

# **Life Cycles in Social Insects**

## **Behaviour, Ecology and Evolution**

*Edited by Vladilen E. Kipyatkov*



St. Petersburg University Press

**Life Cycles in Social Insects:  
Behaviour, Ecology and Evolution**

On the cover:  
The nest of *Ropalidia marginata* (photo R. Gadagkar)

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***Life Cycles in Social Insects: Behaviour, Ecology and Evolution***

**Proceedings of the International Symposium, St. Petersburg, Russia 22–27 September 2003.**

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**Жизненные циклы общественных насекомых: Поведение, экология и эволюция**

Материалы международного симпозиума, Санкт-Петербург, 22–27 сентября 2003 г.

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В сборнике опубликованы статьи, написанные авторами проблемных докладов, прозвучавших на международном симпозиуме, состоявшемся 22–27 сентября 2003 года в Санкт-Петербургском университете. Статьи посвящены вопросам теории жизненных циклов в применении к общественным насекомым. Рассмотрены поведенческие и экологические аспекты эволюции жизненных циклов общественных насекомых.

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## Preface

This volume consists of papers written by the authors of the invited lectures presented at the International Symposium, "Life Cycles in Social Insects: Behavioural, Ecological, and Evolutionary Approach", St. Petersburg, Russia 22–27 September 2003. The symposium was organised and sponsored by the Russian Language Section of the International Union for the Study of Social Insects. It was held at St. Petersburg University – the oldest University in Russia, founded in 1724 under the decree of Peter the Great along with Russian Academy of Sciences and the Academic Gymnasium. The symposium has attracted attention of many specialists and distinguished experts in the field from Europe, North and South Americas, Australia and Japan (see the List of Participants on p. xii).

The main purposes of the symposium were to bring together the people interested in the study of seasonal and life cycle evolution in social insects, including leading experts, to create the opportunity for productive discussions, to evaluate the present-day status of the empirical and theoretical research and to stimulate further studies in this important field. In his report below (pp. ix–xi) Christopher Starr describes the symposium and main presentations delivered by the participants at greater length.

The traditional life history theory generally ignores social insects. So we really need the new theoretical approaches to be developed specially for life cycles evolution in social insects. It is our strong conviction that the major approach which is worth developing in the first place is the study of the life cycle of a whole colony, not of colony members. The papers included into this volume may represent the first step in the development of a general theory of life history evolution in social insects. Anyhow, I hope that this book will stimulate further research, both empirical and theoretical, in this important and promising field.

With the publication of this book, I wish to thank all contributing authors as well as the referees for their help. My special thanks are due to Dr. Elena Lopatina (St. Petersburg University) for the constructive discussions and practical help in the editing of this book.

Vladilen Kipyatkov  
June 2006



*Life Cycles in Social Insects: Behaviour, Ecology and Evolution.*

V. E. Kipyatkov (Ed.), St. Petersburg University Press, St. Petersburg, 2006, pp. ix–xi.

## **The International Symposium, "Life Cycles in Social Insects: Behavioural, Ecological, and Evolutionary Approach". St. Petersburg, Russia 22–27 September 2003**

The symposium, sponsored by the Russian Language Section of the International Union for the Study of Social Insects (IUSSI), was ably organized by Vladilen Kipyatkov and Elena Lopatina. Both are on the faculty of the University of St. Petersburg, the venue of the symposium. St. Petersburg, a thriving city of 5 million, had a special vibrancy at the time, as it was celebrating the 300<sup>th</sup> anniversary of its founding by Tsar Peter I (known as Peter the Great). The city is built on the delta where the Neva River meets the Gulf of Finland, and the many canals running through it give it a character very much its own. The university is the oldest in Russia, founded in 1724 by Peter, who took a keen interest in science and its development.

There were some 40 participants representing more than 15 countries (see p. xii). These included about ten students from Russia, Ukraine and elsewhere in Europe. In addition to the 26 invited oral presentations, there were about a dozen poster presentations.

The opening session was held in the ornate Peter the Great Hall in the main university building. With a marble bust of Peter himself looking on, Vladilen opened the symposium. Randy Hepburn (South Africa) then spoke on ecological correlates of absconding, migration, and swarming in honey bees. He was followed by Raghavendra Gadagkar (India), who described his research into how division of labour is regulated in *Ropalidia marginata* wasps. Subsequent sessions were held in the university's Conference Centre. Our meals were served in the dining room adjacent to the meeting room. Completing a convenient triangle was a comfortable lounge where participants could chat and sample Russian beer, wine, and vodka during breaks and before meals.

Most social insect taxa were treated by at least one speaker. Bill Foster (UK), speaking on social aphids, argued that a defensible gall is a prerequisite for the evolution of the soldier caste and that investment in soldiers is negatively correlated with rate of colony growth and level of attendance by ants. Turning to the social thrips, Tom Chapman (Australia) gave evidence that altruistic soldiers are likely to evolve in species that occupy small galls, and have high reproductive skew and low rates of inbreeding.

In addition to Randy Hepburn's talk on *Apis*, Yaacov Lensky (Israel) described how he narrowed the list of active components in the alarm pheromone of *Apis mellifera* to 11 volatiles. Paul Schmid-Hempel (Switzerland), arguing that parasites affect virtually all aspects of the life histories of their hosts, made a strong case for the need to include the effects of parasites in any study of life histories of social insects.

Social wasps were well represented. Catherine Bridge (UK) showed that, while females on the small colonies of *Liostenogaster flavolineata* normally exhibit an age-based queue for the inheritance of dominance and reproductive rights, "queue-jumping" occasionally occurs. Stefano Turillazzi (Italy) described his lab's work on behavioural and physiological adaptations of *Polistes* social parasites. For example, parasite larvae get more visits from host workers, yet secrete less saliva, than do host larvae. Lidia Rusina (Ukraine) compared colony survival and productivity in three *Polistes* species from southern Ukraine. Differences among them in nest sites, mode of colony founding, and predators lead to different responses to year-to-year variations in climate. Jim Hunt (USA and Germany) tracked the major transitions in the evolution of eusociality in wasps by mapping salient traits onto the phylogeny of the group. Fernando Noll (Brazil) showed how the swarm-founding Epiponini fall into five groups according to the degree of caste differentiation. Bob Jeanne (USA) provided evidence that Michener's "reproductivity effect", in which colony productivity per individual is negatively correlated with colony size, does not hold for swarm-founding wasps.

On the ground with the ants and termites, Jürgen Heinze (Germany) described how variations in life history traits among species of *Leptothorax* match predictions made by concession models. Kazuki Tsuji (Japan) modelled life history evolution in social insects with perennial colonies, taking spatial structure and colony dynamics into account. Blaine Cole (USA) teased apart the relationships between mating frequency, growth, size, productivity, and fitness in colonies of *Pogonomyrmex occidentalis* in Colorado. Diane Wiernasz (USA) followed with a description of her work on sex allocation in the same population of *P. occidentalis*. Graham Elmes (UK) analysed adaptations of *Myrmica* brood cycles to cold, fluctuating climates.

Moving closer to the venue of the symposium, Vladilen Kipyatkov (Russia) discussed the evolution of seasonal life cycles in boreal ants, and Elena Lopatina (Russia) described her investigations into the control by *Myrmica* queens over the development of larvae. Noting that permanent workers had at least three independent origins in the termites, Yves Roisin (Belgium) presented evidence that a prerequisite for the evolution of the worker caste was foraging for food away from the nest. In a second presentation, Yves offered an alternative to the Boomsma-Grafen model for the evolution of split sex ratios in ants. Serge Aron (Belgium) presented results that miniaturization in inquiline parasitic ants does not explain how the sexuals of these parasites escape culling by host workers.

The presentations varied in how closely they focussed on life histories of social insects, the central theme of the symposium. Blaine Cole raised the issue fittingly by quoting John Tyler Bonner that "the life cycle is the central unit in biology". Kazuki Tsuji put it right in our laps by pointing out that "life history is a blind spot in insect sociobiology". In the same vein, Jürgen Heinze lamented that books on social insects rarely cover life history issues and, conversely, that the standard life history texts (e.g. those of Stearns and Roff) barely mention social insects. Chris Starr (Trinidad & Tobago) reiterated these points and called for a "general theory of the colony cycle" in social insects. Highlighting Jürgen's observation, Chris argued that what is missing is a centralised database, and he called on the IUSI to establish and support an online repository for life history data on social insects. A lively discussion of the pros and cons of this proposal developed and was carried next door to the bar.

The symposium was not exclusively work. Entertainment included a welcome party, an enjoyable performance by a Russian folk trio, and an Italian opera. Two tours during the week gave us a chance to see a few of the many beautiful palaces and cathedrals for which St. Petersburg is noted. Many found time to make our way across the Neva to sample the famous art collections in the Hermitage museum.

The capstone social event was a Friday evening banquet at a well-known folk restaurant in the town of Pavlovsk, just to the south of the city. In this lovely wooden building we spent a delightful evening enjoying multiple courses of excellent Russian cuisine, listening to serenades by folk singers, and raising a great many toasts from the abundant bottles of Russian vodka and Georgian wine. The next day, most of the group took the opportunity for a real field excursion with Vladilen and Elena to one of their research sites in the taiga (boreal forest) south of the city.

I believe most who attended will agree that the symposium was very successful. There was good scientific content, the sharing of exciting recent results as well as provocative ideas, and, not least, the opportunity to get to know and interact with our Russian and Ukrainian colleagues. Our hats are off to Vladilen and Elena for doing such an excellent job of organizing and hosting the gathering. Peter the Great would have approved.

Edited version of a report by IUSI archivist  
Christopher K. Starr

**The International Symposium "Life Cycles in Social Insects:  
Behavioural, Ecological, and Evolutionary Approach"  
St. Petersburg, Russia 22-27 September 2003**

**List of Participants**

1. **Takashi Abe**, Japan
2. **Emilia Z. de Albuquerque**, Brazil
3. **Edward James Almond**, United Kingdom
4. **Serge Aron**, Belgium
5. **John Breen**, Ireland
6. **Catherine Bridge**, United Kingdom
7. **Thomas W. Chapman**, Australia
8. **Blaine J. Cole**, USA
9. **Elena Diehl**, Brazil
10. **Francis Drummond**, USA
11. **Dmitry Dubovikoff**, Russia
12. **Graham W. Elmes**, United Kingdom
13. **Lesja Firman**, Ukraine
14. **William Foster**, United Kingdom
15. **Raghavendra Gadagkar**, India
16. **Nicola Gammans**, United Kingdom
17. **Manuela Giovanetti**, Italy
18. **Eleanor Groden**, USA
19. **Myriam Harry**, France
20. **Jürgen Heinze**, Germany
21. **H. R. Hepburn**, South Africa
22. **James H. Hunt**, USA
23. **Robert L. Jeanne**, USA
24. **Manfred Kaib**, Germany
25. **Vladilen E. Kipyatkov**, Russia
26. **Alexander Komissar**, Ukraine
27. **Yaacov Lensky**, Israel
28. **Elena B. Lopatina**, Russia
29. **Andrei Maysov**, Russia
30. **Emma Napper**, United Kingdom
31. **Fernando B. Noll**, Brazil
32. **Tatiana Novgorodova**, Russia
33. **Tanja Pishcheva**, Ukraine
34. **Yves Roisin**, Belgium
35. **Virginie Roy**, France
36. **Lidia Rusina**, Ukraine
37. **Paul Schmid-Hempel**, Switzerland
38. **Oksana Skorohod**, Ukraine
39. **Christopher K. Starr**, Trinidad & Tobago
40. **Kazuki Tsuji**, Japan
41. **Stefano Turillazzi**, Italy
42. **Diane C. Wiernasz**, USA

*Life Cycles in Social Insects: Behaviour, Ecology and Evolution.*

V. E. Kipyatkov (Ed.), St. Petersburg University Press, St. Petersburg, 2006, pp. 1–20.

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

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**Abstract** – *The fundamental character 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, we are only at the beginning of an attempt at a theoretical understanding of how colony cycles are shaped by natural selection. It is proposed to initiate this process by taking advantage of a) a structural resemblance between colony cycles and the life cycles of individual organisms, and b) the substantial 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 by analogy 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 some kinds of hypotheses about colony cycles that are suggested by analogy.*

*Finally, an appeal is made for the establishment of a permanent central database for social-insect colonies, partly in the service of advancing a general theory of the colony cycle. It is suggested that this can be a feasible, cost-effective undertaking for the International Union for the Study of Social Insects (IUSSI).*

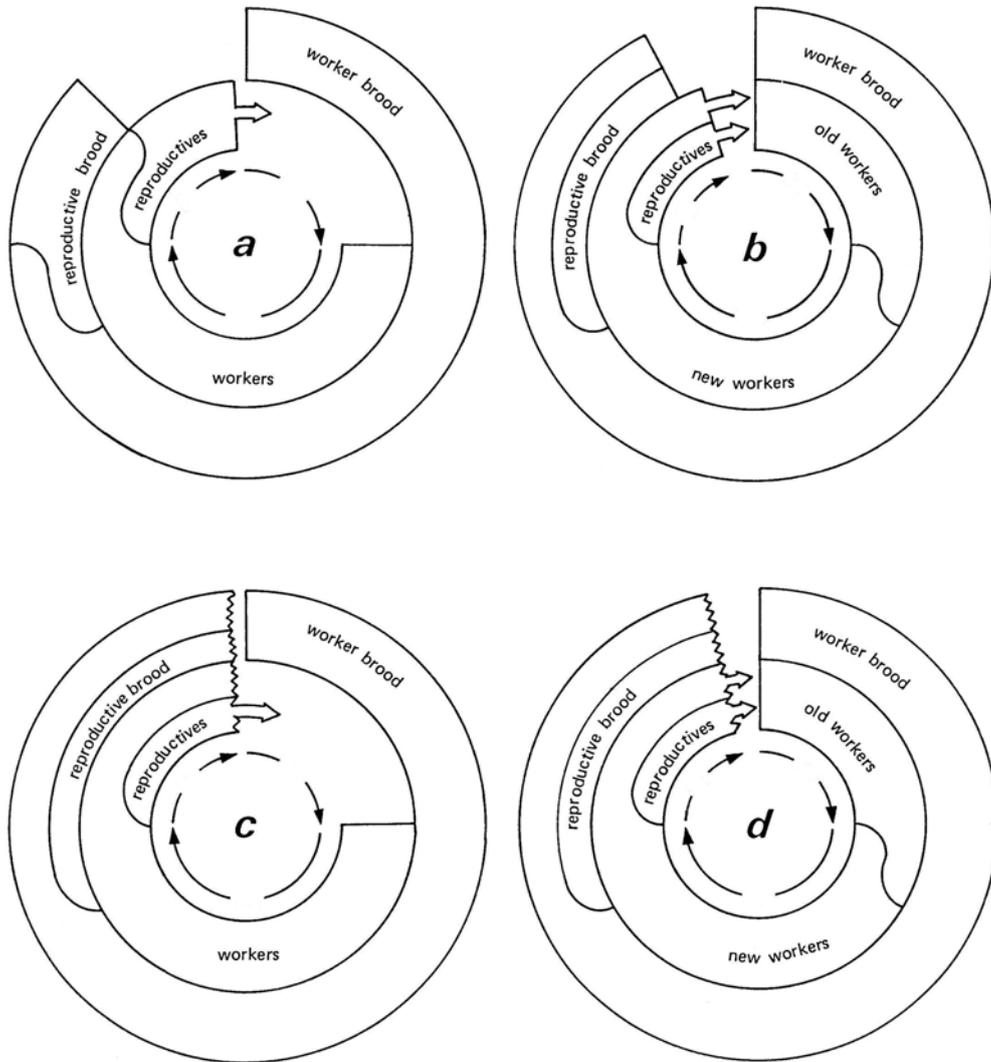
**Keywords:** colony cycle, life history, social insects, sociometrics.

### **Introduction**

"A comprehensive life history theory for social insects should aim to explain, first, why the basic ant [colony] cycle is [indeterminate] and [independent founding] .... Next, it should explain the nature, timing and scale of each part of the basic [colony] cycle, and especially how resources are partitioned between investment in growth (worker production) and investment in reproduction (sexual production). Lastly, it should uncover the reason why variants in the basic pattern evolve." Bourke and Franks (1995: 300)

The social insect colony typically comprises a queen or royal pair, a large number of workers (and sometimes soldiers), immature brood at various stages, and sometimes new reproductive individuals, all enveloped in a stationary nest.

These different types of individuals are more or less constant in form, while the colony as a whole is not. For any species, a colony of a given size has a characteristic mix of phena, and it resists any disturbance of this mix. However, overall colony size is not constant.



**Figure 1.** Schematic representation of four types of colony cycles.

- a. Determinate independent-founding, exemplified by paper wasps (*Polistes*).
- b. Determinate swarm-founding, exemplified by nocturnal hornets (*Provespa*).
- c. Indeterminate independent-founding, exemplified by most termites.
- d. Indeterminate swarm-founding, exemplified by honey bees.

The outer and inner circles indicate which types of brood and adults, respectively, are present. Labelled arrows inside the inner circle name the phases in the colony cycle, as follows: Fo – founding, Gr – growth, Rp – reproductive. A jagged line across the two circles indicates that the original colony continues past the end of the reproductive phase.

The relative numbers of different sexes, castes and life stages change and with them the character of the colony.

There are some marked regularities in these changes, so that it is meaningful to speak of a species-characteristic colony life cycle, or colony cycle. Fig. 1a shows a relatively simple colony cycle with three distinct phases, or stages, based on unequivocal events. While different authors have given these phases different names, there is little disagreement about their identity.

The cycle illustrated in Fig. 1c differs in one respect: A healthy colony undergoes several distinct reproductive phases, rather than disintegrating after just one. And that shown in Fig. 1d differs from this latter in that a new colony is founded not just by one or more queens (and kings in termites) but by a group of queens together with workers, so that workers are continuously present.

**Table 1.** Colony cycles classified according to two major variables (see Fig. 1). Known or supposed examples are given within each box.

	Independent founding	Swarm founding
Determinate	<i>Stenogastrinae</i> <i>Polistes</i> <i>Mischocyttarus</i> many <i>Ropalidia</i> Vespinae except <i>Provespa</i> social Halictinae <i>Bombus</i>	<i>Provespa</i> a few ants
Indeterminate	most ants most (all?) termites	many <i>Ropalidia</i> most Epiponini <i>Apis</i> Meliponini Dorylinae Ecitoninae

These three patterns describe the cycles of the great mass of eusocial insect species (Tab. 1). We can readily extract two basic points from a comparison of them:

1. In most species, we can meaningfully conceive of the establishment of a new nest as the start of the cycle (founding) and the production of new colony propagules as the event toward which the cycle is directed. Accordingly, it is convenient to define colony death – the end of the cycle – as the time when there are no longer any workers present.

2. Variation among taxa is expressed in two main parameters. First, Fig. 1a illustrates a determinate cycle, ending after one reproductive phase, while in Figs. 1c and 1d the cycle is indeterminate, with the possibility of many reproductive episodes. (The frequently used terms "annual" and "perennial" are a geographic special case of the same distinction.) Second, there is a distinction between independent-founding (Figs. 1a, 1c) and swarm-founding (Fig. 1d) species, depending on whether the founding group includes workers. (In non-parasitic

ants, "dependent founding" is a synonym of "swarm founding".) Except in a few species of ants, social insects do not appear to make frequent use of both founding modes.

A virtue of these two parameters is that each represents a distinct dichotomy.

Recognition of two main parameters suggests a fourth pattern, a determinate cycle with swarm founding. Does this type of colony cycle exist in nature? It is characteristic of at least two of the three species of nocturnal hornets, *Provespa* (Matsuura, 1991, 1999) and is known or expected from a few ants (K. Tsuji, pers. comm.). However, the association of swarm founding with a determinate colony cycle is evidently a rarity among social insects. It is not hard to suggest plausible reasons why this should be so. However, as far as I am aware, no one has even drawn attention to the fact that this particular pattern is so very rare.

The colony cycle is generally recognized as a fundamental property of social insects. Nesting biology is at the heart of insect sociobiology, and the colony cycle forms the framework of nesting biology, so that the proposition that colony cycles are a product of natural selection – with the corollary that this part of the phenotype should be as open to comparative treatment as are nest structure, foraging behavior, etc – is uncontroversial. It is, in fact, almost a first principle of insect sociobiology in our time.

The colony cycle of the western honey bee, *Apis mellifera*, has been well known for many centuries. It is now about a century since the main pattern of founding and colony cycle in ants and swarm-founding social wasps has been known at least in outline. Comparable knowledge is older for vespine wasps and bumble bees, somewhat more recent for termites and halictine bees, and about half a century old for army ants. As these examples show, the colony-cycle pattern is well established in all groups that have received major attention. As a result, early in almost any general treatise on a group of social insects – such as vespine wasps (Edwards, 1980; Matsuura and Yamane, 1990; Spradbery, 1973), *Ropalidia* wasps (Gadagkar 2001), bumble bees (Goulson 2003), honey bees (Gould and Gould, 1988; Seeley, 1995), ants (Hölldobler and Wilson, 1990); leaf-cutter ants (Weber, 1972), army ants (Gotwald, 1995) or termites (Grassé, 1982–86; Krishna and Weesner, 1969–70) – one finds a substantial description of the typical colony cycle and important variations on it. The first chapter of Heinrich's (1979) book on bumble bees is titled simply "The Colony Cycle", and Schneirla's (1971) book on army ants is structured around this theme.

At the same time, we still do not have even a rough draft of a general theory of the colony cycle in social insects. This is illustrated by the table of contents of any treatise or textbook on social insects as whole (e.g. Buschinger, 1985; Kipyatkov, 1991; Wilson, 1971). The colony cycle is not treated as a general subject but separately in chapters on different groups. Accordingly, when it was learned that at least some nocturnal hornets typically found new colonies by means of swarms, it was a surprise just because all other vespine wasps appear to be strictly independent-founding, not because of any theoretical reason to expect that the nocturnal hornets or any other vespine should found one way or the other. Stated another way, this question has yet to go beyond the inductivist phase of its development.

My purpose here is quite modest. It is to put the search for a general theory of colony cycles on the agenda of insect sociobiology and suggest some steps in this direction. By "general theory" is meant a framework of ideas that will draw attention to phenomena that require explanation and highlight other fruitful questions. The timing is good for such an undertaking. As seen in remarks by Jeanne (1996), Seeley and Mikheyev (2003), and especially Bourke and Franks (1995: Chapters 9–10), others have been thinking along similar lines, so that the approach taken here will hopefully have a familiar flavor for some readers.

## The superorganism analogy

In the 1870s there arose in sociology the idea that a human society could usefully be analogized with an organism. It was soon seen that the analogy could be extended to embrace societies of other animals (Espinas, 1877), and about a century ago Wheeler (1911) explicitly treated the social-insect colony as a "superorganism" with broad functional similarities to a multi-cellular organism.

This concept of the colony is with us today, although in quite different form from its first incarnation. It is most meaningful with respect to a) organization of the immediate work of the colony, and b) colony cycles. The first is the substance of the thriving research programme of social physiology and self-organization (Camazine *et al.* 2001; Detrain *et al.*, 1999; Moritz and Southwick, 1992; Pasteels and Deneubourg, 1987; Seeley, 1995), with marked advances in our understanding of how colonies forage, build nests, and maintain a suitable microhabitat, all drawing inspiration from the analogy with organisms.

The second, in contrast, has received almost no attention. That is, the modern superorganism concept tends to treat colonies as systems for efficient foraging, nest construction and maintenance of suitable microclimatic conditions, but not as systems geared to replicating themselves. Might this be because there is no body of general ideas on (individual-level) life cycles to suggest analogous features in colony cycles? Not at all.

