). Хотя для многих перепончатокрылых известны факты широкого варьирования числа яйцевых трубочек, для шмелей в известной нам литературе подобные данные отсутствуют. Данные изменения встречались: асимметрия - в 2% случаев, 10 трубочек в 0,4% случаев. Эти факты выявлены пока только у рабочих шмелей, поэтому для выяснения влияния подобных изменений на потенциальную плодовитость маток требуются дальнейшие исследования.

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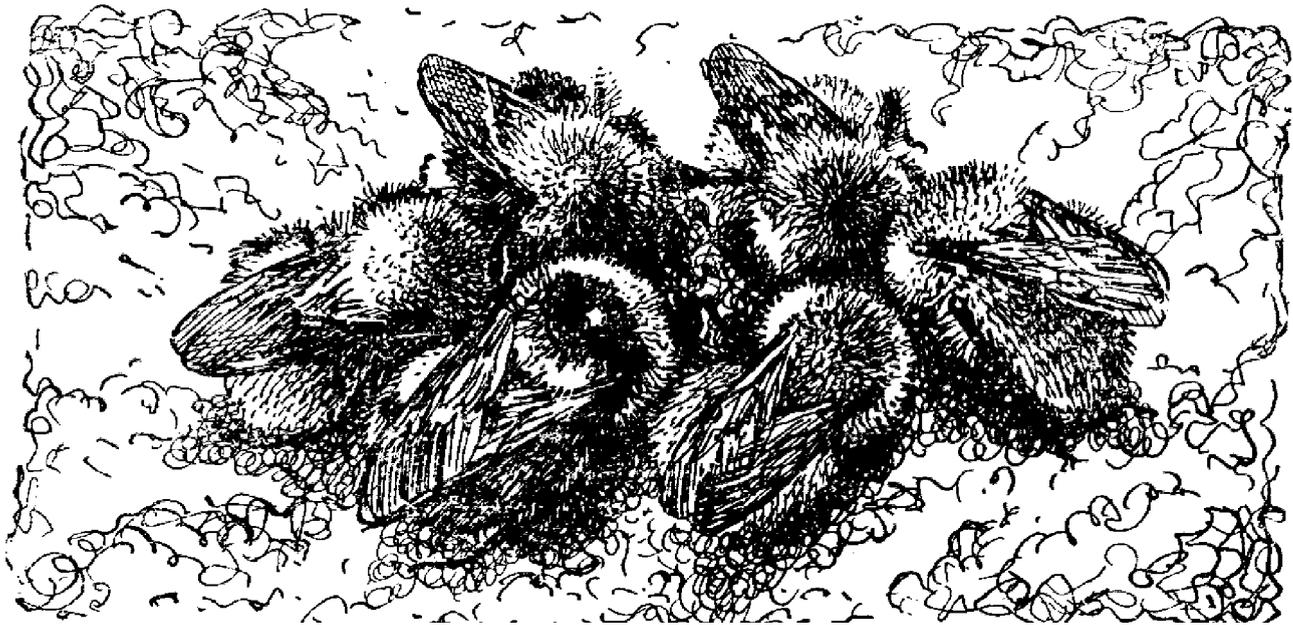
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