## Life-history theory

"[Life history theory] has successfully explained: why organisms are small or large, why they mature early or late, why they have few or many offspring, why they have a short or long life, and why they must grow old and die." (Stearns, 1996)

"Life history theory has been extraordinarily successful in providing a framework within which to understand evolutionary change." Roff (2002: 459)

Half a century ago, Cole (1954) set forth the mathematical framework for analyzing the consequences of differences in life-history traits. Today life-history theory is a robust sub-discipline of population biology with a number of recent book-length treatments (Charnov, 1993; Roff, 1992, 2002; Stearns, 1992). A simple indication of its maturity is seen in the standard set of demographic notation that has long been uniformly accepted.

As Heinze (pp 49–61 of this volume) notes, almost no connection has yet been made between insect sociobiology and life-history theory. The one substantial attempt in this direction of which I am aware is in Bourke and Franks's (1995: Chapters 9–10) book on ants, which demonstrates considerable variation in details within the scope of a common pattern applicable to most species. The reasons for this general mis-connection are not obscure: The colony cycle is not recognized as a topic within life-history theory, and the life-cycles of individual social insects have little relevance apart from the colony cycle.

Still, the large existing body of (individual-level) life-history theory can serve as a ready-made source of inspiration in initial steps toward general formulations regarding the colony cycle. In what follows, my first concern is to propose how we might utilize existing theory as analogical stepping stones. In so doing, I hope we can take our distance from one particular aspect of Bourke and Franks's treatment. Although they do not say so explicitly, it is implied that a general theory of the colony cycle will form an integral part of life-history theory. In my view, it is preferable at present to treat the analogy between developmental

cycles in individuals and colonies as a valuable source of conjectures, to be received with scepticism. It will serve this purpose if the term "life cycle" is no longer applied indifferently to individual organisms and to colonies. Only the first sense is used here.

Allied with this shortcoming is a tacit tendency to equate the colony cycle in some cases with the life cycle of the queen. They are often very closely tied to each other in monogynous colonies without queen replacement, but they are not the same.

I will review some features of life-history theory, with a view to reaching a preliminary judgement of their analogical relevance to the study of colony cycles. In so doing, one is automatically drawn into a sort of triage, setting to one side those features that obviously (perhaps trivially) apply, to the other side those that obviously do not apply, and investing the uncertain ones with especial interest

Two obvious outstanding general differences between a colony and a metazoan animal merit early emphasis.

First, the individual parts of the colony are physically uncoupled. One important result of this is that there is more than one fundamental way to reproduce the colony.

Bonner (1993: 24) noted with some puzzlement that most animals and plants pass through an extreme size bottleneck in their life cycles, by starting out as tiny embryos. Why do they go to all this bother? "Would it not be much easier", he asked, "simply to pinch in two and regenerate the missing half ...?" The answer seems to be that they do so because there is no good way to avoid it. Social insect colonies, in contrast, are not obliged to pass through this bottleneck, and in roughly 10% of species they bypass it through swarm founding. Why, then, is independent founding the rule in social insects? This is among the key questions that any general theory will have to address.

Second, the components are genetically heterogeneous, not a clone, so that there are necessary genetic conflicts of interest within the colony. No one before W.D. Hamilton seems to have given this point any weight, yet it is the largest pillar of today's insect sociobiology (no references needed). Should a general theory of the colony cycle take kin conflict into account? In time, it must. As an example, the colonies of many north-temperate social wasps turn rather abruptly to a phase of brood slaughter – the "couvain abortif" of Deleurance (1950, 1952) – toward the end of the season. A general theory should be able to predict whether such brood cannibalism is adaptive at the colony level or if it only makes sense from the point of view of those adults who kill and eat. For the present, however, I believe we can legitimately set kin conflict aside under the simplifying assumption that it does not shape the main differences between taxa in their colony cycles. Still, this "present" may be short-lived, as we are already seeing attempts to model the role of kinship in shaping colony cycles (e.g. Bourke and Chan, 1999; Crozier and Pamilo, 1996; Herbers *et al.* 2001; Peters *et al.*, 1999; Reuter and Keller 2001).

While Fig. 1 simplifies the diversity of known colony cycles, it is not a gross oversimplification. This narrow variation in colony cycles, compared with what is found in the life cycles of individual organisms, facilitates our purpose. To give an example, alternation of (colony) generations is unknown in social insects. No free-living species has alternating sessile and errant generations, and no social-parasitic species has both an intermediate and a definitive host.

There are today two basic approaches in life-history studies: optimization and genetic. Optimality analyses commonly assume enough genetic variation to let organisms evolve the best combination of features within external constraints. This approach fits social-insect

colonies well and is expected to predominate in colony-cycle studies for the foreseeable period. After all, interactions among life-history variables occur in every individual of every generation over evolutionary time, so that we should expect fine-tuning of those interactions that determine inclusive fitness.

It is noteworthy that theory about social-insect evolution has long been based on genetic models, yet information about genetic bases of social variation has been slow in coming, especially with respect to between-colony differences. The one known case in which dimorphism or polymorphism of a colony trait is controlled by one or a small number of genes – that of the monogyne and polygyne forms of the fire ant *Solenopsis invicta* (Ross and Shoemaker, 1997; Valles and Porter 2003) – is evidently very unusual. There is no indication that distinct polymorphism of colonies within a population is at all common in social insects.

The basic substance of life-history theory is the schedules of birth and death, so that the terms  $l_x$  and  $m_x$  – survival to age  $x$  and reproduction at age  $x$ , respectively – are used without unambiguity and often without definition. Calculation of lifetime fitness involves computing the manner in which birth and death rates change with such factors as age and size. The key parameters in this calculation are: a) size at birth, b) growth pattern, c) age at maturity, d) size at maturity, e) number and size of offspring, f) sex-ratio of offspring, g) age- and size-specific reproductive investments, and h) length of life.

It is plain that each of these parameters except (f) sex-ratio of offspring is analogically applicable to colony cycles. That is, it is meaningful to speak of (a) the number of individuals in a colony at founding, (b) the pattern of increase in number of individuals over time, etc. As an opening conjecture, one can suggest that each of the meaningful analogical parameters will be found to have much the same place in a general theory of the colony cycle as it does in life-history theory.

You can confirm the reasonableness of this view by reading a representative passage from one of the general treatments of life-history theory as if it were about colony cycles. What results in most cases is a series of statements that sound like they might be true and are, in any case, not nonsensical. Still, in hardly any case has the question yet been posed of whether such statements are, in fact, true.

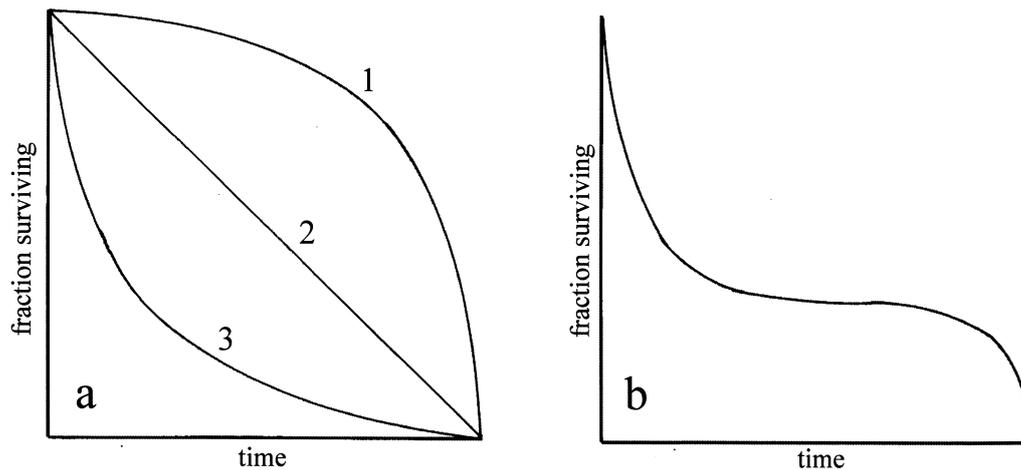
In a spirit of skeptical appreciation, I would like to consider some features of life-history theory, with a view to suggesting how they might serve our purpose.

## Life tables and survivorship curves

Survivorship curves are commonly divided into three types (Fig. 2a). Type 2, which assumes a constant probability of dying in all intervals, is the simplest. It is also the least expected in nature, including at the colony level, as there is good reason to expect that mortality rates will, in fact, be markedly inconstant. Mortality rates of individuals are age-specific, although age per se appears not to be a generally important factor. Rather, other factors that tend to vary with age – such as developmental stage, body size, reproductive status – are key. It seems almost certain that colonies will show a strong analogy in this respect, as has long been known for the western honey bee.

Of the three ideal survivorship curves, Type 3 is probably the most widely applicable to social-insect colonies, and it may be the strong general rule among independent-founding species. Colonies, like organisms, are likely to escape from some important predators as they grow. Anyone who has noticed the huge numbers of ant and termite reproductives that fall

prey to lizards, birds and ants and then has seen large nests of the same species continuously inhabited year after year will have little difficulty with this untested generalization. Consistent with this view, only 1.3% of colonies of the harvester ant *Pogonomyrmex occidentalis* survive to the end of their first year (Cole and Wiernasz 2002).



**Figure 2.** Idealized survivorship curves, with fraction surviving on a logarithmic scale. *a.* The most commonly recognized curves, taken from any textbook of population biology or life-history theory. *b.* Hypothetical colony survivorship curve resulting from i) high mortality in the independent-founding phase, ii) very low mortality during the growth and most of the reproductive phases, and iii) maximum lifespan set by the life of the (irreplaceable) queen.

In the biology of independent-founding social wasps, the founding stage is commonly regarded as a time of exceptionally high colony mortality, although few hard data are available. One clear indication that founding-phase colonies of independent-founding social wasps are at high risk is provided by Queller (1996: Tab. 13.1): In six species in which both haplometrosis and pleometrosis are frequent, pleometrotic colonies have a markedly higher probability of surviving to the growth phase. In one of the very few formulations of a colony-level life table, Miyano (1980: Fig. 1) found patterns strikingly consistent with a Type-3 curve in two of three populations of *Polistes chinensis*, with a clear improvement in survivorship around the end of the founding phase (see also Turillazzi, 1984: Fig. 2.1 on *P. nimpha*). This makes sense if the emergence of the first workers coincides with the colony growing more or less abruptly out of risk from some important enemies.

Accordingly, I propose as a candidate principle of the colony cycle that colony mortality in independent founders is by far highest during the founding phase, the very period in which the colony does not enjoy the advantages of sociality. It is called a "principle" advisedly, as the existence of such a high-risk stage early on must shape the cycle as a whole. Such a principle seems to be in harmony with present thinking about social insects (e.g. Bourke and Franks, 1995: 304), although it remains without broad empirical support.

A comparable general hypothesis for swarm-founding species is not so readily at hand. It seems likely that the colony is at somewhat greater risk right after division than right

before, but it is far from obvious whether this difference should usually be large. Furthermore, if there is a substantial risk involved, is it mainly from decreased colony size or the loss of the nest? This question would seem quite open to experiment with a species in which one can induce either an in-place reduction in size or an intact absconding swarm. However, even in so intensively studied a species as the western honey bee, I am aware of no strong evidence pointing to a Type-3, Type-2 or Type-1 survivorship pattern. If the death of wild colonies is usually due to senescence of the queen, the latter curve would seem to apply. What does seem obvious is that there is no reason to propose that swarm founders in general are at any extraordinary risk during the founding or any other phase of the colony cycle.

It should be noted that these three are not the only possible idealized patterns, and it seems likely that others exist in nature. For example, an ant species might plausibly combine high early mortality with very low mortality after the founding phase and a maximum lifespan set by queen longevity, giving rise to a sigmoid curve with high survivorship in the middle part (Fig. 2b).

### **Relationships among parameters: Trade-offs**

"The basic hypothesis underlying most analyses of the evolution of life history traits is that variation is constrained in large measure by trade-offs between traits." (Roff, 1992:1)

Life-cycle syndromes are "suites of characters that covary and function together" (Dingle, 1986), so that a change in one stage or parameter may well have consequences in another. For example, generation time shows a distinct positive correlation with adult body size across a very broad range of taxa (Harvey and Pagel, 1991: Fig. 1.1). Larger organisms may tend to live longer simply because they must, as a combination of large body size and short life cycle will usually not work.

There are two things of note in this relationship. First, it is allometric. Within a given taxon, and to lesser extent among taxa, many physiological and ecological variables – including those relevant to life-history theory – relate to each other at least approximately by a power function  $y=c+bx^a$ , in which the allometric constant  $a$  is not equal to 1. If  $y$  is generation time and  $x$  is body length, for example, then  $a\approx 0.82$  across a broad taxonomic range of organisms (based on Harvey and Pagel, 1991: Fig. 1.1).

There is now a large literature on how other life-history traits vary with body size (Roff 2002: Tab. 4.10). It is reasonable to expect various colony-level variables to vary with colony size in similarly lawful ways, yet the exploration of these relations has only just begun. As an example, parasite load in some social insects is known to increase allometrically ( $a > 1$ ) with colony size (Schmid-Hempel, 1998, pp. 37–48 of this volume).

Second, any such relationship between two parameters can be posed so that the correlation is negative. In the example just cited, the fraction of parasite-free colony members correlates negatively with colony size.

In itself, this second is a trivial feature, but it serves to highlight a central concept from life-history theory that can be imported intact and without hesitation into any general theory of the colony cycle. A trade-off is a causal relationship that constrains simultaneous evolution of two or more traits. This is a very accessible concept, with many examples available in such areas of everyday life as home economy and sport. A successful decathlete,

for example, is celebrated for minimizing the consequences of a series of trade-offs. What it means for our purposes is that the colony cannot do everything, that choices must be made. A trade-off is not a compromise, although it may demand a compromise.

Charnov (1993: Tab. 5.1 and 5.4) compared the expected and observed correlations between pairs of four life-history variables for mammals. With the exception of one pair, in which the expected correlation was uncertain, the direction of the observed correlation matched the expected.

**Table 2.** *Life history traits involved in trade-offs. A trade-off is demonstrated or inferred between each pair of these nine traits, a total of 45 pairs. From Stearns (1992).*

- |                         |
|-------------------------|
| 1. Current reproduction |
| 2. Parental survival    |
| 3. Future reproduction  |
| 4. Parental growth      |
| 5. Parental condition   |
| 6. Number of offspring  |
| 7. Size of offspring    |
| 8. Offspring condition  |
| 9. Offspring survival   |

The most studied trade-offs in organisms are: a) current reproduction vs parental survival, b) current reproduction vs future reproduction, c) reproduction vs growth, d) reproduction vs offspring condition, and e) number and quality of offspring (Stearns, 1992; Tab. 2). A noteworthy feature of such trade-offs is that, despite the very strong logic behind them, it can be surprisingly difficult to demonstrate them in practice. To give two illustrations from Roff (1992: Tab. 6.3 and 6.8), a) a review of studies of correlation between reproduction and survival in 17 animal species showed the expected negative correlation in only four species, against a positive correlation in four, and no significant correlation in the other nine, and b) in only seven of 13 studies of the manipulation of brood size in birds was a significant effect on the next brood shown.

**Table 3.** *Suggested colony-level states of some social-wasp genera with respect to r-selected traits. The traits are: 1) rapid development, 2) a high rate of increase, 3) early reproduction, 4) small size, and 5) semelparity (Pianka 1970). The scoring is based on my own experience as an observer of social wasps and in places is more impressionistic than quantitative. IF – independent-founding species, SF – swarm-founding species.*

Genus	1	2	3	4	5
<i>Polistes</i>	+	+	+	+	+
<i>Mischocyttarus</i>	+	+	+	+	+
<i>Ropalidia</i> IF	+	+	+	+	+
<i>Ropalidia</i> SF	-	-	?	-	?
<i>Polybia</i>	+	-	+	-	-
<i>Vespa</i>	+	+	+	-	+
<i>Vespula</i>	+	++	+	-	+
<i>Dolichovespula</i>	+	+	+	±	+
<i>Parischnogaster</i>	?	-	?	++	+

Despite these practical difficulties, the study of possible trade-offs at the colony level is a necessary part of understanding the colony cycle. I suggest that the most demonstrable trade-offs are likely to be: a) production of many small vs few large workers, b) in termites, production of workers vs soldiers, c) reproduction vs further growth, and d) size of colony propagules, with emphasis on independent-founding vs swarm-founding. Especially in ants, it should be feasible to manipulate features of the colony to test these propositions. The focus below is on aspects of the last two kinds of trade-offs.

At the same time, there is a limitation inherent in the study of simple trade-offs within pairs of parameters. This is recognized in the concept of r- and K-selection, as outlined in almost any population-ecology textbook. The focus of these opposing terms shifted after they were first proposed to describe selection in density-regulated and -unregulated environments (MacArthur and Wilson, 1967), so that they came to be associated with suites of characters (Tab. 3). The terms have fallen into some discredit, yet a presumption remains that two alternative sets of traits approximating these represent a widespread reality (Stearns, 1992).

If not too much is made of it, it is a reasonable working hypothesis that analogous sets of characters are to be found at the colony level in social insects, something that must have occurred to many in our discipline. The pattern of conjectures shown in Table 3 is consistent with the view that a general theory of the colony cycle will develop around the functional understanding of syndromes of characters much more sophisticated than the simple beginning illustrated in Fig. 1.

### **Reproduction: Now or later?**

"We are still far from understanding why some organisms are semelparous and others are iteroparous. In particular, does semelparity result from extreme reproductive effort, or is death inevitable and extreme reproductive effort a response to it?" (Roff, 1992: 394)

"One way to understand the adaptive design of the life history of a social insect colony is to view the colony as having an investment policy whereby it allocates limited resources among the various physiological functions fostering its growth, survival, and reproduction." (Seeley and Mikheyev 2003)

The presumed trade-off between present and future reproduction is at the heart of the distinction between semelparity and iteroparity (or monocarpy and polycarpy, respectively, in plants). Iteroparity – the tendency to reproduce in several episodes over an extended period – appears to be more common, overall, in multicellular organisms. Examples of semelparous species – in which all reproduction comes in a single burst toward the end of the parents' life – are many insects, Pacific salmon, bamboos, some oak trees, and annual plants. As with much else in life-history theory, it is very easy to enumerate the relative advantages of each habit and very difficult to say why a given habit is found in these taxa but not in these others. A closely analogous situation is seen in the distinction between determinate and indeterminate colony cycles.

The question of the circumstances in which it is worthwhile to devote less or more of one's resources to reproduction goes back at least to Fisher (1930). Reproduction by an organism is logically assumed to come at a cost to its future reproduction and/or expected longevity. If it did not, the organism should start reproducing as early as possible, which most do not. Reproductive effort (RE) is the proportion of available energy devoted to

reproduction, rather than into self-maintenance or growth, during a given period (Hirshfield and Tinkle, 1975). This is often taken to refer only to surplus energy, beyond that needed to keep the organism alive, so that it becomes primarily a question of growth versus reproduction. The age schedule of reproduction is a reflection of how this trade-off is resolved.

As a rule, organisms and colonies become larger with age, and fecundity tends to increase with size. We expect, then, a definite positive correlation between age and fecundity, even if the causal link is weak. The relationship between size and fecundity has been extensively studied at the organismal level (Roff, 1992:126–28). As expected, there is a distinct tendency for larger individuals to reproduce more. The allometric constant varies widely among taxa, with a suggestion that larger individuals tend, on the whole, to be more fecund per body mass. There is no necessary problem in the allometric nature of the relationship or in the great variation between taxa, as long as size and fecundity remain positively correlated.

Colonies face the same question as do organisms with respect to the timing of reproduction: Is it better to reproduce a smaller number of propagules early or to delay in expectation of producing more when one is bigger? In its direct form, with relation to single organisms, this question has been with us for at least 50 years. With respect to colonies in relatively non-seasonal environments, it is almost untried, although I imagine that most of us have puzzled over it, as did O. W. Richards. Based on his experience with many species of social wasps in Guyana, he asked why colonies of some species persist for a year or more and grow to very large size, while others stay small and break up after a few months (Richards and Richards, 1951; Richards, 1953). It is easy enough to frame a conjecture in terms of bet-hedging, as is often done where attacks by army ants are common and irresistible, but why do species in the same locality hedge their bets so variously? Richards's sketch of a working hypothesis was that small-colony species tend to have a higher RE and invest less in such things as resistance against natural enemies, but my own experience leaves me far from satisfied that any such clear trend exists. Still, I am not aware that we have even a plausible alternative hypothesis in this important question.

Models of social insects in strongly seasonal environments predict that the colony should delay the reproductive phase as long as external conditions allow it to remain productive (Bourke and Franks, 1995; Oster and Wilson, 1978). One of the very few broad theoretical generalizations about colony cycles is that it is optimal for the reproductive phase to start abruptly, with no new worker eggs laid after the first reproductive eggs (Macevicz and Oster, 1976; Oster and Wilson, 1978; modified by Cassill 2002 to accommodate indeterminate colony cycles). This "bang-bang" hypothesis is accessible and attractive, yet it remains almost untested. This is really quite puzzling, as in most social insects it is exceptionally easy to detect the change-over from worker to reproductive production in the colony. In the one explicit test of which I am aware, Greene (1984) found only an indifferent fit between the observed and expected patterns in vespine wasps and gave reasons to predict a departure from bang-bang. Archer (1981) similarly found an overlap in the initiation of worker and reproductive brood in two other vespines.

My own more casual observations with independent-founding social wasps are consistent with those of Greene and Archer, as is implied in Fig. 1a. That is, although few workers are produced after the start of reproductive production, there is significant overlap. I suggest that the now rather sterile question of whether social insects adhere to a bang-bang pattern or not should give way to a more fruitful comparative one: What is the diversity among

species in departure from strict bang-bang, and how can it be explained? To begin with, it should be easy to devise a one-dimensional goodness-of-fit index and apply it to coexisting species of independent-founding polistine wasps, or to conspecific populations in different habitats. Predicting or explaining differences in departure from strict bang-bang – or even saying why there should be differences at all – will be more of a challenge.

At the colony level the size-frequency allometry is at the heart of a long-standing conundrum. In surveying data on reproductive output in social hymenoptera, Michener (1964) found that as a colony grows its total reproductive output increases, but output per adult female decreases. Accordingly,  $a < 1$ , where  $y$  is number of colony offspring and  $x$  is colony size. Unlike at the individual level, this "reproductivity effect" (Wilson, 1971: 338) poses a problem. While a large multicellular plant or animal does not have the option to divide into two or more smaller individuals, social-insect colonies usually can do just this. If  $a < 1$ , any large colony would do better to break up immediately into smaller units, so that no species should characteristically develop large colonies. Similarly, swarm founding should not exist, as the parent colony would do better to invest in independent-founding queens.

Discussions of the reproductivity effect tend to focus on the fact that Michener's analysis did not take into account colonies that have zero reproductive output because they fail early, and to suggest that larger colonies enjoy greater survivorship. The tacit assumption, then, is that colony survivorship approximates a Type-3 curve. However, I am unaware of any attempt to reach a more definite solution to this problem.

Social insects would appear to have exceptional flexibility in the allocation of resources to reproductive vs non-reproductive brood, according to the immediate situation. The developmental period is short, relative to that in metazoan animals of the same cumulative body mass. And in swarm-founding species the decision regarding the fraction of workers to allocate to the swarm can wait until close to the time of departure. It is as if an animal could wait until the moment of giving birth to decide what fraction of her substance to invest in the offspring.

The trade-off between reproduction now or later may also in many cases be a question of reproduction vs survival. Although it can be difficult to demonstrate, it seems very likely that for colonies of most species reproduction poses distinct risks to survival. What is far from clear is whether these risks are generally high, and it will probably be difficult to seek answers in a well-controlled fashion.

## **The number and size of offspring**

Do larger colony propagules fare better? This question would seem to be especially acute for swarm-founders. Swarms are necessarily very few in number, and any swarm substantially depletes the size of the parent colony. It appears almost self-evident that a larger swarm will have greater reproductive value (expected lifetime reproductive output) than a smaller one. This is corroborated in the few species studied to date (Winston, 1987:189; Jeanne and Nordheim, 1996), and there is every reason to expect that such a positive correlation is general and strong.

Given such a correlation, what is the shape of the curve? It would be hard to explain any simple curve, as this would select either for independent founding or for the whole colony as a swarm, and a straight line would seem decidedly unnatural. It is predicted that colony reproductive value as a function of swarm size will show a sigmoid function, with modal

swarm size where the slope is steepest. This can be tested experimentally by the induction of absconding swarms of varying size in a swarm-founding wasp. The difficult part, it seems to me, will be to devise a convenient index of colony productivity that is proportional to expected reproductive success.

In independent-founders, as well, the colony has a choice of investing in many smaller or few larger reproductives, and it is generally supposed that in queens, at least, larger size confers an advantage. As a rule, males are about the size of workers, but in most ants and some other social hymenoptera queens are substantially larger. The common question with respect to this discrepancy has to do with why workers are so small, but let us turn this around and ask why queens are so large.

The evidence, while mostly fragmentary and indirect, seems unequivocally in favour of the view that larger queens do better than smaller ones, as in organisms as a whole, as the founding stage is likely to put severe demands on a their body reserves (Wheeler and Buck, 1996). In one of the few direct studies of this question, Wiernasz and Cole (2003) found a strong positive correlation between size and survivorship in *Pogonomyrmex occidentalis* queens. In addition, as a rule in ants, queens are significantly larger in haplometrotic than pleometrotic species (Wiernasz and Cole 2003). The working hypothesis suggested by these results is that colonies of independent-founding species produce large queens at a cost in numbers because large queens have a decided advantage in the founding stage. The observation that the (short-lived) males are smaller is consistent with this hypothesis. Against this hypothesis, it would appear, is the observation that in termites, queens and kings are usually the same size and not strikingly bigger at final moult than workers.

At the individual level among related species, those with larger females tend to produce larger offspring and at the same time to produce more of them, so that investment per offspring is a compromise between a constant absolute amount and a constant proportion (Clutton-Brock, 1991; Fox and Czesak 2000). Does a similar pattern obtain at the colony level? With correction made for phylogenetic effects, this seems like quite a tractable question in both independent-founding and swarm-founding taxa.

### **Conclusion: What is to be done?**

"Animal sociology remains, in comparison [to human sociology], at its very beginning. To be sure, outstanding specialists have accumulated an enormous mass of facts and have published a great many substantial works in recent decades, from which we have gained deep insights into the biology and organization of animal societies. However, it is only in very recent times that we have seen any attempt to analyse this material from a sociological perspective." (Eidmann, 1928)

"There are virtually no general predictions in life history theory, because some organism can always be found with a tricky and unexpected trade-off that violates the assumptions, because the predictions themselves depend on the state of the life history, and because we do not yet have reliable source laws to predict the critical trade-offs." Stearns (1992: 208)

This, then, is the present status of our understanding of colony cycles in social insects:

1. The basic pattern is well known in a wide variety of taxa.
2. The analogy with individual-level life cycles remains very little exploited.
3. Where the analogy is recognized, the untested assumption that results can be carried over from individual-level life-history theory prevails.

4. The task of explaining differences in colony cycles among taxa has hardly begun.

Michener's (1964) reproductivity effect has been subject to very few tests. On the one hand, this is baffling, as the reproductivity effect has never been treated as comfortable conventional wisdom. At most, it seems to be uncomfortable conventional wisdom and so should serve as an attractive target of new inquiries. On the other hand, it is no mystery why no one has set out to replicate and expand Michener's analysis from existing data. The data are scattered, fragmentary and often ambiguous for the purposes of any broad comparative test. Similarly, anyone testing for colony-level trade-offs across a variety of taxa would likely find the task rather frustrating. Like much of population biology, life-history theory is very fact-intensive, and it is not yet close to a state where the mass of facts ceases to bewilder.

The relevant parameters are by no means obscure or peripheral, yet, as Tschinkel (1991) has noted, the collection and publication of any basic data that do not serve an immediate hypothesis have become quite unfashionable in insect sociobiology. As a result, even such a valuable and easily measured parameter as average colony size at maturation is calculated in very few independent-founding social wasps, for example, and virtually never unless it serves to address an immediate question.

To cite another example, Hölldobler and Wilson's (1990: Tab. 3–2) compilation of colony sizes in ants probably represents the bulk of published data. To anyone outside of our discipline, it would probably appear shocking that this fundamental data-set comprises just 135 species – of which 57 are based on just one colony and another 19 on two – with about 40% derived from a single paper (Wilson, 1959), and is not consistently based on mature colonies.

The key problem is not exactly a paucity of data. Rather, what is missing is a centralized database of colony-level parameters. That is, it is mainly an information-retrieval problem. When researchers undertake a broad comparative study, the customary approach to amassing the data is the same as it was a generation ago: survey the literature and then put out an appeal for unpublished or obscurely published data. Electronic search and communication methods contribute speed to this procedure, but it is fundamentally archaic. A freely accessible repository for both published and unpublished data could do much to promote and democratize the analysis of insect societies.

There is a good model for such a database. The Human Relations Area File (HRAF, <http://yale.edu.hraf/>), based at Yale University, has existed since 1949 to accessibly store data on human societies. The HRAF stores data on about 365 ethnic and religious groups according to a detailed classification. Nothing even remotely comparable exists for the study of insect societies. It is a brake on progress in our discipline that well-rounded, publishable data-sets and especially more fragmentary, obscure, and unpublished data do not automatically go into a central database and are therefore not accessible with Internet ease.

It is certainly not because of any intrinsic difficulty that the HRAF model has not been emulated in insect sociobiology. The number of "species" is of course larger, but the number of data categories would certainly be much smaller (see Tschinkel, 1991: Tab. 1, and the appendix to this paper) than the hundreds recognized by the HRAF. All in all, this is not a daunting enterprise. The main value of such a database would likely be in the understanding of colony cycles, but the uses of a good data-set commonly go well beyond those originally conceived.

The central practical problem is that a general database on social insects is not the obvious responsibility of anyone in particular. Who, then, should manage it? One option is

to seek an institutional base, like that enjoyed by the HRAF and a new electronic database of ant taxonomy (<http://www.antbase.org>). An alternative is to adopt it as a major, permanent initiative of the International Union for the Study of Social Insects (IUSI), the organizing body for our discipline.

This second option may seem quite radical in an age when scientific societies have long since almost entirely stopped organizing research and restricted themselves to facilitating discussion and publication. Nonetheless, there is much in favour of it. Management of the database need not be especially expensive – requiring perhaps one full-time staffer – and until such a resource has the weight of tradition there are risks in entrusting it to the hospitality of an institution. It seems fair to predict that a well-run database would quickly gain enough popularity among insect sociobiologists to ensure outside funding and its continuation by the IUSI.

This proposal is hereby laid before the IUSI as a formal motion for implementation.

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## Appendix

*Draft list of sociometric parameters for a database on social insects. The list is limited to that part of the database needed for a description of the colony cycle, leaving aside such areas as nest structure, feeding habits, and within-colony kinship. For an alternative classification of much the same subject area see Tschinkel (1991: Table 1).*

Modal numbers of colony-founding group members

- a) Queens, b) males/kings, c) minor workers, d) major workers, e) brood according to each stage (in swarm-founding species, distinguish between mother and daughter colonies).

Modal numbers of colony members at the start of the growth phase

- a) Functional queens, b) males/kings, c) minor workers, d) major workers/soldiers, e) brood according to each stage.

Modal numbers of colony members at the start of the reproductive phase

- a) Functional queens, b) males/kings, c) minor workers, d) major workers/soldiers, e) brood according to each stage.

Modal weight of colony-founding group members

- a) Functional queens, b) males/kings, c) minor workers, d) major workers/soldiers, e) brood according to each stage.

Modal weight of colony members at the start of the growth phase

- a) Functional queens, b) males/kings, c) minor workers, d) major workers/soldiers, e) brood according to each stage.

Modal weight of colony members at the start of the reproductive phase

- a) Functional queens, b) males/kings, c) minor workers, d) major workers/soldiers, e) brood according to each stage.

Forms that undergo seasonal diapause

Duration of seasonal diapause

Mean egg-to-emergence time

- a) Queens, b) males/kings, c) minor workers, d) major workers/soldiers.

Schedule of production (sequence of emergence) of new individuals according to sex and caste

Ratio of minor/major workers (or workers/soldiers) according to colony age

Ratio of minor/major workers (or workers/soldiers) according to colony size

Mean duration of the founding phase

Mean duration of the growth phase

Mean colony generation time

Colony survivorship through the founding phase  
(in swarm-founding species, distinguish between mother and daughter colonies)

Colony survivorship through the growth phase

Colony survivorship according to age

Colony survivorship according to number of workers

Number of colony propagules according to age

Number of colony propagules according to number of workers

*Life Cycles in Social Insects: Behaviour, Ecology and Evolution.*

V. E. Kipyatkov (Ed.), St. Petersburg University Press, St. Petersburg, 2006, pp. 21–36.

## **Life history strategy and evolution of insect societies: Age structure, spatial distribution and density dependence**

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### **Introduction**

Research in insect sociobiology has been isolated from that on life history evolution. With a few exceptions (Oster and Wilson, 1978; Bourke and Franks, 1995; Akimoto, 1996; Tsuji and Tsuji, 1996; Keller and Genoud, 1997; Horiuchi *et al.*, 2002) theories of life history strategies have almost never been referred to in the literature on the evolutionary biology of social insects. Simultaneously, life history strategy theories almost never have tackled complex phenomena observed in social insects such as castes and division of labor (Heinze, Starr this volume). The aim of life history strategy theories – to explain any pattern of phenotypic variation (Stearns, 1992) – implies that they should also include evolutionary theories of social behavior. Though kin selection is an important aspect of evolution, however, I suggest it can be integrated as a special aspect of evolutionary theories of life histories. This does not mean that studies of social evolution are less important than those of life history evolution in general. As humans are also social, understanding animal social behavior will always be an ultimate goal of our intellectual activities driven by the inevitable curiosity to know ourselves. This quite parallels medical science, which is largely a specific discipline of biology but is often more important for us than biology as pure science.

Theories of insect sociobiology are either explicitly or unconsciously based on various simplified assumptions about the life histories of the study animals. Simple assumptions enabled us to tackle phenomena, which are indeed complicated, while simultaneously led us to disregard issues that are important in life history strategy theories. In this article I examine age structure, a subject that hitherto has been largely ignored in studies of social evolution. I set out a number of testable hypotheses about the effect of population demography and spatial structure on the evolution of individual and colonial characteristics of social insects. In addition, I propose a preliminary model in which I attempt to integrate some aspects of life history strategy and kin selection theories. I hope that with this approach we can find a breakthrough to a number of issues that are still difficult to understand in the paradigm of social evolution.

## Age structure as a blind spot in social evolution theories

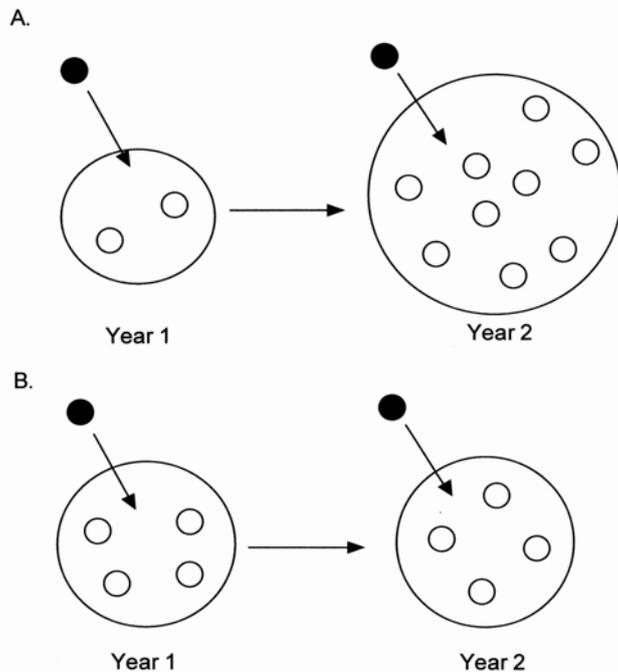
Insect sociobiologists need to pay more attention to age structure. Ants, honey bees, termites and possibly also many tropical social wasps and bees, have age-structured populations. Age structure involves phenomena, such as overlapping generations, perenniality and iteroparity. Life history strategy theory is less straightforward than single-trait optimality theories, because it has to simultaneously handle many parameters. Among its topics the evolution in age-structured populations is a theoretical challenge, because in an age structured population it is difficult to define fitness, “the currency” of adaptive evolution or the predictor of allele frequency change (Stearns, 1992; Charlesworth, 1994).

The parameters in inclusive fitness models or Hamilton’s rule ( $br-c > 0$ ) are individual fitness and relatedness. A good measure of individual fitness (fitness of genotype) in empirical studies is usually the number of offspring, i.e. the lifetime reproductive success or the net reproduction rate ( $R$ ) (Grafen, 1984; Clutton-Brock, 1988). However, this holds only true in the absence of age structure. Theories of life history strategy suggest that under age structure lifetime reproductive success is only a good measure of fitness when the population size is kept constant by some density-dependent processes. When the population size changes in a density-independent way, the timing of reproduction as well as the number of offspring is both important fitness components. More precisely, in an increasing population, the intrinsic rate of natural increase ( $r$ ) is the appropriate measure of fitness in many circumstances (Caswell, 1989; Stearns, 1992; Charlesworth, 1994). I try to illustrate, why timing is important for replicating genes in Figure 1.

As the per-gamete impact on the population gene frequency change is larger as the population is smaller (Fig. 1), in an increasing population fitness per gamete is larger the earlier gamete production ( $r$ -selection). The simplest mathematical expression of this is as follows. The strategist who dies at age  $t$  just after leaving  $R$  offspring will have  $R^{(t)}$  descendants after  $t$  years. When  $R > 1$ , the number of descendants after a given time, increases with decreasing  $t$ . In theories of life history strategy, it is often discussed that earlier reproduction is more effective to increase fitness than increasing lifetime fecundity (Pianka, 1974; Wilson, 1975). In the next section, I will discuss the variation in dispersal behavior in social insects as a possible case in which timing of reproduction can be an important fitness component.

## Dispersal behavior and density dependence

Ants and termites are dominant in terrestrial ecosystems in the world, expanding to various ecological niches from tropical rain forests to more arid boreal habitats. It seems to me difficult to believe that all of them live in environments where population size is regulated by a density-dependent process. The common occurrence of the coexistence of multiple reproductive females, polygyny, in ants and termites has been discussed as the challenge of kin selection theory (e.g. Nonacs, 1988; Roisin, 1993; Keller, 1995). I have pointed out in the collaboration with Nobuyuki Tsuji (Tsuji and Tsuji, 1996) that the issue of ant polygyny might be more easily understood in the context of life history strategy evolution under age structure rather than the kin selection context. This section is an abstract of Tsuji and Tsuji.



**Figure 1.** Graphic illustration of the effect of population size fluctuation on the gene frequency change.

A. Each small circle represents a gamete. The mutant (closed circle) that left a gamete in the gene pool at Year 1 can increase the gene frequency by ca. 0.333, while can change the gene frequency only by 0.1 at Year 2. This is because the population density is increasing: the latter the little per gamete impact on gene frequency changes due to "dilution".

B. In contrast, when population density is constant, over years, the impact on gene frequency change per gamete is also unchanged.

The number of queens in an ant colony often reflects the mode of colony founding (Keller, 1991; Keller and Vargo, 1993). In monogynous species, new colonies are usually founded by one or multiple queens after dispersal on the wing (independent founding, Hölldobler and Wilson, 1990), while many polygynous species reproduce by fission or budding (swarm founding in the terminology of wasps and bees) in which new queens are recruited to an established colony and later may leave the colony accompanied by workers to found a new colony (dependent founding, Hölldobler and Wilson, 1990). These alternative dispersal tactics are sometimes observed within a single species. Queens of monogynous society are subject to high mortality (for example see Wiernasz and Cole, 2003) due to their long distance dispersal and the absence workers that assist during colony founding. However, once the colony is established, the queen can obtain a large lifetime reproductive success, living long as the primary reproducer of their colonies (Keller and Genoud, 1997). In contrast, the colony-founding success of dependently founding queens of polygynous society will not be as low as that of independently founding queens, because they are assisted by a force of workers. However, the reproductive success per queen is small in polygynous societies and queens are often short-lived (Keller and Vargo, 1993). In addition to the costs and benefits of the alternative tactics, Tsuji and Tsuji (1996) pointed out another important difference between the two. Independent foundresses have a longer generation time than dependent foundresses. This is because the former need longer time before they produce their first sexual offspring after colony founding. In Japan, many species need at least 5 years (Tsuji and Tsuji, 1996) and *Pogonomyrmex* harvester ants might need even longer (B. J. Cole, personal communication). In species with dependent founding, the young queens that are newly recruited to the colony reach the maximum oviposition rate soon after their adult emergence (Keller and Passera, 1990) and can produce sexual offspring even in the reproductive season

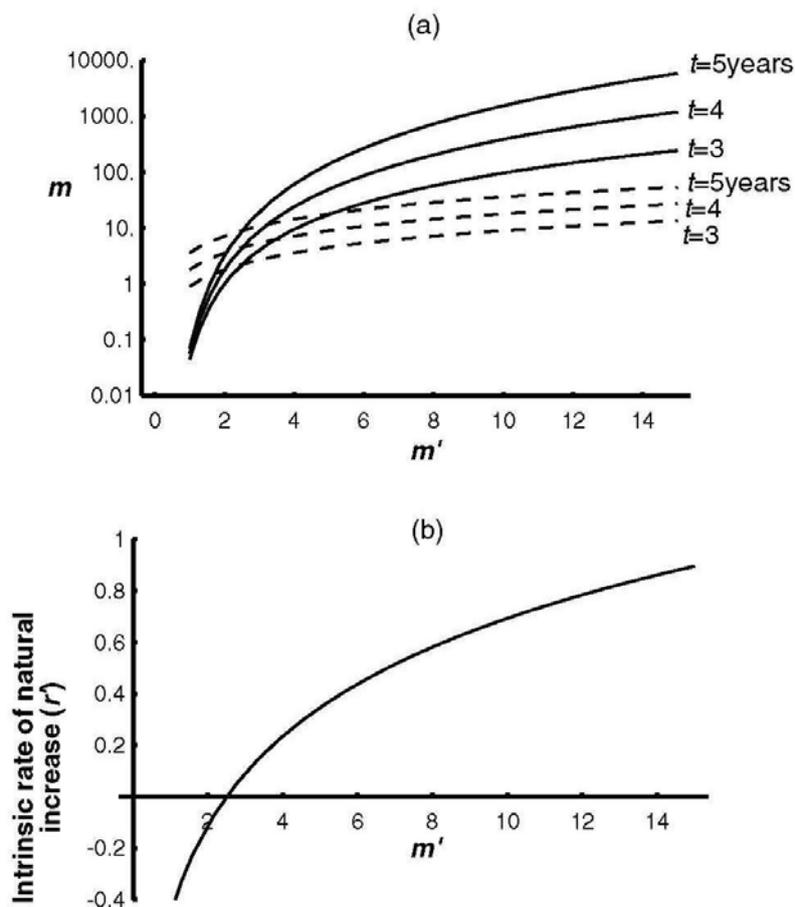
following their emergence (i.e. the next year). In an increasing population, this short generation time of dependently founding species may lead to higher fitness. Tsuji and Tsuji (1996) compared the intrinsic rate of natural increase ( $r$ ) between independent and dependent founding strategies of ants under various parameters ranges and found that this can be true at least in theory. The intrinsic rate of natural increase is equal to the growth rate of the population of haploid, clonal organisms of the respective strategist. In other words,  $r$  should follow Euler's equation:

$$\sum_{X=0}^{\infty} l_X m_X e^{-rX} = 1$$

where  $l_X$  is the survival rate to age  $X$  and  $m_X$  is the average fecundity of a queen at age  $X$ . Figure 2 shows an example of the results. In this figure, to highlight the selective advantage of dependent founding we assumed that dependently founding queens live only for one year, i.e. they die after leaving reproductive offspring in the year following their adult emergence, while it was assumed that independently founding queens are iteroparous with maximum life span of  $T=10$  after the first production of reproductive offspring. The solid curve indicates the threshold where both strategies give the same value of  $r$  in the given parameter setting. The independent strategy is advantageous in the area above the curve, while the dependent strategy is favored in the area below. The longer new colonies of independent strategists need to reach the reproductive stage ( $t$ : the time from colony founding to the onset of the production of reproductives), the larger is the area where the dependent strategy is favored. On the other hand, the broken lines show the condition where lifetime reproductive success (the expected number of reproductive offspring produced in a queen life) of the two strategies is the same. Note that with positive population growth rate ( $r > 0$ ) the areas where dependent strategies are advantageous are larger in terms of maximizing  $r$  than in terms of maximizing lifetime reproductive success. This is due to the shorter generation time associated with the dependent strategy ( $r$ -selection). The terms “ $r$ -selected and  $K$ -selected” (MacArthur and Wilson, 1967) usually mean to indicate the patterns observed in sets of life history traits. However, here by “ $r$ -selection” I mean a situation when selection operates to maximize  $r$  but not to maximize net reproduction rate. Low survival to colony maturity in the independent strategy also makes the dependent strategy advantageous. This is consistent with discussions assuming density-regulated populations (Nonacs, 1988; Keller, 1995). The number of reproductive offspring ( $m$ ) produced per year also positively influences  $r$  of both strategies. However, in an increasing population the effect of earlier reproduction on  $r$ , as the fitness measure, is more important than that of increasing fecundity ( $m$ ) in many parameter settings. In Figure 2, the dependent strategy that produces four offspring in at age 1 and thereafter dies can obtain almost the same fitness as the independent strategy that produces 100 individuals every year after age 5. Interestingly, in an increasing population, the number of reproductive cycles or the life span of queens after the first production of reproductives scarcely contributes to queen fitness measured as  $r$  (Tsuji and Tsuji, 1996).

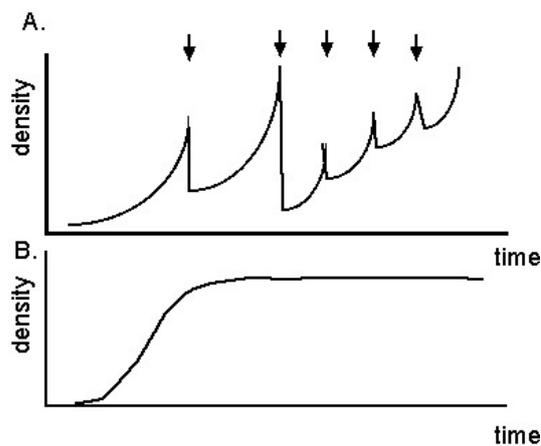
The short life span of queens of polygynous ants has yet been explained by intracolony conflict (selection of more related queens by workers, Nonacs, 1988), or by a higher external mortality of queens due to frequent nest movements (Keller and Genoud, 1997). From Tsuji and Tsuji's perspective two new hypotheses can be proposed. The first suggests that selection for a long queen life span is relaxed in an increasing population. The accumulation

of mutations through genetic drift might corrode the physical ability of queens to live long. The second hypothesis suggests a trade-off between early reproduction and longevity. In a density-independent population, it can be advantageous to reproduce earlier even at the cost of a shortened life span. This argument is a specific case of the general premise of life history theories that negative correlations between life history traits and traits adaptive in a specific environment are explained either through relaxing selection or a trade off (Rose, 1991).



**Figure 2.** A. Solid lines represent where the  $r$  of the two strategies is the same. Dashed lines show the condition where lifetime reproductive success of the two strategies is equal. The  $m$  is the per-year fecundity of an independent strategist, while  $m'$  is that of a dependent strategist. Other parameters are assumed for both strategies as: the annual survival before producing sexual offspring ( $p=0.5$ ), the annual survival after this ( $q=0.8$ ). Independent strategists are assumed to produce maximum 10 times (10 years), while dependent strategists are assumed to reproduce only once. The quantity  $t$  is the time from colony founding to initial production of reproductive offspring in the independent strategy. B. The population growth rate ( $r$ ) as the function of  $m'$ . Figures are from Tsuji and Tsuji (1996) with permission of Blackwell Publishing.

In which environments do real populations increase? Sociobiologists may suppose that an ever-increasing “elastic” population is unrealistic (e.g. Queller, 1993 p. 72, lines 18–21). However,  $r$  selection can operate also when population-size is limited. Disturbed habitats might be a good example. When disturbance occurs at random, mortality caused by the disturbance is likely independent of both population density and genotypes (since by



**Figure 3.** Illustration of (A) density-regulated population and (B) density unregulated population with random disturbances. Arrows indicate random disturbance events.

definition it is “random” mortality). When such stochastic processes, occasionally decrease population size and are followed by relatively long-lasting increases of population size, selection operates only during the increasing phases. As mentioned earlier, this selection is density-dependent (when population size dynamics is density-independent) (Fig. 1).

I illustrate this in Figure 3. Tsuji and Tsuji (1996) considered that ants living in open habitats are subject to more frequent disturbances, including human interference, than those living in forests. They tested their model and suggested that in subtropical Okinawa Island polygynous species are very dominant in open habitats while there are more monogynous species nesting in forests. A similar trend is observed in tropical Asia (K. Tsuji, unpublished data). Note that the two alternative

strategies in Tsuji and Tsuji’s model can either occur in different species or result from intraspecific variation, whereas other hypotheses explaining the ecological domination of fission founding unicolonial ants (e.g. Holway *et al.*, 1998; Holway and Suarez, 2004) mostly focus on interspecific competition. A large proportion of polygynous species found in open habitats of Okinawa Island are so called “tramp species”, such as *Anoplolepis gracilipes*, *Pheidole megacephala* and *Tapinoma melanocephalum*. Tramp species belong to various ant taxa and are characterized by polygyny, polydomy and colony reproduction by fission. In addition, they are often unicolonial (characterized by loss of colony boundaries due to the absence of intraspecific aggression, Bourke and Franks, 1995). They are also known as disturbed habitat specialists, which enables them to spread throughout the world with human activities (Passera, 1994). Unicoloniality usually leads to low relatedness, which is a largely unsolved puzzle in sociobiology. I believe that the here suggested concept of density-dependent selection will allow an empirical and theoretical approach to understand this phenomenon.

Testing Tsuji and Tsuji’s model with interspecific comparative data have some drawbacks. First, one has to control for phylogenetic relationships. Second, ecological requirements other than the traits on which the model focus (such as generation time) might differ from species to species. In fact, although the absence of tramp species in natural forests is also reported in other studies (Reimer *et al.*, 1990), unicolonial tramp species may sometimes invade forests (e.g. O’Dowd *et al.*, 2003). Therefore other factors, possibly depending on the specific history of each local ecosystem, will affect the ecological dominance of tramp

species. For example, tramp species that introduced to oceanic islands such as Hawaii (Reimer *et al.*, 1990, Krushelnycky *et al.*, 2004) generally seem to have left far stronger impact on local ecosystems than observed in Okinawa which is a continental island.

### **Polygyny can evolve also in density-regulated environments**

The density-dependent selection hypothesis by Tsuji and Tsuji has not attracted much attention in ecology of social insects and was never tested except by Tsuji and Tsuji (1996) themselves. One reason might be that the hypothesis seems inappropriate to explain unicoloniality of *Formica* and *Myrmica* that live in temperate to subarctic climate regions, while most unicolonial tramp species have a tropical or subtropical origin. Unicolonial *Formica* and *Myrmica* often construct nest mounds that seem quite stable and last for many years in the same place (e.g. Rosengren and Pamilo, 1983). Two alternative explanations might be possible for this phenomenon. First, the stability of population size and population density in ants should be measured as the number of reproductive individuals, but we have little empirical information on this sort of population demography. Even if the number and the size of nests seem to be unchanged over long, period, the population-wide number of queens might fluctuate in a density-independent way. I assume that cold winter can cause random mortality or disturbances in the low temperature regions where *Formica* and *Myrmica* are found. Indeed, queen number per colony varies with time in *Myrmica* (Elmes and Keller, 1993). The fact that in central Japan unicolonial *Camponotus yamaokai* lives in higher altitudes than its monogynous and multicolonial sibling species *C. nawai* (Satoh, 1989) supports my hypothesis. Both species are arboreal and live inside twigs and branches and will more directly experience cold winter temperature in higher altitudes, while species nesting underground can probably better buffer cold temperature by hibernating hiding deeper in the ground (However, some researchers such as Heinze and Buschinger (1988) suggested that cold temperature can lead to polygyny by other causations). Second, Tsuji and Tsuji's model might not account for unicoloniality of *Formica* and *Myrmica*, and their populations are stable and regulated by density-dependent processes. Assuming that populations of those ants are saturated and almost constant, the strategy will evolve that most effectively maximizes population density (carrying capacity:  $K$ ) at a given resource (Stearns, 1992; Charlesworth, 1994). Even when the carrying capacity in terms of the number of nests is unchanged,  $K$  in terms of reproductive individuals increases with the number of queens per nest. Buschinger (1990) has discussed that polygyny in *Leptothorax* ants is a  $K$ -selected trait. In saturated environments, the colony-founding success of independently founding queens will be low. Therefore, this idea parallels discussions based on reproductive skew models (e.g. Reeve and Ratnieks, 1993), which argue that low founding success of dispersing queens is the major driving force for the evolution of ant polygyny (Bourke and Heinze, 1994; Keller, 1995).

To test if an ant population is regulated by density-dependent processes or subject to density-independent fluctuation will not be easy in most situations. One approach to test Tsuji and Tsuji's  $r$  selection hypothesis and other hypotheses is to focus on longevity. If the driving force for the evolution of unicolonial, dependent strategy were to maximize  $r$ , queens of dependent founding species would have a shorter life-span than those of their independently founding sibling species. If ant polygyny were the queen's strategy of maximizing her own lifetime reproductive success and/or  $K$  in a density-dependent

population, the life-spans of polygynous queens would be as long as monogynous ones. However, conflict among relatives can cause queen mortality in density-regulated populations, either because workers choose more related queens (Nonacs, 1988) or more fertile queens (Forsyth, 1980). As mentioned earlier, myrmecologists have long noticed the short life of polygynous queens (Keller and Vargo, 1993) and some authors have attempted to explain this by the evolutionary theory of senescence (Keller and Genoud, 1997). The short life-span of polygynous queens under  $r$ -selection (Tsuji and Tsuji, 1996) is explained either by relaxed selection for a long life or a trade-off between early reproduction and longevity but not by high external mortality. Empirical data on queen longevity are still scarce (Keller, 1997) and further empirical studies are needed to test these ideas.

### Inclusive fitness model with density dependence

Tsuji and Tsuji's ecological model incorporated density-dependent selection but was not able to treat relatedness asymmetries and conflicts among relatives that have been hot topics among sociobiologists studying hymenopteran societies. This might be another reason why their theoretical approach has left little impact on empirical studies of myrmecology so far. Here, I propose a tentative but straightforward method of inclusive fitness modeling in populations with age structure.

Let me assume an iteroparous social insect with overlapping generations. Production of reproductive offspring is assumed to be seasonal, so that the population consists of discrete cohorts. Life history strategy theories often deal with fitness pay-off to resource investment. A model to analyze "inclusive fitness rewards" to investment was proposed by Taylor (1988) and has been used in the context of sex allocation conflict (Boomsma and Grafen, 1991; Crozier and Pamilo, 1996). I suggest extending Talyor's model to populations with age structure.

According to Taylor the inclusive fitness rewards to investment of  $y_i$  units of resource in offspring of the  $i$ th sex is

$$W = \sum_{i=1}^2 b_i v_i f(y_i) \quad (1)$$

where  $b_i$  is the regression relatedness of offspring of the  $i$ th sex to the focal individual who invests the resources,  $v_i$  is the sex specific reproductive value of the  $i$ th sex, and  $f(y_i)$  is the sum of reproductive success of offspring of sex  $i$  as a function of  $y_i$ . Population density will affect inclusive fitness only through the component  $f(y_i)$ . In a finite population with random mating  $f(y_i)$  can be expressed as

$$f(y_i) = y_i / Y_i \quad (2)$$

$Y_i$  is the sum of investment in  $i$ th sex in the entire population. In the context of sex allocation, the denominator  $Y_i$  of the right-hand side of Eq. 2 represents Fisherian frequency dependence, because as the ratio of offspring of sex  $i$  in the population to the other sex increases, the reproductive success of offspring of sex  $i$  per unit investment decreases. When individuals reproduce more than once, lifetime inclusive fitness is

$$W = \sum_{j=1}^M \sum_{i=1}^2 b_{ij} v_i f(y_{ij}) \quad (3)$$

The subscript  $j$  denotes the  $j$ th reproductive season, and  $j=0$  is the season (or the year when reproduction occurs annually) the focal individual was born. Reproduction may begin at  $j=1$  and  $M$  is the physiological end of life. When lifetime reproduction is considered, mortality should be taken into account. Here, we define  $y_{ji}$  as the expected investment in offspring of the  $i$ th sex in the  $j$ th season, i.e., if the investment in sex  $i$  ( $i=1$  is female and  $2$  is male) is constant as  $y_i$  over reproductive seasons,  $y_{ij}$  means  $y_i x$  (survival probability to season  $j$ ), which corresponds to  $l_x m_x$  in demography models. Under random mating

$$W = \sum_{j=1}^M \sum_{i=1}^2 b_{ij} v_i y_{ij} / Y_{ij} \quad (4)$$

$Y_{ij}$  is the expected total investment in sex  $i$  offspring in the population in season  $j$ . As in Eq. 1  $Y_{ij}$  in the denominator leads to frequency-dependence. Here, one notices that when focusing on one sex the denominator  $Y_{ij}$  can also simulate density-dependent selection. The larger the absolute population investment in sex  $i$  is, the smaller is the reproductive success through per capita investment in offspring of sex  $i$  ( $y_{ij}/Y_{ij}$ ). In short, a single gamete has a higher value the fewer gametes are in the gene pool (see Fig. 1a). Assuming that the population investment  $Y_{ij}$  is a function of population density ( $N_j$ ) (because the more colonies, the more reproductive offspring will be produced in the entire population), Eq. 4 represents density-dependent selection. It is, however, unlikely that animals can accurately assess the future population density and determine seasonal investment in order to maximize their lifetime inclusive fitness. It is more realistic to assume that, when population density is expected to change at a constant rate, natural selection causes animals to adopt the life history pattern that maximizes their expected lifetime inclusive fitness. Here I assume the simplest situation where the rate of population growth per season ( $\lambda = N_{j+1}/N_j$ ) is in proportion to the increase in the rate of population investment ( $Y_{ij+1}/Y_{ij}$ ). Lifetime inclusive fitness is

$$W = \sum_{j=1}^M \sum_{i=1}^2 b_{ij} v_i y_{ij} / Y_{i0} \lambda^j \quad (5)$$

$Y_{i0}$  is the initial value at season 0. More generally, when there are no discrete seasons and colonies can reproduce at any time, as in many tropical social insects, the lifetime inclusive fitness is

$$W = \sum_{i=1}^2 \int b_{it} v_i y_{it} / Y_{i0} e^{rt} \quad (6)$$

where the subscript  $t$  is time, which is a continuous variable, and  $r$  is the instantaneous rate of population increase.

To focus on the issue of the timing of reproduction, we assume sex ratio to be always 1:1, i.e.  $y_{1j} = y_{2j} = x_j/2$  and  $Y_1 = Y_2 = X_j/2$ . The quantity  $x_i$  is the investment in sexual offspring made by the focal individual at season  $j$  and  $X_j$  is that done by the entire population in the same season. The ratio of reproductive values  $v_1/v_2$  is 2 and also assumed to be constant, ignoring worker reproduction and reproduction of males in more than one season (Pamilo, 1991).

The expression

$$\frac{1}{2} \sum b_{ij} v_{ij} = G_j$$

denotes the average life-for-life relatedness of offspring summed over the two sexes produced in the  $j$ th season. According to the previously mentioned logic the population wide

investment  $X_j$  is assumed to be proportional to population density ( $N_j$ ). Thus  $X_j = aN_j$  ( $a$  is a positive constant) and Eq. 5 becomes

$$W = \sum_{j=1}^M 2G_j x_j / aN \lambda^j$$

$N$  is initial population density that is a positive constant. When  $aWN/2$  is replaced by  $w$ , the equation can be simplified as

$$w = \sum_{j=1}^M G_j x_j / \lambda^j \quad (7)$$

I call Eq. 7 inclusive fitness with density dependence. Below I discuss the effect of change of population density on the evolution of social behavior, using this quantity as a predictor of the direction of gene frequency change. For simplicity, I assume that animals can live for a maximum of 2 seasons and can maximally reproduce twice. Their lifetime inclusive fitness therefore is

$$w = G_1 x_1 + G_2 x_2 / \lambda$$

When population density is constant ( $\lambda=1$ ) and relatedness does not vary with time ( $G_1=G_2=G$ ), the value of per capita (expected) reproductive investment of the first year is equal to that of the second year. However, in an increasing population ( $\lambda>1$ ), the value of the first year offspring is higher. If there is a simple trade off ( $x_1+x_2=\text{constant}$ ), the optimal strategy is to invest all resources in the first offspring. From this view, social insects like ants that experience a long ergonomic stage (the stage producing only workers) should compensate for this delay of reproduction by later producing a huge number of offspring, particularly when the population size is increasing. Social insects generally fit the pattern “K-selected” through slow growth, delayed reproduction, large (colony) size, and extended parental care (Pianka, 1974), though they do not produce a small number of large-sized offspring. They should be adapted to density-regulated stable environments. This idea comes in line with Alexander (1974) who suggested that the ultimate factor of the evolution of altruism and cooperative breeding is population saturation, which leads to food shortage. However, Alexander also stated that in cooperatively breeding mammals and birds resource shortage often causes overt fluctuation of population density, with many animals being killed by hunger (see also Emlen, 1991, 1997). If my view that populations are constant and stable were correct, such an occasional reduction of population density would not random fluctuation, but rather an aspect of density-dependent population regulation that can be detected in a much longer term.

The above equation can also handle conflict between relatives. Let me assume insects that have an annual life cycle like *Polistes* wasps of temperate regions. Individuals are assumed to be able to reproduce at most twice (first brood  $x_1$  and second brood  $x_2$ ). First, I discuss the adaptive value of parental manipulation. An over-wintered foundress female sacrifices the reproductive ability of her first brood to produce more offspring  $x_2$  in the second brood. The lifetime inclusive fitness of this female ( $w'$ ) is

$$w' = 0.5 x_2' / \lambda$$

where  $\lambda$  is the population growth ratio between the two successive seasons. On the other hand, the inclusive fitness of non-manipulating females is

$$w = 0.5 x_1 + 0.5 x_2 / \lambda \quad (8)$$

Parental manipulation is favored when  $w' > w$ , i.e.

$$x_2' - x_2 > x_1 \lambda$$

If the population size is constant ( $\lambda = 1$ ), the above condition is  $x_2' > x_1 + x_2$ , i.e. the tactic, which maximizes the production of offspring in the lifetime, is favored. However, this does not hold true in an increasing population ( $\lambda > 1$ ). A female has to increase the production of the second brood not by  $x_1$  but by more than  $x_1 \lambda$  to compensate the loss of her first reproductive brood, which makes parental manipulation less advantageous. This supports discussions of Alexander (1974) that evolution of altruism through parental manipulation is more likely to occur in a saturated population whose density is near the carrying capacity.

Next, let me focus on the first brood's point of view. How can the daughters in the first brood maximize their inclusive fitness – by helping their mother to increase the second brood or by leaving the nest to reproduce themselves? This corresponds to Hamilton's kin selection assumption that daughters can decide options by themselves.

When a daughter immediately leaves the nest to reproduce by herself in the second brood season, her lifetime (inclusive) fitness is

$$w_1 = 0.5 x_2'' / \lambda \quad (9)$$

where  $x_2''$  is the expected production of offspring (I assume that females cannot over-winter after reproduction).

When the daughter forgoes reproduction and instead helps to increase the second brood of her mother by  $\Delta x_2$ , her lifetime inclusive fitness  $w_2$  is (I assume helpers cannot over-winter)

$$w_2 = G \Delta x_2 / \lambda \quad (10)$$

where  $G$  is the average life-for-life relatedness of the second brood (sibs) from the helper's point of view.

From equations 9 and 10, altruism is favored if  $w_2 > w_1$ , thus  $G \Delta x_2 > 0.5 x_2''$ . As one can notice, the population growth parameter  $\lambda$  is eliminated. In other words, Hamilton's rule is fulfilled. For instance, if the second brood are full-sibs of the focal worker,  $G = 0.5$  and the condition is  $x_2 > x_2''$ . Altruism is favored if the mother queen can increase the second brood more than the direct offspring of her solitary reproducing daughters could produce.

An alternative option for the first brood daughter would be not to participate in the second brood production of the year either directly or indirectly through helping, but to simply over-winter and reproduce next year. Taking this option her inclusive fitness is

$$w_3 = 1 / \lambda \quad (11)$$

The numerator of the right-hand side of Eq. 11 is 1, because instead of sending offspring to the gene pool (the over-wintering population), she sends herself ( $G = 1$ ). From Eqs. 10 and 12, altruism is favored if  $G \Delta x_2 > 1$ . Again, Hamilton's rule holds true,  $\lambda$  having been eliminated. In the specific situation when  $G$  is 0.5 (under monandry and equal sex ratio), altruism pays when mothers leave more than 2 additional sibs through the sacrifice of the focal daughter. Eq. 11, however, might be difficult to compare with Eq. 9 or Eq. 10, since the former evaluates the value of survival and the other measures that of reproduction. Finally, I assume a constant population growth even during winter and measure the inclusive fitness from the amount of reproduction in the next year. The inclusive fitness of the over-wintered daughter

is

$$w_3 = 0.5x_3' / \lambda^2 + 0.5x_4' / \lambda^3 \quad (12)$$

where  $x_3'$  and  $x_4'$  are the expected investments in offspring of the first and the second brood, respectively. From Eqs.10 and 12, the condition under which altruism is favored is  $G\Delta x_2 - 0.5x_3' / \lambda - 0.5x_4' / \lambda^2 > 0$ . When  $G=0.5$ , it becomes  $\Delta x_2 > x_3' / \lambda - x_4' / \lambda^2$ . Interestingly, when the population is increasing ( $\lambda > 1$ ), altruism can more easily evolve than predicted by Hamilton's rule. This is because by helping her mother, the daughter can (indirectly) participate in reproduction earlier. I do not show math but the lodger, a hopeful reproductive, i.e. a female staying in the mother's nest without helping and waiting for her own chance to inherit the mother's resource, e.g. territory, is clearly maladaptive in an increasing population, because this option makes early reproduction (direct or indirect) impossible. In general, timing of reproduction, regardless of whether direct or indirect, is important in age-structured populations. Increasing populations make earlier participation in reproduction advantageous. With the same logic, the opposite will be true in a decreasing population: late-reproduction is favored. However, I am unable to imagine a real example of an ever-decreasing population in social insects.

In sum, there is a marked contrast between the effects of population growth on kin selection and parental manipulation in age-structured populations. Parental manipulation is less likely favored in an elastic population, whereas voluntary reproductive sacrifice is favored by kin selection when Hamilton's rule holds regardless of the population growth rate, and in some situations altruism can evolve more easily through kin selection when the population is growing. This introduces a new approach for testing kin selection and parental manipulation theories. If "primitive" social insect taxa like polistine wasps and halictine bees have populations with rapid density fluctuations, kin selection is a more likely explanation rather than parental manipulation. Itô and Kasuya (2005) recently detected a relatively strong density dependent population regulation in *Ropalidia fasciata* that rather supports parental manipulation hypothesis. However, this sort of demographic data are needed also in other species. My prediction works only when parental manipulation entails a delay of "real" reproduction. If the behavioral options changed the timings of direct and indirect reproduction in different ways this prediction would not hold.

The discussion above proposes the possibility of a new type of conflict between mother and daughters. In an increasing population, daughters might be willing to be helpers, while the mother might be reluctant to keep the daughters as helpers. In mammals and birds, parents sometimes attack offspring to induce their dispersal, which can be explained by the classical concept of parent-offspring conflict over the optimal period of parental care (Trivers, 1974). My model proposes an alternative hypothesis, i.e. parent's refusal of offspring's altruism, which in some rare situations might be adaptive in cooperatively breeding vertebrates, e.g.. when populations experiences random fluctuations.

How accurately my models (the basic models are Eq. 5 and 7) can approximate the exact solution of a rigorous population genetic model will be the subject of future studies. However, I hope that my tentative approach is useful to tackle the evolution of social behavior in age-structured populations.

## Dispersal and disturbance

In addition to clonal reproduction, the model by Tsuji and Tsuji (1996) had another unrealistic assumption, i.e., the spatial structure of the population was not taken into account. In ants, fission foundresses can disperse only short distances on foot, while independent founding by winged queens results in long dispersal. Generally, long-range dispersal is believed to be adaptive in spatially or temporally heterogeneous “disturbed” environments (Southwood, 1962; Dingle, 1980; Roff, 1994). Tsuji and Tsuji’s conclusion that dependent founding with short-distance dispersal can evolve in disturbed habitats (due to its high  $r$ ) stands in contrast to this conventional belief. Intuitively, fission reproduction may have some disadvantages for ants. First, offspring colonies stay in close spatial proximity of the mother colony, therefore, both mother and her offspring colonies are likely eliminated by a single disturbance event. In other words, fission reproducers are less likely to avoid disturbance risks. Second, fission reproducers might be more likely to suffer from density-dependent effects due to local environment saturation. Nakamaru, Beppu and Tsuji (submitted) made a computer simulation model that incorporates both disturbance and spatial structure to see if fission is still favored in disturbed environments or not, despite the expected costs of short-distance dispersal. They used a special version of lattice model in which a colony can occupy a single site of the two-dimensional lattice space (in contrast of conventional lattice models in which a single individual can occupy a lattice site).

Lattice models are useful to analyze the effects of spatial structure on population and evolutionary dynamics, and can treat dispersal distances as quantitative variables (e.g. Fahring, 1992; Bolker and Pacala, 1999; Harada, 1999; Hiebeler, 2004). The new feature of the model by Nakamaru *et al.* (they call their model the colony-based lattice model, contrasting to ordinal individual-based lattice models) is the incorporation of size information. Colonies are assumed to grow in each site and there can be size variation between colonies. They assumed two strategies: L (long dispersal independent foundress) and S (short dispersal fission foundress). When the colony size exceeds a certain threshold (reaching colony maturity), an L colony sends a propagule of minimal size to an empty site chosen at random in the entire lattice space, reducing the size of mother colony by the minimal unit. In contrast, an S colony exceeding the threshold size divides itself into two half and sends one half to a neighboring site, the other half remaining in the original site. Colonies are assumed to follow a logistic growth curve independent of the strategy. Natural colony mortality is assumed to be a function of colony size, with small colonies being more likely to go extinct. Nakamaru *et al.* (submitted) introduced additional mortality caused by disturbance that is controlled by two stochastic parameters ( $p$ : the occurrence probability of disturbance, and  $q$ : spreading probability of disturbance to a neighborhood). In short,  $p$  controls the frequency of disturbance and  $q$  affects the spatial scale of disturbance. A combination of a large  $p$  and a small  $q$  means that the population experiences many small-scale disturbances, while a small  $p$  with a large  $q$  implies the occurrence of a few large-scale disturbances. Disturbance kills all colonies on the respective sites and creates new empty sites.

Computer simulations with this colony-based lattice model with various parameter settings revealed that despite the possible costs of short-distance dispersal, fission is favored in environments with an intermediately degree of disturbance (Nakamaru *et al.* submitted). The reason is as follows: Offspring colonies in the L strategy start from the minimal size so that they take a long time to initiate the production of offspring colonies, as compared with

S colonies. They are more likely to go extinct by disturbance or by the size-dependent colony mortality before they leave offspring colonies. In other words, temporal avoidance of disturbance by reducing the generation length of a colony is more effective than spatial avoidance by long-distance dispersal. Again, the lattice model approach suggested that earlier reproduction is a key factor for the evolution of fission reproduction in social insects with overlapping generations.

The colony-based lattice models made several interesting predictions other than the above. When we assumed that the S strategy can disperse randomly like the L strategy, relaxing the assumption of trade-off between size and dispersal distance, made fission strongly adaptive, because such a strategy can avoid disturbance both temporally and spatially. This may hold true for wasps and bees, especially those with relatively long lasting colonies in the tropics or those with perennial colonies. Since they can fly, unlike ants, fission does not limit their dispersal distance. In support of this prediction, many wasps and bees with long-lasting large colonies, such as honey bees, stingless bees, Neotropical polistine wasps with large colonies are mostly “swarm” founders. This hypothesis needs to be tested by a rigorous analysis taking phylogenetic information into account.

## Concluding remarks

So far sociobiologists have mostly approached the diversity of life histories in social insects from a kin selection perspective. I have discussed that a more comprehensive understanding will be possible by taking population dynamics and spatial structure into account. For this aim I proposed a tentative approach combining population dynamics (density-dependent selection) and kin selection and stressed the importance of timing of reproduction in an elastic population. Assuming ant life histories, it was suggested that disturbance does not necessary favor dispersal, which is a new finding in the evolutionary theories of dispersal behavior. Future theoretical studies should integrate spatial structure and relatedness issues into a single model. As I have illustrated here, the interplay between social evolution theories and other evolutionary theories will be fruitful, not only to better understand social insects but also to improve general evolutionary theories. Sociobiology now comes to the stage of such new syntheses.

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## **Parasitism and life history in social insects**

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**Abstract** – *Parasites are ubiquitous and present a formidable challenge for social insects. Studies, especially on the model system of the European bumble bee, *Bombus terrestris*, and its parasites have shown that parasitism affects almost any trait that characterizes the life history of social insects. For example, infection by the trypanosome, *Crithia bombi*, reduces founding success of the queen in spring. Parasitization of workers by brood of conopid flies is associated with a shift in the timing of reproduction in natural populations. Even the use of the immune defence machinery alone elicits severe changes, such as a shift in reproductive timing, a severe reduction in colony reproductive performance and leads to an increased investment in immune defence capacity of offspring. How such selective pressures have shaped social insect life history is still an unanswered question that represents a challenge for future research.*

**Keywords:** Parasite, social insect, life history, coevolution, bumble bees.

### **1. Life history diversity in social insects**

Social insects are the dominant fauna in many habitats. Part of their success is explained by the social life style that has enabled them to cope with the challenges in their environment in unprecedented ways (Oster and Wilson, 1978). As a consequence, social insects have conquered a large range of habitats and show a huge diversity of life styles. For example, ants live in rainforests and deserts. Most species use underground nests but others prefer arboreal nesting sites (Wilson, 1971). The same is true for the termites or the social bees, the latter varying further in their ability to arrange brood cells in loose clumps (such as the bumble bees) or highly regular arrangements (such as in the honey bees and the stingless bees) (Michener, 1974). Not only nesting habitats vary, but also the diet of social insects cover a vast array of items, from the nectar- and pollen-harvesting bees to the fungus-cultivating leaf-cutter ants (Hölldobler and Wilson, 1990). Furthermore, colony size is an intriguing character that varies by several orders of magnitude, from small colonies found in almost any of the groups to the huge colony sizes of marauding army ants (Hölldobler and Wilson, 1990). Some of these characters show regular patterns, such as the increase in colony size with latitude in ants (Kaspari and Vargo, 1995), or the scarcity of ground-nesting bees in the tropics (Roubik, 1989).

Regardless of the adaptive meaning of any of these traits, the choice of nesting site, diet or colony size - to mention just a few - exposes social insects to different kinds and varying

degrees of parasite pressure. For example, ground-nesting seems to be associated with increased parasitisation by nematodes (Schmid-Hempel, 1998), while the closed nests of termites seems to be associated with an increased burden of fungi (Boomsma *et al.*, 2004). Hence, there is a clear connection between social insect life style and the presence and pressure exerted by parasitism. Here, some of the elements of this relationship are explored. Parasites are ubiquitous. The diversity of organisms affecting social insects is just as wide as those attacking any other insect species. The range includes viruses, bacteria, fungi, protozoans, helminths and also other insects, such as parasitoid wasps and flies. In addition, social parasitism is widespread among social insects and could be added to the list. Here, only the issue of “real” parasitism by alien organisms is discussed.

Parasitism as an evolutionary force shaping social insect forms has long been neglected and therefore represents still an expanding field of enquiry (Schmid-Hempel, 1998). Our knowledge on the occurrence and effects of parasites is therefore rather limited, even though new insights are added every year. The number of parasite species identified for any single host species varies widely (Schmid-Hempel, 1998) and certainly represents an underestimate due to the lack of sufficient study. Furthermore, in most cases, it is simply not known what the effect of the parasite actually is unless the effect is very drastic and hard to overlook, such as *Varroa* mites killing entire colonies of honey bees (Ball and Allen, 1988; Kraus and Page, 1995). In many cases, the really important effect of a parasite often may appear in a different context than investigated (Brown *et al.*, 2003). Quite clearly, there is still a lot to discover about which parasites affect social insects and what their effects may be.

## 2. The questions of life history theory

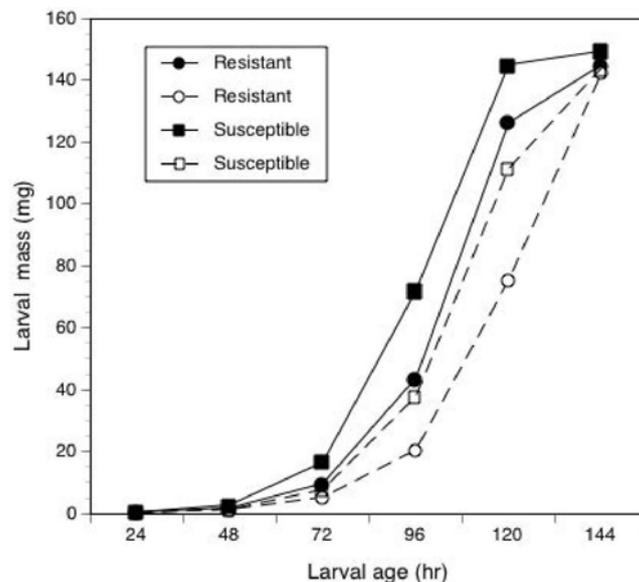
A life history is described by the pattern of birth, development, maturity, reproduction, senescence and death. What kind of process shape these patterns is the question that life history theory asks. To structure the problem, life history theory usually investigates a number of important traits. These include age and size at maturity, the pattern and number of reproductive periods, the size and number of offspring produced, senescence, death of the organism and the associated variation in life span. All of these parameters have been shaped by natural selection and affect important elements of the dynamics of populations (Stearns, 1992).

Also among species of social insects, these parameters vary widely. For example, all of the ants and termites, and many social bees (e.g. the honey bees) and social wasps (e.g. some species of swarm-founding Polistinae, Jeanne, 1991) have a perennial life cycle with repeated reproductive periods, that is, they are iteroparous. The life history also may be perennial but with only one reproductive period (e.g. *Polybia occidentalis*, Jeanne, 1991) and, hence, represent a semelparous life cycle. Many species of bees and wasps, finally, are annual with one (e.g. the bumble bees) or two (some Halictids, Michener, 1974), reproductive periods. Annual ants or termites have so far not been described.

Whilst the patterns of social insect life history can be described readily, the search for the selective factors and processes underlying these patterns is more demanding. A major assumption is that life history variation is due to variation in the strategies of allocation of scarce resources to competing needs of the organism. For example, the same amount of nutrition cannot at the same time be invested into growth and maintenance, or to reproduction. Similarly, an investment into defense against parasitism cannot at the same

time be allocated to some other life history parameter. In fact, defense against parasites has been shown to be costly in a variety of organisms (Schmid-Hempel, 2003). This is also the case for social insects.

In a series of classical studies, Rothenbuhler and his collaborators demonstrated genetic variance for defense against American Foulbrood (a bacterial disease) by way of hygienic behaviour in the honey bee. In this context, it was also shown that larval growth was reduced in honey bee lines that had been selected for increased resistance against foulbrood (Sutter *et al.*, 1968) (Fig. 1).



**Figure 1.** The effect of selection for increased resistance against American Foulbrood in the honey bee under controlled conditions. Larvae of lines selected for resistance (circles) generally grow more slowly than larvae from the control (susceptible) lines (squares). The colony environment also plays a role, depending on whether the larvae are raised in susceptible (open symbols, dashed lines) or resistant (filled symbols, solid lines) foster colonies (modified from Sutter *et al.* 1968).

The effect was also dependent on the environment in which the larvae were raised. Such tests show that when an experimenter selects lines for increased resistance, a cost in some other fitness-relevant life history parameter emerges. Hence, evolving the capacity for defense against parasitism is itself costly even when the defense is not used (Kraaijeveld and Godfray, 1997).

In addition to a cost of evolving the immune defense, studies in social insects have also shown that using the immune defense itself is costly. This is the case in bumble bees forced to work (foraging) that show a concomitant reduction in their ability to ward off an experimental implant (König and Schmid-Hempel, 1995). Similarly, when bumble bee workers are forced to use their immune system, even when not infected by a real parasite, their life span is severely shortened – albeit only when resources are too scarce to compensate for the cost of this challenge (Moret and Schmid-Hempel, 2000). In both cases, defense against parasitism bears a cost independent of any pathological effect of the parasite itself.

The two examples also illustrate two major components of defense against parasitism in insects (and thus in social insects, too). On one hand, there is the general response to an immune challenge with the activation of the pro-Phenoloxidase cascade that eventually leads to the production of intermediate compounds toxic to micro-organisms. Eventually,

encapsulation of an invader results (Tzou *et al.*, 2002) (Schmid-Hempel, 2003). On the other, insects can activate a more specific cascade that leads to the production of anti-microbial peptides able to kill a wide range of bacteria or fungi (Schmid-Hempel, 2003). Both arms of the immune defense system are easy to measure and can be manipulated experimentally in a straightforward manner.

A second important assumption of life history theory is that the respective traits are heritable and that genetic variation exists. This is the case for parameters characterizing the immune defense in social insects. For example, colonies typically vary in their ability to defend themselves against parasites and some of this variation is known to be genetic (Baer and Schmid-Hempel, 2003a; Schmid-Hempel and Ebert, 2003). Therefore, it is to be expected that life history characteristics may also be under selection by parasites and that evolutionary change may result from this selective regime.

### 3. Life history and effects of parasitism in *B. terrestris*

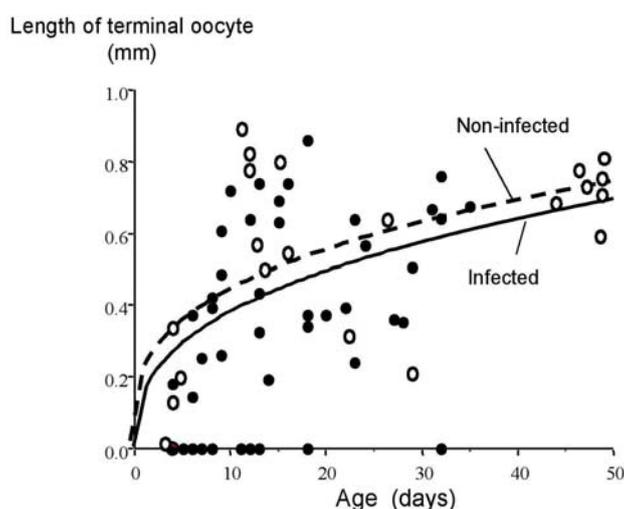
Here, I will discuss the results of studies done on the model system of the European bumble bee, *Bombus terrestris* L., and some of its major parasites, especially the trypanosome, *Crithidia bombi* (Lipa & Triggiani, 1980).

The life cycle of *B. terrestris* is annual with one reproductive period. In spring, the hibernated and fertilized queens emerge from their winter quarters and start a colony on their own. *B. terrestris* is a below-ground nester that preferentially uses abandoned rodent burrows as their nesting sites (Alford, 1975). As the season progresses, the queen's daughters, the workers, take over the tasks of collecting resources and raising brood. Finally, around July to August, reproduction occurs when the production of males (the drones) and sexual females (the young queens or gynes) starts. Not all colonies, however, will succeed in producing any sexual offspring and a small fraction will manage to produce males only.

During the queen's solitary life and the subsequent colony cycle, parasitism is an ever constant threat. During hibernation, for example, the queens can become infected by the nematode *Sphaerularia bombi* that is specialized in finding and infecting bumble bee queens in the soil (Alford, 1969; Poinar and Van der Laan, 1972). If the infection is successful, the queen emerges from its hibernation quarter and starts to search for over-wintering sites rather than nest sites. She will never lay any eggs and is therefore virtually castrated (Lundberg and Svensson, 1975). But even when the queen succeeds in starting a colony, she may either carry a legacy of a *C. bombi* infection with her from the previous year, or she becomes infected with this parasite when feeding on flowers (Durrer and Schmid-Hempel, 1994). A large-scale experiment showed that queens infected by *C. bombi* were much less likely to found a colony and that the effect was strongest if the hibernation regime was shorter (Brown *et al.*, 2003). This change in life-history suggests that *C. bombi* inflicts a heavy fitness toll right at the beginning of the colony life cycle and may also act as a partial castrator, since the affected queen will never have offspring.

A subtle effect of *C. bombi* is that it reduces the development of ovaries in its host (Fig. 2). As a consequence, the point at which the social fabric of the colony breaks apart – the competition point (Duchateau and Velthuis, 1988) – is delayed in infected colonies, since the workers are unable to lay their own eggs. In other words, parasitization by *C. bombi* can even lead to a more socially cohesive colony in favour of the queen's interests (Shykoff and Schmid-Hempel, 1991b). This delay, however, does not lead to more efficient and more

productive colonies because infected colonies still have a lower reproductive output than their uninfected counterparts, at least in controlled experiments (Brown *et al.*, 2003).



**Figure 2.** The average size of the oocytes in workers increases with age, but more slowly in animals infected by *Crithidia bombi* (filled circles) as compared to uninfected controls (open circles). As a result, the first worker egg indicating the emergence of a reproductive conflict within the colony appears some 5 days later in infected ( $38.2 \pm 2.0$  days after the laying of the first eggs) as compared to uninfected ( $33.6 \pm 3.2$  days) colonies. This maintains the social fabric of the colony for a longer time (after Shykoff and Schmid-Hempel 1991b).

In the course of a season, workers of bumble bees colonies are exposed and become infected by a wide variety of parasites. Examples include the microsporidian *Nosema bombi* that presumably has a similar effect and transmission biology as *C. bombi*. Its prevalence is not large but the parasite is present consistently (Shykoff and Schmid-Hempel, 1991a) and can take a heavy toll on infected individuals and colonies. Workers that collect pollen and nectar on flowers during the summer months are subject to parasitization by conopid flies (*B. terrestris* is attacked mostly by *Sicus ferrugineus* and *Physocephala rufipes*) (Schmid-Hempel and Schmid-Hempel, 1996a). A successful infection invariably leads to host death within 10–12 days (Schmid-Hempel and Schmid-Hempel, 1996b) and the emergence of one adult parasitic fly in the next year. The incidence of conopid parasitism can be quite substantial and presumably affects entire populations (Schmid-Hempel *et al.*, 1990; Schmid-Hempel, 2001).

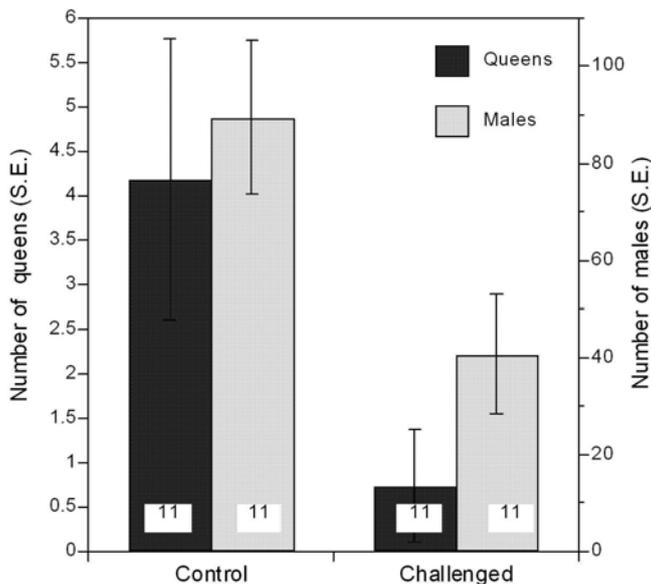
#### 4. Variation in life history due to defence against parasitism

How does parasitism affect life history parameters? On one hand, the question is straightforward when there are pathological effects, such as the reduction of ovary size in workers leading to a reduction of conflict within colonies (Shykoff and Schmid-Hempel, 1991b). Similarly, infection by *C. bombi* is likely to have a direct effect on the energy budget in its host, thus reducing the likelihood of colony foundation for infected spring queens. However, a number of studies show that the effect of parasitism is much more subtle. In fact, the effects may relate to the defence against infection itself rather than the effects of the parasites per se.

Indeed, when an insect host is infected, a range of immune defence mechanisms is set in action (Söderhall, 1998; Tzou *et al.*, 2002). These processes can be elicited experimentally,

enabling the design of studies on the effects of the immune defences themselves. For example, implanting a piece of nylon as a surrogate for an infection by a macro-parasite triggers the proPO-cascade that eventually leads to melanization of this implant. The darkness of the piece gives a useful estimate of the strength of the immune response (Schmid-Hempel and Schmid-Hempel, 1998). Alternatively, the immune system can also be triggered by injection of antigenic molecules that are recognized by the anti-microbial defence system. Such molecules are, for example, the purified surface molecules of bacteria, such as LPS (lipopolysaccharides). Injection of LPS leads, through a signalling cascade (Tzou *et al.*, 2002), to the synthesis of anti-bacterial peptides that are very potent in killing micro-organisms. This tool can thus be used to mimic an attack by bacteria and to study its effects.

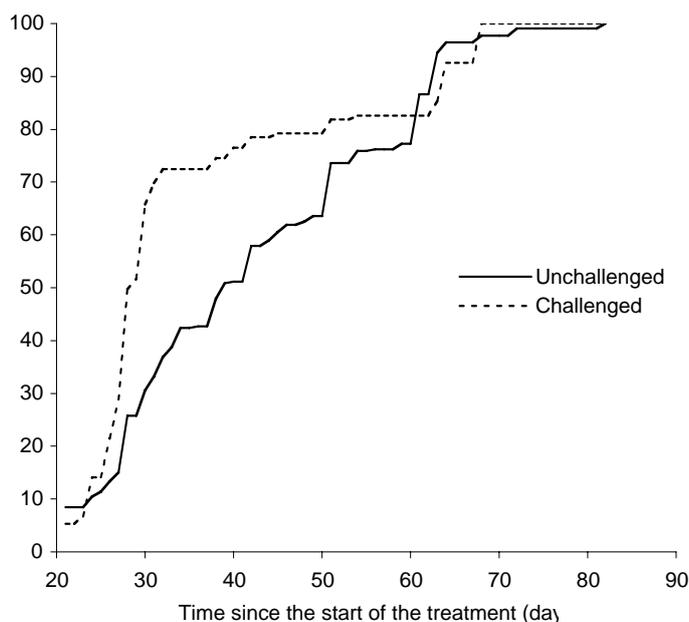
Using the split-colony design for the entire life cycle of the colony (Schmid-Hempel and Schmid-Hempel, 1998), Moret and Schmid-Hempel (2001) permanently challenged one half of a colony by injection of LPS into its workers whilst the other half served as a control (by injection of insect Ringer alone). Moret and Schmid-Hempel (2001) then studied the resulting change in the life histories of the two colony halves. In fact, the immune challenge resulted in a number of far-reaching consequences. For example, the entire colony suffered a severe fitness loss when immune-challenged even though no real infection had taken place (Fig. 3). Therefore, running the immune system seems to require a substantial amount of resources that cannot be invested otherwise.



**Figure 3.** A constant antigenic challenge of the workers of a colony (“challenged”) leads to a massive reduction of the reproductive success (daughter queens, males) as compared to controls (“Control”) in the bumble bee, *B. terrestris*. Numbers in bars are sample sizes (number of colonies) (after Moret and Schmid-Hempel 2001).

Quite unexpectedly, Moret and Schmid-Hempel (2001) also found that not only was there a loss in fitness but also a change in the patterning of life history events as a result of the challenge. The challenged colony halves started and finished reproduction earlier than the control halves, even though they lived in the same environment (Fig. 4). The fitness consequences of such a life-history shift are not yet understood, since it is associated with a generally lower reproductive output (this is a confusing statement that could use some clarification). However, similar cases are known from other organism. For example,

Minchella (1985) found that aquatic snails infected or just exposed to their trematode parasites also advanced their reproductive timing. Their interpretation was that this reduces the expected negative effects of parasitism, since the trematode will eventually castrate the snail later in the season. Similarly, Polak and Starmer (1998) discovered that infection by mites in *Drosophila* lead to an increased reproductive effort. Therefore, also in *B. terrestris*, it might be the case that a real infection by bacteria, such as mimicked here by injection of LPS, is commonly associated with a reduction of future reproductive performance or even complete sterility once the infection gets out of control and develops into a heavy parasitaemia. If such is the case, also colonies of social insects may choose to advance their reproduction to minimize the effects of the infection. Clearly, this issue would deserve further studies. Perhaps as a corollary to these experimentally demonstrated shifts in life history, natural populations of bumble bees show a correlation between the relative time of reproduction (measured against the length of the entire life cycle at any one location) and the rate of parasitism in this population (in this case, measured as the prevalence of conopid fly brood in the workers) (Durrer and Schmid-Hempel, 1995).



**Figure 4.** A constant antigenic challenge of the workers of a colony (“Challenged”) leads to advancing the reproductive events as compared to controls (“Unchallenged”) in the bumble bee, *B. terrestris*. Shown is the cumulative fraction of males produced by the colony until a given day after the start of the experimental treatment (which started with the first brood) (after Moret and Schmid-Hempel 2004).

A very unexpected effect also resulted from immune-challenging the colonies in that sexual offspring produced by this colony showed increased immune performance (Moret and

Schmid-Hempel, 2001). In particular, the males had elevated activity levels of the PO-enzyme that is a crucial component of the insect immune system. It thus appeared as if the challenged colony invested more into the quality of its offspring and especially with respect to defence against parasitism. This pattern is similar to the pattern known from vertebrates. For example, mammals are known to transfer antibiotics in the mother milk (Hanson, 1998; Coste *et al.*, 2000) and, similarly, bird females can add antibiotics to their eggs (Rollier *et al.*, 2000). Hence in this respect, social insects may be more similar to the brood-caring vertebrates than previously thought. Indeed social insects are characterized by a large investment in brood care.

## 5. Parasitism and the biology of social insects

The few examples mentioned above demonstrate the potential role of parasites in affecting the life history of social insects. It is therefore interesting to speculate about the potentially co-evolved traits that characterize social insect biology. For example, social group size in mammals correlates with disease pressure (Côté and Poulin, 1995). The same may be true for social insects, as it appears that colony size is a correlate of parasitic infection, such that large colonies tend to be more frequently affected by parasites (Schmid-Hempel, 1998) although the situation may not always be as simple (Hughes *et al.*, 2002). Similarly, genetic diversity generated by female multiple mating has been shown to reduce the level of parasitism (Baer and Schmid-Hempel, 1999). In addition, nesting ecology, foraging behaviour and diet is also decisive to affect the level of parasitism (Michener, 1985). In a recent review, Boomsma *et al.* (2004) surveyed some of these correlates more closely.

In addition to overall characteristics of social insect biology, the internal transmission dynamics also affects the outcome of an infection. Certain modes of colony organisation that lead to a partitioning of the colony into more or less separate entities can lead to a reduction of within-colony transmission (Schmid-Hempel and Schmid-Hempel, 1993; Schmid-Hempel, 1998). How strong this effect is remains to be further investigated. The evidence so far is quite spotty (Hughes *et al.*, 2002; Boomsma *et al.*, 2004). Nevertheless, it is obvious that traits so typical for social insect biology such as colony size, organisation of the division of labour, genetic diversity and kinship all play an important role for how parasites affect the colonies. It may therefore be possible that, for example, variation in colony size is in important ways driven by parasitism. In fact, variation in colony size remains poorly understood in functional terms although some correlates such as geographic latitude have been identified (Kaspari and Vargo, 1995). On the other hand, small colony size and low-density populations may protect against being “found” by parasites and therefore could represent an unexpected anti-parasite strategy.

One problem that has comparably attracted little attention is the fact that a colony also must maintain its integrity – both, socially and ergonomically. Parasites clearly disrupt this integrity in many ways by imposing increased mortality rates and reducing fecundity. In fact, there is one element of the co-evolution between host and parasite that is quite unique to social insects. Queens of social insects – with very few exceptions (mainly in the termites) – mate only during a single reproductive period and before starting their colony. This means that the genotype of the colony, that is, the genotypes of the workers and sexuals remain “fixed” for the duration of the colony cycle. This is the case because the queen’s genotype (or those of the many queens in polygynous species) cannot change during the life time of

the queen's tenure. (In some species, such as in the honey bees, queen supersedure occurs, which of course changes the available genotypes.) Also the available male genotypes represented by their sperm in the queen's spermatheca remain the same. Furthermore, in the social hymenoptera – the ants, bees and wasps – effective recombination (producing new combinations for offspring) is possible only in the diploid females while the males, being haploid, cannot produce new variants in this way. In other words, as long as the colony exists and the heading queen is not replaced, the genotypes present in the colony will remain within a limited range of possible types.

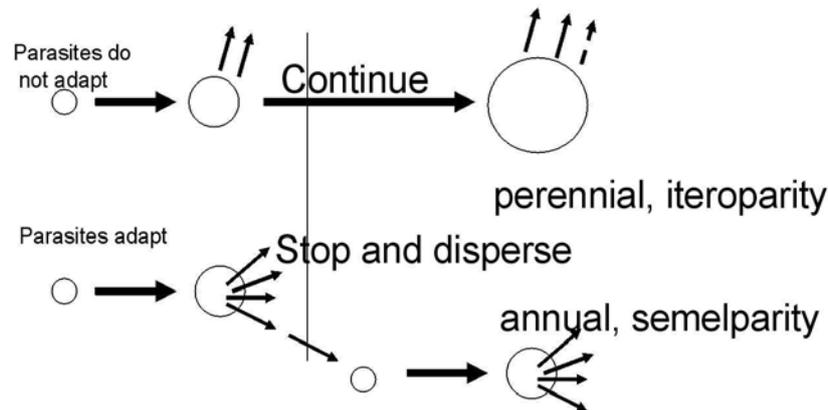
On the other hand, parasites and especially micro-parasites – being numerous, short-lived, and constantly renewable by mutations and in form of novel infections picked up during the colony's life cycle – can continue evolving against a relatively constant genetic background of an established colony. Parasites are therefore expected to adapt to the prevailing genetic background of the host colony. Depending on several factors, this could, but must not necessarily, lead to an increased virulence for the infected colony (Ebert, 1994; Lipsitch *et al.*, 1995; Lipsitch *et al.*, 1996; Ebert, 1998a). In fact, many experiments have shown that serial passage of a parasite through a new, constant host background leads to increased virulence in this host and an associated loss in an original host (Ebert, 1998b). Whether or not this is also the case in the situation of a social insect colony as described above remains to be investigated, but is used as a working hypothesis here.

When parasites adapt to a given colony's genetic background and increase in virulence, a novel problem arises. Defence against parasitism is costly (Schmid-Hempel, 2003). It is to be assumed that increased virulence of the parasite may also increase the costs of defence. This is likely when virulence is, for example, a direct consequence of an increased rate of parasite multiplication, that is, more propagules being produced within the same time. If this is the case, then being infected not only imposes a simple and constant cost (Moret and Schmid-Hempel, 2000), but also would require increasingly more resources to combat and clear the infection as the colony cycle unfolds and parasites keep adapting. Looking at the relationship of cost and success, the level of a standardized immune response indeed appears to correlate with the success of a colony, suggesting that a good immune defence (presumably entailing a high cost) increases survival and reproductive success (Baer and Schmid-Hempel, 2003b).

Expanding on this scenario, a consequence of such adaptation by parasites to a colony would mean that ever more resources have to be allocated to defence, just to ensure the colony's mere survival in the face of parasitism. At some point, all available resources would be committed to defence and nothing left for further maintenance and growth. Therefore, the hosts may opt out of this race and decide to stop the colony cycle. We may observe this consequence as resulting in a shift from a perennial and iteroparous life cycle to an annual and semelparous cycle (Fig. 5). In this way, the colony avoids an ever-increasing cost of immune defence and instead evades parasites by stopping the cycle and dispersing to a new location. This scenario is of course quite speculative and remains to be investigated. However, it could help shedding some light on why there is so much variation in the life cycles of social insects.

This process would leave its traces mainly in the observed variation among taxa that are exposed to different parasite pressures, that is, are exposed to ecological variation. Such variation does certainly exist in closely related species that occupy different niches and thus vary in their ecology. However, variation in life history parameters is mainly visible at higher

taxonomic levels, for example, among the groups of termites, ants, bees and wasps, or – within these groups among tribes. We do not know at present whether the co-evolutionary scenario could explain these patterns (Boomsma *et al.*, 2004). A closer look would be worthwhile.



**Figure 5.** A possible connection between the adaptation by a parasite to its host colony and the colony life cycle. When parasites adapt rapidly and impose ever increasing costs of defence, adopting an annual, semelparous life cycle may be superior to a perennial, iteroparous life cycle.

In all, parasitism affects almost any aspect of social insect biology and, most notably, almost all parameters that characterize a life history, such as age at reproduction, colony size, or division of labour. The consequences of this selective pressure are still unclear in most cases and vaguely understood in some (Schmid-Hempel, 1998). The present article has listed just a few items, mainly worked out for the model system of the bumble bee, *Bombus terrestris*, and its parasites. It leaves open a huge variety of species, life styles and potential host-parasite interactions. Shedding more light into these questions will be a challenge for future research.

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## **Life in a nutshell – social evolution in formicoxenine ants**

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**Abstract** – *Ants of the myrmicine tribe Formicoxenini are suitable model systems to investigate life history evolution in social insects. Though the evolution of queen numbers is to some extent constrained by phylogeny, environmental conditions explain variation in queen number and reproductive skew in Leptothorax and Temnothorax. Hibernation mortality in boreal habitats appears to be associated with multiple-queening in both genera. Nest site limitation promotes high skew (functional monogyny) in Leptothorax, but leads to colony take-over and fusion in monogynous Temnothorax nylanderii.*

**Keywords:** *Leptothorax*, social organization, life history evolution, polygyny, reproductive skew.

### **Introduction**

Social Hymenoptera (ants, bees, and wasps) have become important models for the investigation of self-organization and pattern formation in biological systems (Bonabeau *et al.*, 1997; Page and Mitchell, 1998; Sendova-Franks and Franks, 1999), the proximate and ultimate aspects of phenotypic plasticity (Wheeler, 1986; West-Eberhard, 2003), the mechanisms underlying complex behavior and chemical communication (Hölldobler and Wilson, 1990; Hammer and Menzel, 1995; Wehner, 2003), and the role of inclusive fitness in social evolution (Hamilton, 1972; Wilson, 1975; Bourke and Franks, 1995; Crozier and Pamilo, 1996). Social Hymenoptera, in particular ants, have been recognized as keystone taxa in ecology and conservation biology (Hölldobler and Wilson, 1990; Kaspari and Majer, 2000) and various species, such as fire ants and the Argentine ant, are investigated in detail to understand which conditions predispose a species to become successful invaders or tramps (Chapman and Bourke, 2001; Holway *et al.*, 2002).

In short, social insects have been scrutinized from countless angles and in countless contexts, not the least because many simple life history traits of social insects exhibit such an enormous variation between species that model systems to study certain biological questions are readily available. For example, in ants alone, body size within the two female castes ranges from 2mm to more than 3cm and average longevity in queens varies thirty-fold, from a few months in *Cardiocondyla* (unpublished observations) to close to thirty years in *Lasius* (Hölldobler and Wilson, 1990). Ant queens exhibit tremendous inter- and intraspecific variation in reproductive tactics and dispersal strategies, from wingless,

stationary queens with intranidal mating, which never leave their established colonies, to efficient fliers, which mate on the wing and found their own society solitarily (Buschinger and Heinze, 1992; Heinze and Tsuji, 1995; Heinze and Keller, 2000). On the level of the society, fundamental life history traits exhibit even more surprising plasticity. Colony size at maturity ranges over eight powers of ten, from less than 10 in *Thaumatomyrmex* (Jahyny *et al.* 2002) to several million individuals in driver ants or *Formica* supercolonies (Higashi and Yamauchi, 1979). Age at maturity extends from a few months in colonies that undergo budding to several years in colonies of many monogynous species, such as fire ants, and propagule size and the pattern of reproductive allocation (i.e., allocation of resources towards reproduction vs. growth and maintenance) vary accordingly.

It may therefore be astonishing that life history evolution in social insects is only poorly studied and not well understood. Textbooks on life history evolution (Stearns, 1992; Roff, 2001) hardly ever mention social insects at all, and likewise, the topic of life history evolution is rarely given a methodical, general treatment in books on social insects (for one of the few notable exceptions see chapters 9 and 10 in Bourke and Franks, 1995). Not counting the comprehensive theories on sex allocation and reproductive skew (Crozier and Pamilo, 1996; Johnstone, 2000), we are presently lacking broadly applicable models on social insect life history evolution. For example, though colony size has vital impact on many fundamental parameters of social life (Bourke, 1999) we have little insight into what determines colony size. Even more disturbing is the broad lack of empirical information on such simple life history traits as the age structure of populations (Tschinkel, 1991), which can often easily be obtained in other organisms.

The myrmicine tribe Formicoxenini is a particularly well studied group of ants, which provides some of the best known examples of dominance hierarchies among workers and queens (Cole, 1981; Franks and Scovell, 1983; Bourke, 1988; Heinze and Smith, 1990; Heinze *et al.*, 1997), queen dispersal polymorphism (Heinze and Buschinger, 1989; Hamaguchi and Kinomura 1996; Rüppell *et al.*, 2001ab), inter- and intraspecific social parasitism (Buschinger, 1986; Foitzik and Heinze, 1998), host-parasite co-evolution (Foitzik *et al.* 2001, 2003a) and variation in sex allocation (Pearson *et al.*, 1995; Herbers and Stuart, 1996; Chan *et al.* 1999, Foitzik and Heinze 2000; Foitzik *et al.* 2003b, 2004), queen number, and reproductive skew (Buschinger, 1968, 1974; Heinze and Buschinger, 1989; Bourke and Heinze, 1994; Heinze and Oberstadt, 2003). According to a recent taxonomic revision (Bolton, 2003), which confirms previous ideas by Smith (1950) and others (Baroni Urbani, 1978; Francoeur *et al.*, 1985; Buschinger, 1987; Douwes and Stille, 1987), most of the non-parasitic representatives of *Leptothorax* in its traditional sense from boreal and temperate habitats are currently classed into two separate genera, *Leptothorax* (formerly *Leptothorax* s. str.) and *Temnothorax* (formerly *Leptothorax Myrafant*). Species of these taxa inhabit preformed cavities in the soil, decaying wood, or rock crevices. Average colony size, between a few dozen and a few hundred individuals, 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.

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 (Buschinger, 1973, 1974; Heinze and Ortius, 1991), Formicoxenini – and in particular *Leptothorax* and *Temnothorax* – provide suitable model systems to investigate

ultimate and proximate aspects of life history variation. The data base on sex allocation ratios, variation in queen numbers and reproductive skew appears sufficiently robust and has encouraged a number of tests of models of particular life history traits. In the following, I review the results of recent research on the behavioral, genetic, and ecological correlates of social structure in these two genera, including previously unpublished details from ongoing projects.

### **Queen number in formicoxenine ants**

Queen number has been considered to be a rather labile trait in evolution, which easily evolves in response to changed selection pressures (Ross and Carpenter 1991). The occurrence of both obligatorily monogynous and facultatively polygynous species in various ant genera supports this view, though there is little well documented evidence for monogynous / polygynous pairs of sibling species. In *Leptothorax*, colonies in all studied species may have several queens, while in *Temnothorax*, most species are strictly monogynous (Buschinger 1968, 1974; Heinze and Buschinger 1988). Only a few nearctic species, e.g., *T. longispinosus* and *T. rugatulus*, which occur throughout deciduous forests in temperate North America, and the palearctic species *T. tuborum* and *T. interruptus*, which occur in Central Europe and Southernmost Scandinavia, are facultatively polygynous.

It was suggested that cold climate favors polygyny in that solitary colony founding under adverse environmental conditions is avoided. This view is corroborated by the observation that most ants from habitats near the tree-line in North America and Eurasia are facultatively polygynous or social parasites and that similar patterns are observed in mountainous areas (Heinze, 1993a; Heinze and Hölldobler, 1994). Workers of *L. canadensis* survive artificial hibernation better in groups than in isolation (Heinze *et al.*, 1996a). If the same were true for young *Leptothorax* queens, multiple-queening and subsequent budding under more favorable conditions in spring and early summer would strongly increase the reproductive success of a colony.

### **Reproductive skew in multi-queen colonies of *Leptothorax***

The partitioning of reproduction (reproductive skew) among queens in *Leptothorax* societies has been investigated using ESS models on optimal skew (Bourke and Heinze, 1994). While queens in colonies of *L. muscorum* and *L. canadensis* contribute more or less equally to the colony's offspring (polygyny) (Heinze, 1994; Lipski *et al.*, 1994), queens in colonies of *L. gredleri* and an as yet undescribed *L. sp. A* from New England and Eastern Canada form rank orders, in which the most dominant queen monopolizes reproduction (functional monogyny, Buschinger, 1968; Heinze and Smith 1990; Heinze *et al.* 1992). In *L. acervorum* and probably also other species, queen number and the degree of reproductive skew differ considerably between populations, with some populations being almost completely monogynous (Heinze *et al.* 1995), others facultatively polygynous (Buschinger, 1968; Bourke, 1991; Heinze *et al.*, 1995; Bourke *et al.*, 1997), and still others functionally monogynous (Ito, 1990; Heinze and Ortius, 1991; Felke and Buschinger, 1999).

According to ESS models on optimal skew, how reproduction is partitioned among group members is determined by the relatedness among cooperative breeders, their respective fighting strength, the effect subordinates have on the dominant's reproductive success, and

ecological constraints, i.e., the costs of emigration from the group and solitary breeding (Vehrencamp, 1983; Reeve and Ratnieks, 1993; Johnstone, 2000). How these factors influence reproductive skew depends, for example, on who is in control of reproduction. When the dominant can determine the maximum share subordinates have in the group's offspring, skew is expected to increase with increasing relatedness. In contrast, when the subordinates may claim unsanctioned reproduction, higher relatedness will lead to lower skew (Johnstone, 2000).

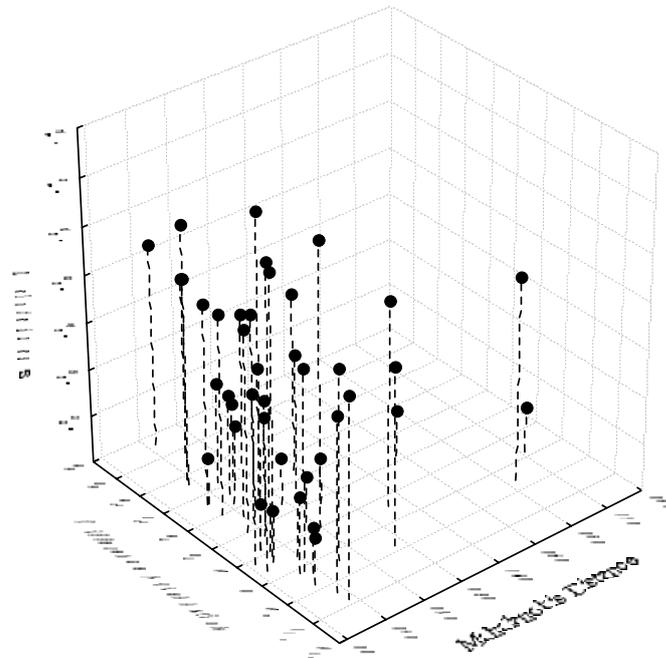
Observations suggest that dominant queens of functionally monogynous *Leptothorax* typically can restrain the subordinates' behavior and are therefore in control of reproduction. Rank orders are formed by overt or ritualized aggression, such as antennal boxing, biting, and sting smearing (Heinze and Smith, 1990; Heinze *et al.*, 1992; Heinze, 2004). Within a few weeks after the end of hibernation, such hierarchies become stable, queen-queen aggressions cease, and the alpha-queen begins to lay eggs. Workers, which previously were indifferent to queen antagonism, may now ally with the dominant queen and attack and expel "disobedient" subordinates that develop own eggs in the presence of an already fertile dominant queen (Heinze and Smith, 1990; Heinze *et al.*, 1992; Ortius and Heinze, 1995). The formation of such coalitions between the reproductive queen and the workers appears to rely on chemical signals, which reflect the fecundity of the dominant queen. In an analogy to Forsyth's (1980) explanation of queen killing in pleometrotic associations, workers benefit most from supporting the queen that is the first to lay eggs after hibernation, as in most cases this will be their own mother.

### **Chemical signals in functionally monogynous ants**

Such fertility signaling eventually overrides differences in queen aggressiveness and physical strength. This can be nicely demonstrated by permitting subordinate queens to reproduce in the presence of a non-laying dominant. To do so, young queens *L. gredleri* from Sommerhausen, Germany were returned into their orphaned, maternal nests after mating in the laboratory in late summer and allowed to establish hierarchies. Before the behaviorally dominant queen had laid her first eggs, the colonies were subjected to artificial winter conditions. After several weeks of hibernation, half of the workers and the most subordinate queen of each colony were transferred to more favorable spring conditions and allowed to lay eggs, before the more dominant queens and the remaining workers were added. Interestingly, in each colony the initially most subordinate queen remained the only egg-layer without engaging in aggressive interactions with the former dominants, while the latter were attacked and finally expelled by workers (unpublished results). The independence of physical dominance and reproductive potential and the role of fertility signaling in the division of reproductive labor and the maintenance of high skew has also been demonstrated in *Leptothorax* sp. A (Ortius and Heinze, 1999).

Chemical communication appears to play a major role also during the establishment of hierarchies. When queen-queen fights in *L. gredleri* escalate, one individual may use her sting to spread substances from the Dufour's gland onto the cuticle of an opponent (Heinze *et al.*, 1998). These secretions appear to be colony-specific, and it was suggested that young queens, after somehow succeeding in sneaking into and becoming adopted in an alien colony, use such secretions to mark the resident queen and have her replaced by her own workers (Heinze *et al.*, 1998). The application of Dufour's gland secretions might thus

constitute an intraspecific equivalent to information warfare by propaganda substances in socially parasitic ants (Regnier and Wilson, 1971; Allies *et al.*, 1986).



**Figure 1.** The role of Dufour's gland secretions in the regulation of reproduction in *Leptothorax gredleri*. Queens of this ant species apply chemical secretions from their Dufour's glands onto the cuticle of other queens and thus induce aggressive reactions by workers. For details see text.

However, in a subsequent investigation with 41 queens from 11 colonies, the secretions of queens distantly related to the colony's workers did not produce a stronger response (inspective or aggressive antennations in five minutes elicited by secretions corrected for the number of antennations elicited by water) when applied onto a focal worker than the secretions of related nestmate queens. Furthermore, there was no association between the degree of similarity between the queen's secretions and those of an average nestmate worker and aggression (multiple regression,  $R=0.1367$ ,  $p=0.6984$ ; Mahalanobis distance:  $\beta=-0.126$ ,  $p=0.441$ , genetic distance:  $\beta=0.034$ ,  $p=0.834$ ; Oberstadt, 2003). In contrast, multiple regression on data from only the colony with the largest queen number suggested that secretions from fertile queens differ most and elicit more aggression (seven queens,  $R=0.9354$ ,  $p=0.072$ , chemical distance:  $\beta=-1.449$ ,  $p=0.021$ ; genetic distance:  $\beta=-0.4987$ ,  $p=0.126$ ; ovary development:  $\beta=1.0258$ ,  $p=0.0589$ ). Dufour's gland secretions may thus be used by the fertile queen to punish subordinate queens as in the queenless ant *Dinoponera quadricaps* (Monnin *et al.*, 2002).

## Optimal skew models and *Leptothorax*

In any case, while functional monogyny is initially established by overt and ritualized fighting among queens, it is later maintained by the workers, which react to pheromonal signals from the dominant by attacking potential rivals. Dominant *Leptothorax* queens thus are capable of punishing subordinates either alone or assisted by workers and appear to be in control of the partitioning of egg laying. *Leptothorax* societies can therefore be used to test the respective predictions from concession models that reproductive skew increases with relatedness and the magnitude of ecological constraints (e.g., Vehrencamp, 1983; Reeve and Ratnieks, 1993; Johnstone, 2000).

The first prediction is not supported by estimates of queen-queen relatedness based on allozyme genotypes. Queens in both low-skew and high-skew species are on average equally closely related (Heinze, 1995). Though in an experimental set-up with two-queen colonies of *Leptothorax gredleri* aggression during hierarchy formation was significantly more frequent among related than unrelated queens ( $8.1 \pm 4.5$  attacks per hour vs.  $5.3 \pm 1.2$  attacks per hour,  $n_1 = n_2 = 12$ , Mann-Whitney U-test,  $z = 0.30$ ,  $p = 0.003$ ), the final outcome – complete reproductive skew – was independent of relatedness (Oberstadt, 2003). Relatedness thus seems to be relatively unimportant for the details of social structure, as previously also shown in several other social insects (Field *et al.*, 1998; Nonacs *et al.*, 2004; Korb and Heinze, 2004).

In contrast, ecological conditions give a better explanation for the observed differences between species and populations (Bourke and Heinze, 1994). According to concession models skew increases with the probability that solitary breeding fails, which again depends on ecological conditions. Facultatively polygynous *Leptothorax* live in large and homogeneous coniferous forests, where queens that disperse on the wing may easily find a suitable nest site for colony foundation. Quite the opposite, functionally monogynous species occur predominantly in patchily distributed boreal habitats. These include the partly shaded, *Cladonia*-covered edges of rocky outcrops or clearings, south-exposed blackthorn and rose thickets, isolated, open pine stands, dry patches of *Polytrichum* moss in *Sphagnum* spruce bogs, or, in the case of the related, xenobiotic genus *Formicoxenus*, the nests of *Formica*, *Myrmica* and *Manica*. Such patches are typically small and provide only a few nest sites, which can be quickly utilized by already established colonies through budding. Dispersal and solitary founding are difficult in such habitats, as no empty nest sites are available close by and long-range dispersal may lead a winged queen into unsuitable habitat. Dispersal risks are reflected in the striking wing polymorphism of queens of some functionally monogynous *Leptothorax* and *Formicoxenus* (Francoeur *et al.*, 1985; Heinze and Buschinger, 1989; Buschinger and Francoeur, 1991): in addition to the typical winged female sexuals, wingless "intermorphic" queens with a morphology intermediate between that of winged "gynomorphs" and the "ergatomorph" worker phenotype occur. In *Leptothorax* sp. A and probably also other queen-polymorphic Formicoxenini, wing polymorphism has a genetic basis and is associated with alternative reproductive strategies (Heinze and Buschinger, 1989). While more than 90% of all *L. sp. A* queens are wingless on wind-exposed rocky outcrops along the shores of St. Lawrence and Saguenay Rivers in Québec, winged queens clearly outnumber wingless queens in more homogeneous pine forests (Heinze, 1993b). Coarse-grained environmental heterogeneity with different dispersal success of long-winged queens appears to maintain the genetic polymorphism.

Through dispersal risks and nest site limitation, habitat patchiness therefore appears to be associated with increased costs of solitary nesting. Together with hibernation mortality, ecological constraints appear to be so severe in patchy boreal habitats that subordinate queens benefit more from tolerating the monopolization of reproduction by a related dominant than from attempting solitary founding. This leads to the association between functional monogyny and habitat patchiness suggested by skew models (Bourke and Heinze, 1994). Rather than risking to fail at solitary founding, young subordinate queens might increase their average inclusive fitness by staying in the maternal nest and helping. Indeed, the presence of a subordinate queen appears to boost the reproductive output of the dominant queen more than the presence of an additional worker (Heinze and Oberstadt, 2003). Furthermore, subordinates might queue as "hopeful reproductives" to replace the present dominant in the future (Kokko and Johnstone, 1999), though in *Leptothorax* the probability that a certain subordinate will take over the alpha-position falls with time as in each year new queens are recruited from the dominant's offspring.

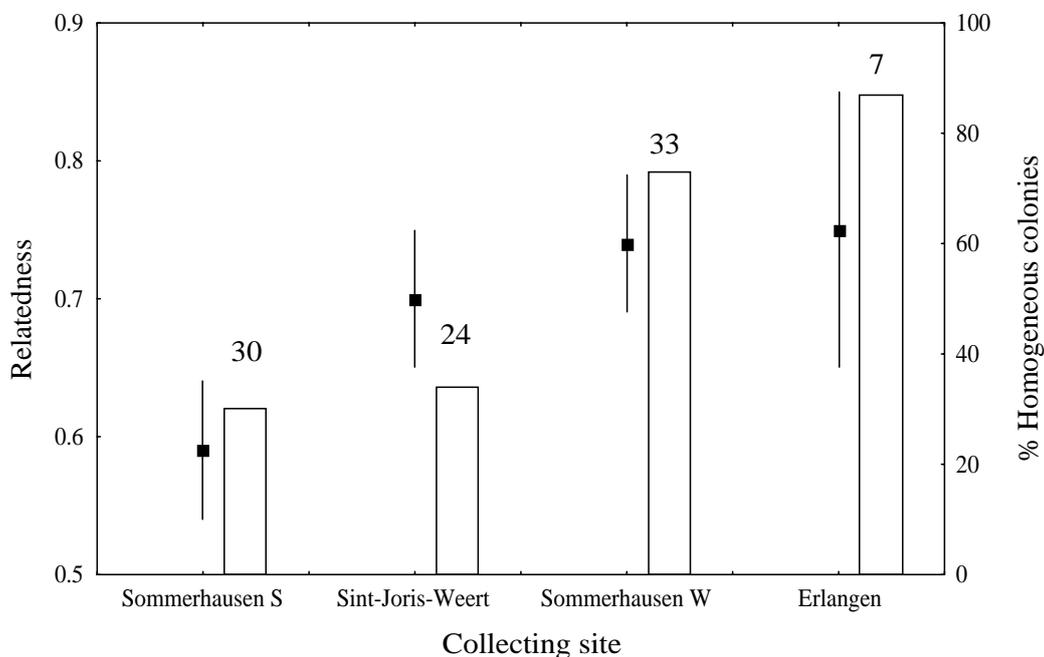
### **Nest site limitation in monogynous *Temnothorax nylanderi***

Hibernation mortality during solitary founding, which appears to be a considerable factor promoting polygyny in boreal *Leptothorax*, is presumably less important in temperate ants, such as Central European or Mediterranean *Temnothorax*. Only a few species in this genus have evolved facultative polygyny, apparently in response to adverse climate (Herbers, 1986a) and nest site limitation (Herbers, 1986b; Foitzik *et al.*, 2004). Polygyny is often associated with alternative dispersal tactics and a pronounced queen size dimorphism (Hamaguchi and Kinomura, 1996; Rüppeil *et al.*, 2001ab). As in other queen-polymorphic ants, small queens typically return into their maternal nests after mating in the vicinity, while a considerable part of large queens disperse and found solitarily (Rüppeil and Heinze, 1999; Rüppeil *et al.* 2001). Though queens appear to avoid each other in polygynous *Temnothorax curvispinosus* (Wilson, 1974), social or reproductive rank orders have as yet not been observed and reproductive skew is much lower in *T. rugatulus* than in functionally monogynous *Leptothorax* (Rüppeil *et al.*, 2002).

Nest site limitation, probably together with a loss of diversity in genetic odor cues, appears to have promoted the evolution of intraspecific parasitism in *T. nylanderi*, one of the most common ants in Central Europe. This species nests in acorns, hazelnuts and hollow twigs and locally reaches abundances of more than 10 nests per square meter. At such nest densities, all available nest sites are quickly occupied. Furthermore, many fragile nest sites decay over summer and new nests will become available again only in fall or winter, when new nuts, hollowed by beetles, have fallen to the ground. This results in an extreme shortage of nest sites in particular in late summer, when young queens disperse to mate and found their own colonies. Though *T. nylanderi* is obligatorily monogynous (Buschinger, 1968; Plateaux, 1970, 1971), many colonies contain workers belonging to different matriline and two or more queens may temporarily be present in colonies in fall (Foitzik and Heinze, 1998). This results both from fusion of mature colonies and intraspecific parasitism. Young founding queens readily invade established colonies when they do not find a suitable nest site and in several cases have been observed to engage in violent fighting with the resident queen. Through the expulsion or elimination of one of the two queens, multiple-queening quickly reverts to monogyny (Strätz *et al.*, 2002a). The frequency of genetically heteroge-

neous colonies is substantially larger and nestmate relatedness is lower in dense populations (Foitzik *et al.*, 2004; M. Strätz and J. Heinze, unpublished, Fig. 2).

Colony take-over or fusion is apparently facilitated by a strong influence of environmental cues on colony odor. Workers from pairs of field colonies nesting in different types of wood showed significantly more aggression than workers from colonies nesting in the same material. When colonies were split and transferred either into two artificial pine nests or one pine and one oak nests, former nestmates presently living in different nesting material were more aggressive than workers from different pine nests (Heinze *et al.*, 1996b). Colony fusion in the laboratory was also observed in *T. crassispinus*, the Eastern sibling species of *T. nylanderi* (Tichá, 2002; Tichá and Štys, 2002), but at least in populations around Regensburg, Germany, mixed colonies appear to be rather infrequent (Strätz and Heinze, 2004).



**Figure 2.** Association between colony density and the occurrence of intraspecific parasitism in *Temnothorax nylanderi*. In dense collecting sites (Sommerhausen S and Sint-Joris-Weert), the frequency of homogeneous, non-usurped colonies with high nestmate relatedness is lower than in sparsely populated areas (Sommerhausen W and Erlangen; Foitzik *et al.*, 1994).

Genetic analysis did not reveal colony usurpation or fusion in other *Temnothorax* (Heinze *et al.*, 1997; Ruppell *et al.*, 2003, but see Pearson *et al.*, 1997). The common occurrence of colony take-over and the dependence on environmental odor cues for nestmate discrimination might proximately result from a loss of variability in genetic odor cues as suggested for invasive, uniclonal ants (Tsutsui *et al.*, 2000). Indeed, *T. nylanderi* exhibits remarkably little genetic variability throughout Central and Western Europe (Strätz *et al.* 2002b), perhaps due to bottlenecks during post-glacial reimmigration from refugia in Southern Europe.

## Conclusion

Queen number and reproductive skew, two important life history traits in social insects, appear to be generally affected by ecological parameters, such as climate and habitat patch size (Hölldobler and Wilson, 1977). Combinations of optimal skew theory and models on evolutionarily stable dispersal strategies have been useful to identify the ecological causes of varying colony structure in boreal *Leptothorax* ants (Bourke and Heinze, 1994), and similar approaches might help to better understand variation also in other life history traits. In particular, the environmental conditions that lead to the evolution ofinquilines (interspecific queen-tolerant social parasites, such as *Leptothorax kutteri*), slave-makers (such as *Temnothorax duloticus* or *Harpagoxenus*) and murder-parasites (queen-intolerant social parasites, such as *L. paraxenus*) from non-parasitic ancestors might be elucidated in such a way (e.g., Heinze and Tsuji, 1994; Lowe *et al.*, 2002). Though it has been difficult to reliably track the fate of individual colonies in the field over several years, Formicoxenini might provide suitable systems also for the investigation of the evolution of other life history traits, such as colony size, age at maturity, and allocation of resources towards colony growth or reproduction.

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## **The evolution of seasonal cycles in cold-temperate and boreal ants: Patterns and constraints**

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**Abstract** – *The paper is an introduction to the research programme on physiological, ecological and behavioural adaptation of ants to cold-climate environments developed over the past two decades by the research group at St. Petersburg State University. Temperate and cold-climate ants use two main seasonal strategies: the strategy of concentrated brood-rearing (no dormancy in larvae, queens and workers pass the winter in diapause without brood) and the strategy of prolonged brood-rearing (overwintering with larvae in diapause, larvae of rapid brood develop from egg to pupa within the same summer season, slow brood larvae overwinter and pupate the next summer). Most temperate ants depart from the bang-bang strategy of worker and sexual production predicted by Oster and Wilson (1978) and use the strategy of two separated bangs, or else the strategy of spring rearing of sexuals. This strategy has several modifications differing mainly in the time of resource acquisition and allocation in sexuals (autumn or spring). It is proposed that the success of the founding queens can be the main determinant of the seasonal pattern of sexual production observed in temperate climate ants.*

*Simple graphic and mathematical models demonstrate that total annual brood production per colony and per worker should decrease as one goes north. Our field and experimental data on *Myrmica* confirm a gradual decrease in annual production of new adults and in the quantity of rapid brood from 50° and 66° N, with this type of brood disappearing entirely at about the level of the Arctic Circle. The model is developed that predicts that the main consequence of the decreasing annual brood production as one proceeds northward is a diminished mature colony size. Our field studies of *M. ruginodis* show a significant decrease in the number of workers per nest between 56 and 69° N. Beyond the latitude at which some larvae are forced to hibernate twice or more, a much sharper decrease in the annual production of new adults and an abrupt decrease in the size of mature colonies are expected. This should result in a two-fold dependence of colony size on latitude. Since too small colonies seem to be unable to survive and reproduce, this will set a northern limit to distribution. The change from monogyny to polygyny and the decrease in the development time from egg to adult are the most plausible adaptation that might buffer the decrease in mature colony size in far-northern ant populations.*

**Keywords:** ants, cold-temperate, boreal, climates, seasonal cycles, life-history, evolution, constraints, seasonal strategies, sexual production, colony size, latitudinal variation, northern distribution limit.

## Introduction

In the most fruitful theoretical study to date of the colony cycle in social insects, Oster and Wilson (1978) focussed on the scale and timing of the resource allocation between worker and sexual production. For annual species such as vespine wasps or bumble bees, they distinguished three main stages in a colony's life cycle: *founding stage* in which the queen initiates the colony and rears the first brood of workers, *ergonomic stage* in which the colony grows rapidly by producing more workers, and *reproductive stage* in which the colony completely switches to production of sexuals. This latter switch is the key to the *bang-bang strategy* of maximizing the colony's fitness, measured as production of sexuals.

In perennial species, such as ants and termites, the founding stage (or phase) is also followed by an ergonomic stage. However, this latter may last for a number of years, during which the colony grows by producing all-worker broods. When it finally comes, the reproductive stage is typically not the last part of the colony cycle, as in following years the colony again produces a mixture of workers and sexuals. For species with perennial colonies, Oster and Wilson likewise predicted a bang-bang strategy, with a strict alteration of ergonomic and reproductive stages each year after the first reproductive stage. The ergonomic stage within each season should be as long as possible, so that more workers are available to raise sexuals during the second part of the year. Such seasonal switches from worker to sexual production, predicted by Oster and Wilson's model, were indeed observed in several tropical and subtropical ants (Bourke and Franks, 1995). For example, in *Solenopsis invicta* this alternation results in clear oscillations in numbers of worker present in a colony (Tschinkel, 1993).

However, perennial colonies living in cold-temperate and boreal climates – henceforth collectively termed “cold climates” – face some special constraints arising from seasonality. In particular, as one proceeds toward either pole the winter becomes more severe, and the warm season during which the colony can grow becomes shorter. The colony must thus invest more resources in workers in order to promote winter survival and subsequent reproduction, yet it has less time in which to amass those resources. Considering this constraint, Oster and Wilson (1978) only predicted that the switch to producing sexuals should occur later in the growing season as the colony overwintering survival rise. They did not go farther in their analysis.

Little attention has been paid to the role of seasonality in life history evolution in ants. For example, in Hölldobler and Wilson's (1990) definitive review "The Ants", seasonality is not even mentioned as a factor shaping the colony cycle. In "Social Evolution in Ants", Bourke and Franks (1995: 336) emphasized the role of seasonality as follows: "*Myrmica* seasonality is therefore a central feature of life history strategy within the genus. However, ant biologists simply do not know if the complex response to seasonality shown by *Myrmica* ants occurs in other ant species, ... because there are few detailed studies of the social physiology of other ants genera." (Bourke and Franks, 1995:336).

Our group at St. Petersburg State University developed a research programme to eliminate this gap in the ecophysiology and social biology of ants. Over the past two decades we have studied the seasonal cycles in more than 80 species belonging to more than 20 genera from different regions of Russia and the former USSR, ranging from warm-temperate to cold-temperate and boreal climate zones. Special attention has been given to the ecophysiology of cold-climates and boreal ants in European Russia between 50°–69° N. Our

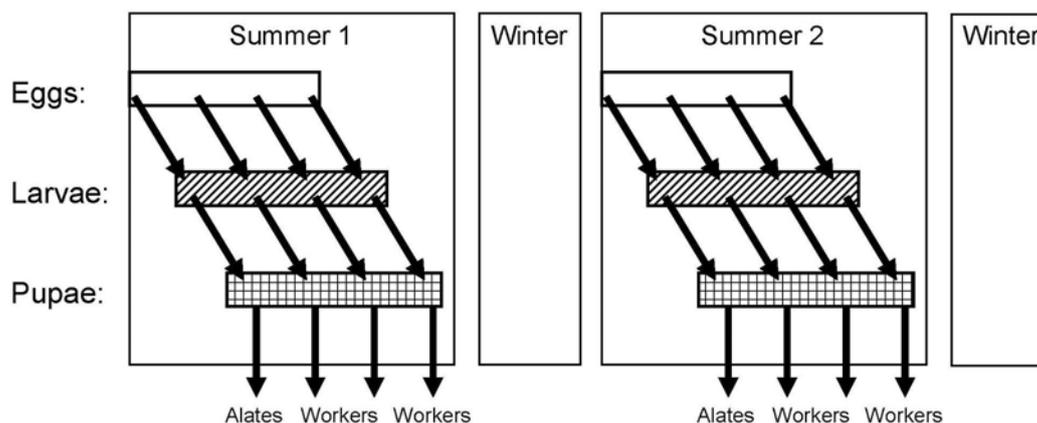
field and laboratory studies have allowed us to map the diversity of annual cycles, to reveal the underlying ecophysiological and social mechanisms of control, and to develop ideas on possible pathways in the evolution of the seasonal cycle in ants (Kipyatkov, 1993, 1994, 1996, 2001; Kipyatkov and Lopatina, 2006). To date, our results have been published mainly in Russian.

The following is an introduction to our research programme on physiological, ecological and behavioural adaptation of ants to cold-climate environments over the past two decades. My purpose here is to present a more broadly accessible review and synthesis of our research program around five questions:

1. What seasonal strategies are available to ants use in cold climates?
2. Do the main patterns of seasonal cycles in temperate and boreal climate ants conform to the predictions of Oster and Wilson's model (1978)?
3. How do seasonal cycles change with latitude, especially toward the far north?
4. Do particular social factors constrain such changes and set a limit to northward extension?
5. Are there identifiable physiological and/or ecological adaptations to overcome these constraints?

## Two seasonal strategies of brood-rearing in cold-climate ants

Most temperate and all boreal climate ants are heterodynamic, with a period of dormancy (winter diapause) in their annual life cycle (Kipyatkov, 1993, 1996, 2001; Kipyatkov and Lopatina, 2006). All cold-climate ants have adult diapause, so that their queens and workers are capable for overwintering, as are alates in some species. Queens and some workers experience diapause several times in their life. On the contrary, the ability of larvae to undergo diapause is not universal in ants. This is a major factor in seasonal-cycle evolution in these insects.

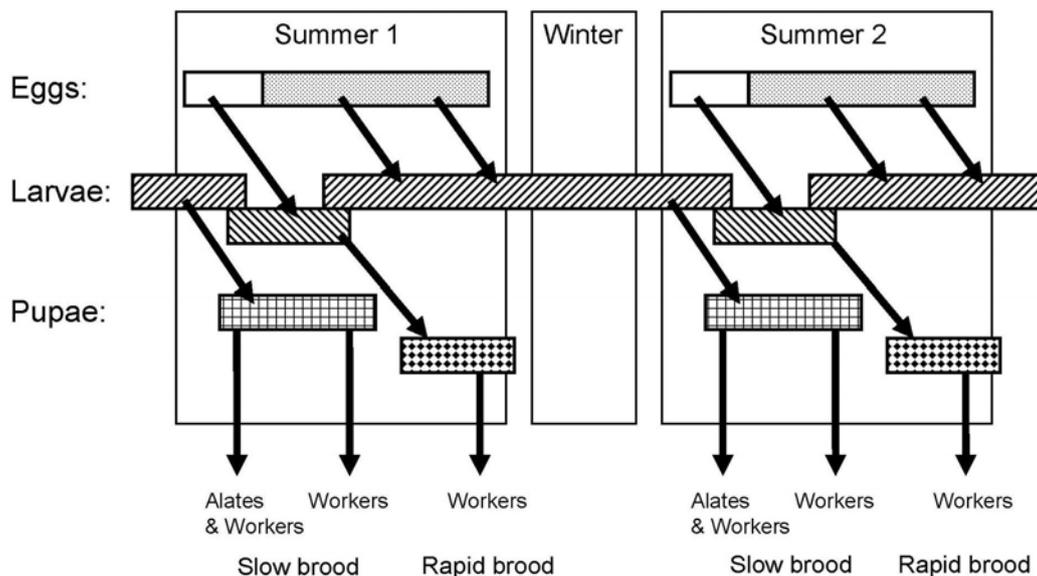


**Figure 1.** The strategy of concentrated brood-rearing. Further explanation in text.

Our own data, as well as those from the literature, support the hypothesis that temperate and cold-climate ants use two main seasonal strategies with respect to brood rearing. The simpler of these is termed the *strategy of concentrated brood-rearing* (Fig. 1). It can be thought

of as a quantitative response to the shorter growing season, or summer, distinguished by the following features:

1. Larvae have no dormancy and complete their development during the summer.
2. The development of all brood stages is thus restricted to the growing season.
3. Only queens and workers are able to undergo diapause and to overwinter.
4. The colony thus passes the winter without brood or adult males.



**Figure 2.** *The strategy of prolonged brood-rearing. Further explanation in text.*

This strategy, however, is not the most common. Rather, temperate and cold-climate ants are more likely to follow the *strategy of prolonged brood-rearing* (Fig. 2), distinguished by the following features:

1. Larval diapause is facultative and controlled by environmental (temperature, photoperiod) and social (worker care, queen influence, pheromones, etc.) factors.
2. Only some larvae develop from egg to pupa within the same summer season without overwintering. This *rapid brood*, or *summer brood*, yields only workers.
3. A large proportion of larvae delay their development, continue to grow in autumn, overwinter in diapause and pupate the next summer. This *slow brood*, or *winter brood*, yields both workers and alates.

According to our observations and published data, concentrated brood rearing is characteristic of the tribe Formicini (*Alloformica*, *Cataglyphis*, *Formica*, *Proformica*) and some species of *Dolichoderus*, *Pogonomyrmex*, *Ponera* and *Prenolepis* (Kipyatkov 1993, 1996, 2001; Kipyatkov and Lopatina, 2006). The onset of diapause in queens is a central point in the cycles of the *Formica* type, as it determines the moment after which new eggs do not appear, the brood gradually vanishes and the ants begin to prepare for overwintering. Queen diapause should not occur too early, as this would effectively waste a part of the growing season. At the same time, if diapause ensues too late many larvae and pupae will be caught by the onset of winter and perish. Evidently, concentrated brood-rearing is only adaptive in

cold climates where development times are very short. Among temperate ants, *Formica* species have the shortest developmental times. Furthermore, development is more temperature dependent, which allows *Formica* workers to rear the brood very rapidly when temperatures are high (Kipyatkov and Lopatina, 1993, in press).

The strategy of prolonged brood-rearing, in contrast, has two evident advantages in cold climates (Kipyatkov, 1993): (1) the larvae can be reared from early spring up to late autumn, thus utilizing the entire growing season, (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 (see Fig. 5).

The larval stages at which diapause can ensue are extremely variable among ants (Kipyatkov, 1996; Kipyatkov and Lopatina, 2006). We distinguish five species-characteristic patterns: (1) diapause in early (1st–3rd of 5) instars (*Lepisiota*, *Plagiolepis*, *Tapinoma*, some *Camponotus*), (2) diapause in middle (2nd–4th of 5) instars (*Camponotus s. str.*), (3) diapause in the late (3rd–4th of 4) instars (*Harpagoxenus*, *Leptothorax*, *Temnothorax*, *Messor*), (4) diapause in the last (usually 3rd) instar (*Manica*, *Diplorhoptrum*, *Leptanilla*, *Monomorium*, *Myrmica*, *Tetramorium*), and (5) diapause in all (of 3–6) instars (*Aphaenogaster*, *Crematogaster*, *Lasius*, *Paratrechina*, *Camponotus* (*Tanaemyrmex*)).

## Seasonal strategies of sexual production

Our field and laboratory data, together with data from the literature, indicate that most temperate ants depart from Oster and Wilson's (1978) predictions regarding seasonal timing of worker and sexual production in two main aspects (Kipyatkov, 1996; Kipyatkov and Lopatina, 2006):

1. Most species raise their alate reproductives not in late summer after the worker brood but quite the contrary, just after overwintering. In a few species the sexuals may develop from the first eggs laid in spring or in most others they originate from the overwintered larvae. In either case, the rearing of alates precedes the main period of worker production in a growing season.

2. The production of sexuals is always accompanied by rearing of workers, often in greater numbers than the sexuals. That is, there is no sharp switch from alate to worker production (see Fig. 5 as an example).

These conclusions are consistent with the two brood-rearing strategies described above (Fig. 1–2), in each of which sexual production precedes production of workers within each growing season (Kipyatkov, 1996, 2001; Kipyatkov and Lopatina, 2006). Since the ergonomic stage is always followed by a long overwintering period which delays the reproductive stage until the beginning of the next growing season, we propose to term such seasonal pattern of sexual production as the *strategy of two separated bangs*, or else the *strategy of spring rearing of sexuals* (Kipyatkov and Lopatina, 2006).

This strategy has been realized in several modifications (Kipyatkov and Lopatina, 2006). In some species, sexuals arise from the first eggs laid by the queen in early spring. This is the case in the tribe Formicini (*Alloformica*, *Cataglyphis*, *Formica* and *Proformica*) and the genera *Dolichoderus* and *Pogonomyrmex*. Consequently, the *spring resource acquisition and allocation in sexuals* is characteristic of all these species. However, the species of red wood ants (*Formica s. str.*) also follow the strategy of spring rearing of sexuals but it is based on the *resource acquisition in autumn*. This is because the workers accumulate food reserves in their

fat bodies during the late summer and autumn and use them for the rearing of sexuals in early spring when there is no food sources in the environment (Otto, 1962; Dlussky, 1967; Schmidt, 1974).

Another, much larger group consists of those ant species in which alates develop from overwintered larvae, in most cases from the largest among them (Kipyatkov and Lopatina, 2006). Therefore, these ants also invest in the growth of alates mainly in spring. At the same time, *Leptothorax acervorum*, and probably other species of *Leptothorax*, significantly differ from other ants in that their sexual larvae grow up to the full size in late summer so that they are able to pupate just after temperature rise in spring without any additional feeding. In fact these ants invest in sexuals mainly at the end of growing season. Only pupation and the development of sexual pupae are postponed until the next spring. Thus, this modification of the strategy of spring rearing of sexuals is distinguished by the *resource acquisition and allocation in autumn* (Kipyatkov and Lopatina, 2006).

The strategy of spring rearing of sexuals demands that the colony's annual cycle should be organized to maximize the quantity of diapausing larvae and new workers produced by the end of each growing season. These new workers will aid in the colony's winter survival and will rear alate females and males from eggs or overwintered larvae the next spring. To this end, brood-rearing should start as early as possible and continue as long as possible in the growing season. At the same time, the brood stages and adults present in the nest at the start of winter should be capable of overwintering. Temperate climate ants have solved this problem by evolving appropriate forms of winter dormancy and efficient mechanisms to control its onset and completion (Kipyatkov, 1993). The forms of winter dormancy and diapause in ants, and the physiological and social mechanisms of their control are treated at greater length by Kipyatkov (2001).

The apparent departure of the seasonal patterns of worker and sexual production in temperate climate ants from Oster and Wilson's (1978) predictions might be explained if we consider not only the optimal allocation of resources within the colony but also the reproductive success of sexuals produced. In temperate and particularly cold-temperate climates the colony-founding by queens after the nuptial flight seems to be more successful if it occurs as earlier in the growing season as possible in most ant species. Earlier founding allows the incipient colonies to attain larger size before the winter and thus increases their overwintering survival. The food resources available for new colonies might also be more abundant in the middle of growing season as compared to its end. Consequently, the success of the founding queens can be the main determinant of the seasonal pattern of sexual production observed in temperate climate ants.

Nevertheless, Oster and Wilson's (1978) model seems to be acceptable in general. It should be only corrected a little taking the colony's responses to seasonality into account. The rearing of new workers in summer and autumn really precedes the production of sexuals in spring, but these two "bangs" are separated by the winter in all temperate climate ants. Although the bang-bang strategy might be optimal in the tropical regions, the strategy of two separated bangs appears more appropriate for temperate and cold climate ants due to the increased fitness of early founding queens and other seasonal factors.

### Latitudinal variation in the seasonal cycle: Ecological constraints

How do seasonal cycles of ants change as we look further north? A simple graphic model of the strategy of concentrated brood-rearing demonstrates that total annual brood production per worker should decrease as one goes north (Fig. 3). The same is evident from an elementary mathematical model developed below.

Let  $D$  be the development time from an egg to an adult ant,  $S$  the duration of the growing season during which brood can be reared,  $N_w$  the mean number of workers in a colony during the growing season,  $q_{NW}$  the proportion of nurses ( $N_{NW}$ ) among all workers (i.e.  $N_{NW}/N_w$ ), and  $L$  the maximum number of larvae a nurse worker is able to care for simultaneously. Then  $q_{NW} N_w$  will be the mean number of nurses per colony, and  $S/D$  will be the number of brood periods (i.e. periods from egg to adult) per season. The maximum total annual production of new adults per colony will therefore be (we do not account here for possible mortality of pupae and callows):

$$P_A = q_{NW} N_w L \frac{S}{D} \quad (1)$$

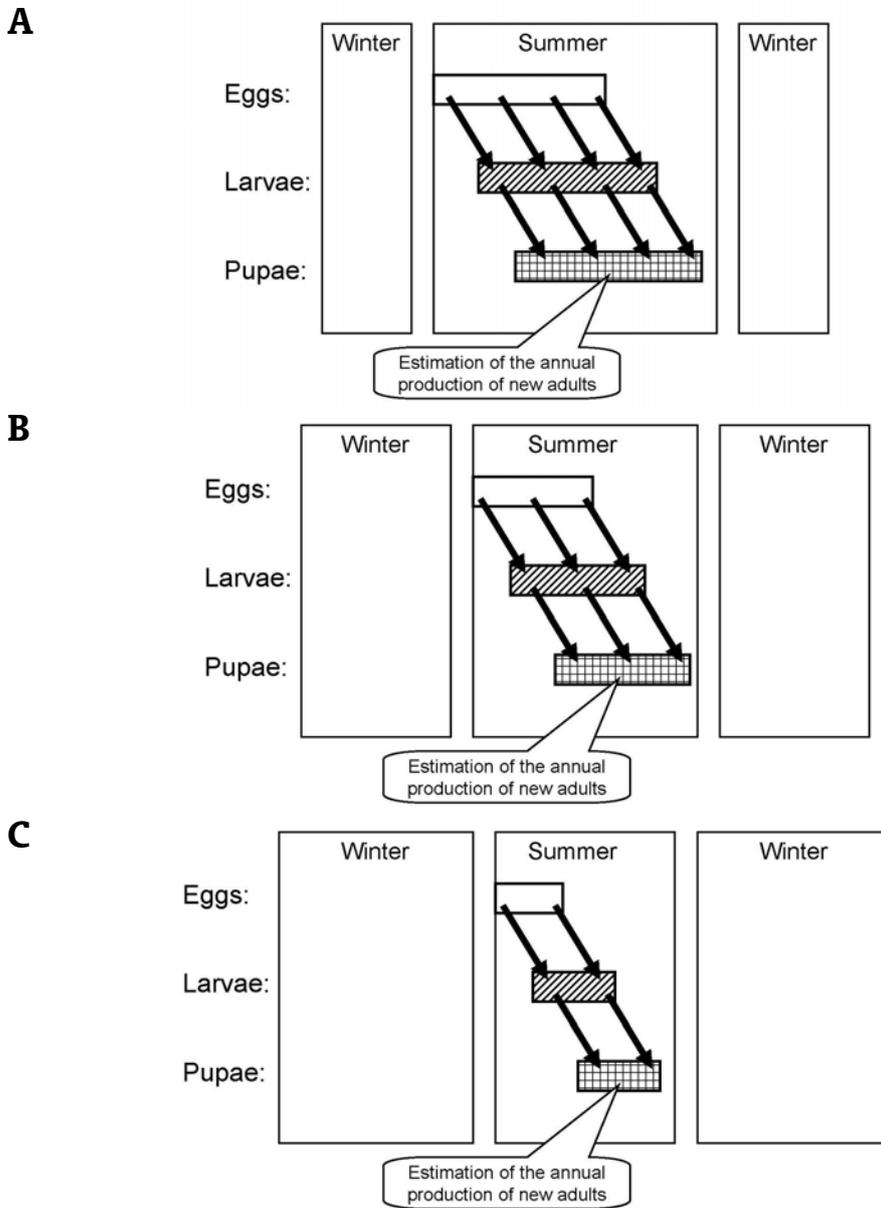
The same value per nurse worker will be:

$$p_A = \frac{P_A}{q_{NW} N_w} = \frac{LS}{D} \quad (2)$$

Let us assume that natural selection favours workers caring for as much brood as they can rear successfully. This sets a limit to the number of larvae that a colony can rear at one time, given the size of its workforce, so that the parameter  $L$  is more or less constant. Let us further assume for a certain time that the development time from egg to adult  $D$  is also constant within a species, regardless of climate or habitat. Then only the duration of the growing season  $S$  varies with latitude in equation 2. Given these assumptions, the mean annual production of new adults per nurse worker  $p_A$  must decrease as we go further north. Shortening the growing season results in decreased total annual production of new adults per worker simply because a colony cannot increase the work load of an individual nurse worker. In exactly the same way the work loads could not be increased for foragers and the workers carrying other social functions in a colony.

Species employing the strategy of prolonged brood-rearing face the same constraint. The mathematical description of the colony cycle becomes more complicated if some larvae extend their development into the next year. However, the same conclusion is seen in a simple graphic model, which also serves to illustrate the main patterns of variation in the seasonal cycle according to latitude (Fig. 4).

This graphic model supports the conclusion that species using the strategy of prolonged brood-rearing should see the following changes in the seasonal cycle structure and brood production as one proceeds northward: (1) a decrease in the annual production of new adults per worker, (2) a decrease in the quantity of rapid brood and thus in the proportion of new adults developing from egg to adult during a single growing season, and (3) above a critical latitude, the entire absence of rapid brood.



**Figure 3.** Effects of a shortened growing season on the total annual production by the colony under the strategy of concentrated brood-rearing.

The width of the rectangles is proportional to the quantity of the respective brood stages in the colony at any moment, so that their area is proportional to total annual production of the respective brood stages. As a species extends its range to the north and the growing season is progressively shortened (from A to C), the total annual production of new adults decreases, as the colony cannot increase the quantity of larvae that the workers simultaneously take care of.

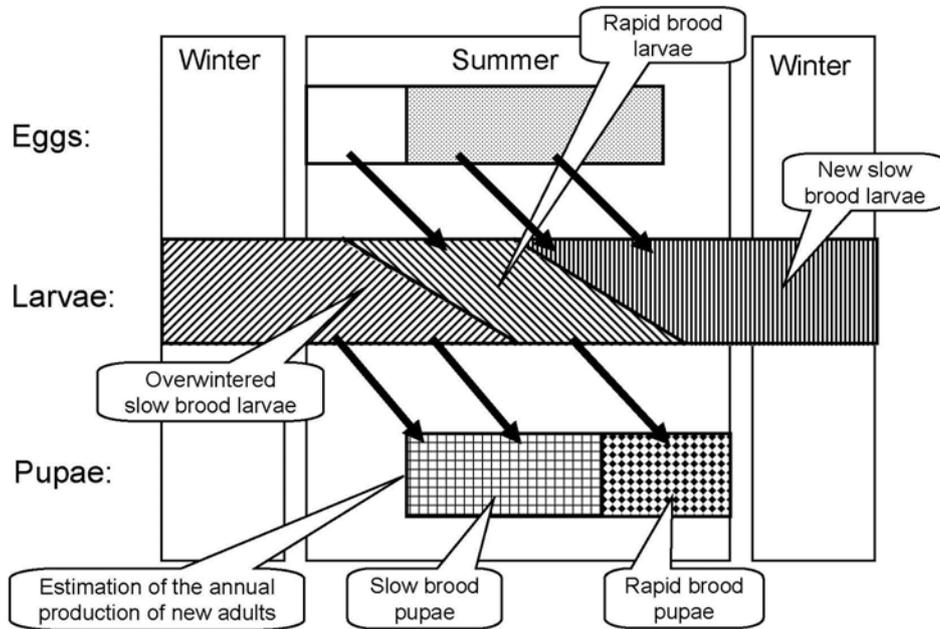
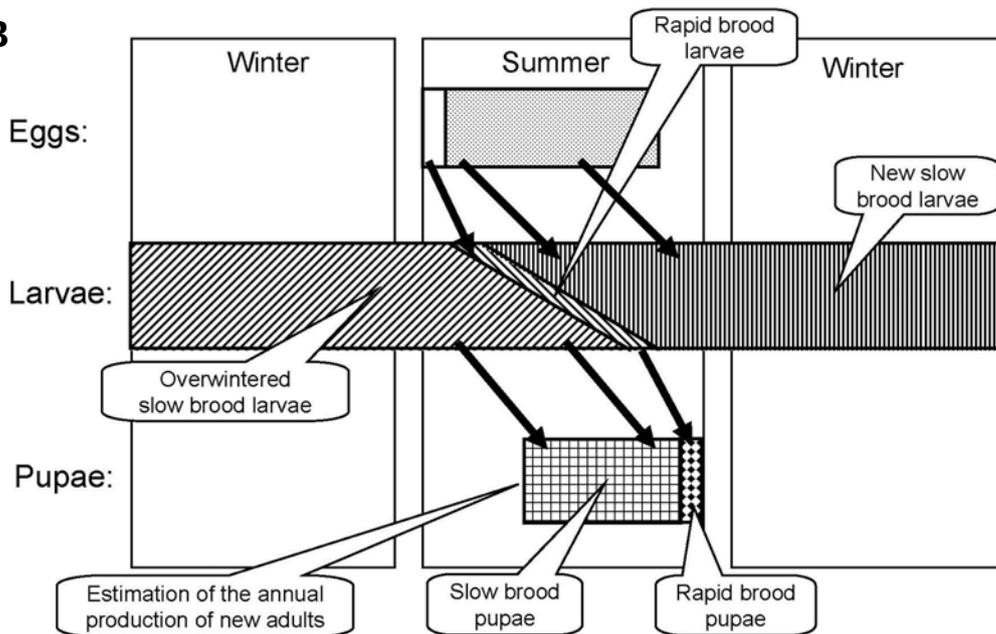
The literature does not provide field data on intraspecific latitudinal variation in brood production in ants. We first studied the phenology of brood development in three *Myrmica* species at different latitudes. These studies confirmed the three predictions stated above. Our data for *M. ruginodis* – the *Myrmica* species that extends furthest north in the western Palearctic Region – provide estimates of the annual production of pupae in colonies at the latitudes of Vladimir, St. Petersburg and near the Arctic Circle. As seen in Table 1, St. Petersburg colonies produced about twice as many pupae per colony and 25–30% more per worker as did colonies further north. This difference was even greater between colonies at the latitudes of the Arctic Circle and Vladimir: nearly twice as more pupae per worker in Vladimir. Thus, a significant decrease in annual production of new adults between 56° and 66° N is evident in our field data.

**Table 1.** Annual production of pupae in *Myrmica ruginodis* colonies at different latitudes.

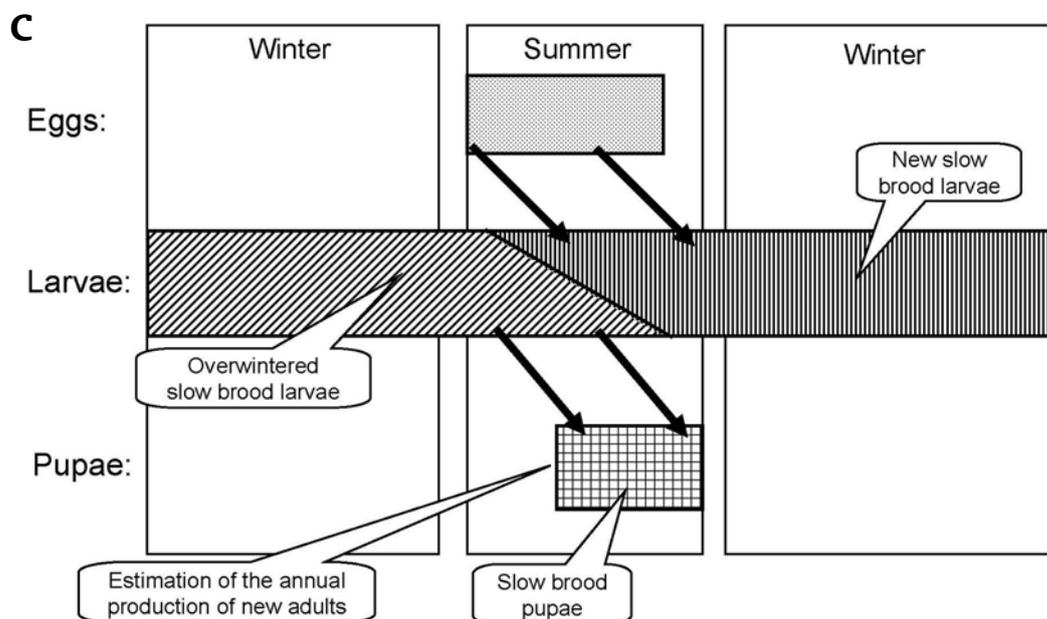
Latitude	Region and Year	Sample size (number of colonies)	Estimated annual production of pupae	
			per colony (mean ± SE)	per worker
56° 15' N	Vladimir, 1996	27	1504 ± 138 <sup>a,b</sup>	2.45 ± 0.23 <sup>a,b</sup>
59° 20' N	St. Petersburg, 1996	42	1269 ± 347 <sup>c</sup>	1.59 ± 0.43 <sup>c</sup>
	St. Petersburg, 1997	49	1299 ± 343	1.63 ± 0.43
66° 15' N	Chupa, 1997	41	595 ± 111 <sup>a,c</sup>	1.27 ± 0.43 <sup>a,c</sup>
66° 33' N	Poyakonda, 1996	56	715 ± 244 <sup>b</sup>	1.27 ± 0.24 <sup>b</sup>

The mean numbers of pupae produced per colony and per worker are significantly ( $p < 0.05$ ) different according to *t*-test if are marked by the same letter ( $p < 0.05$ ). Based on the results of unpublished study.

Predictions 2 and 3 are also upheld by our studies of brood-rearing phenology in *M. rubra*, *M. ruginodis* and *M. scabrinodis* at different latitudes. As an example, let us consider the annual brood-rearing cycle of *M. ruginodis* colonies in four regions near Kiev (50° 30' N), Vladimir (56° 15' N), St. Petersburg (59° 20' N) and Poyakonda (66° 33' N) (Fig. 5). Only the larvae of the third (last) instar overwinter. Near Kiev (Fig. 5a) overwintered larvae begin to pupate at the beginning of June, and both workers and alate larvae have all pupated by 10 July. At this time new third-instar larvae (i.e. from eggs laid by queens earlier in spring, not from the previous season) begin to appear in the colony. They develop rapidly, and many pupate during July and August to yield a rapid brood of workers. However, the majority of new third-instar larvae do not pupate in this season. Rather, they enter diapause and overwinter. By the end of September the brood consists entirely of third-instar larvae in diapause.

**A****B**

**Figure 4.** Effects of a shortened growing season on the total annual production by the colony under the strategy of prolonged brood-rearing.

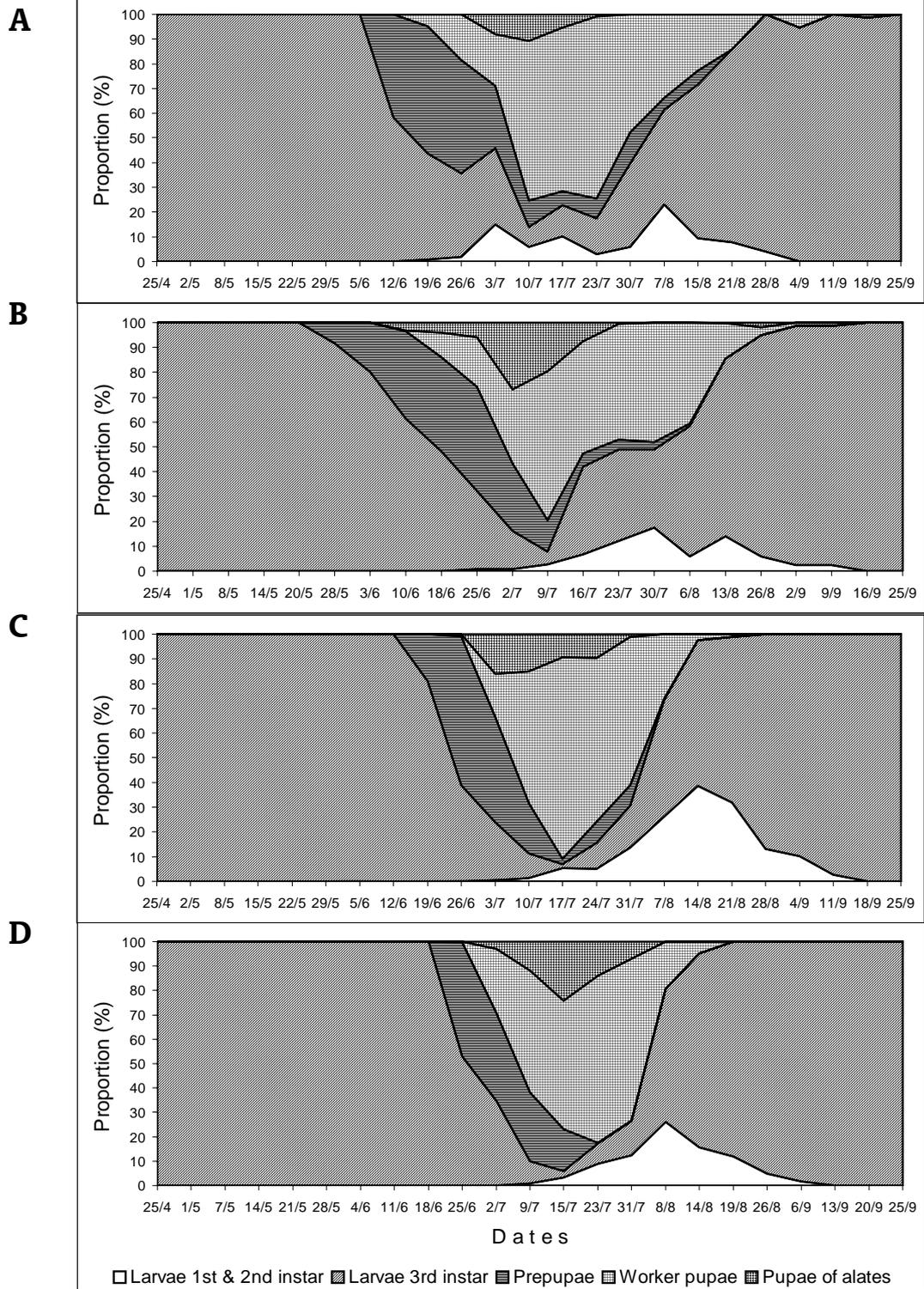


**Figure 4.** Continued.

As in Figure 3, the width of the rectangles is proportional to the quantity of the respective brood stages in the colony at any moment, and their area is proportional to total annual production of the respective brood stages. Thus, as the growing season becomes shorter (from A to C), the total annual production of new adults and the quantity of rapid brood decreases. Rapid brood disappears completely (C) beyond a certain latitude.

The brood-rearing cycle in colonies near Vladimir and near St. Petersburg (Fig. 5b,c) is similar, but in St. Petersburg overwintered larvae begin pupating a week or more later, and all have pupated by mid-July. The major difference is that near Vladimir and near St. Petersburg pupation of new third-instar larvae stops earlier in August, and the quantity of rapid brood is less. Near the Arctic Circle brood-rearing cycle is even shorter (Fig. 5d). Overwintered larvae begin to pupate only after mid-June, and all have pupated well before mid-July. However, the key difference is that new third-instar larvae do not pupate at all, so that rapid brood is entirely absent.

Our experimental studies upheld field observations (Kipyatkov and Lopatina, 1997a,b; Kipyatkov *et al.*, 2003). One could suggest that the significant differences in rapid brood quantity between *Myrmica* colonies from south and north are due to direct influence of very different local climatic conditions on brood development. To investigate this assumption experimentally we used natural colonies of both *Myrmica rubra* and *M. ruginodis* collected near Belgorod (50.5°N) and near St Peterburg (59° 20' N), in spring before the commencement of oviposition. Experimental cultures were maintained at long (20 h light) or short (12 h) days and 17, 20 or 25°C and the workers were allowed to rear the eggs laid by queens, into either rapid brood pupae or diapausing larvae.



Both queen oviposition and brood pupation eventually ceased under all regimes, but short days and low temperature significantly reduced the periods of oviposition and pupation, and consequently the numbers of rapid brood. The most interesting result was, however, that St. Petersburg colonies differed from those from Belgorod by having far shorter oviposition and pupation periods, and much weaker rapid brood production, at the same temperature and photoperiod. Thus, we concluded (Kipyatkov and Lopatina, 1997a) that the dramatic differences in the colony life cycles between Belgorod and St. Petersburg *Myrmica* populations, are not only the results of responses to distinct local climates, but is also due to local adaptation of the innate endogenous mechanisms which exist in ant colonies (Kipyatkov, 1994, 2001).

In another study (Kipyatkov and Lopatina, 1997b) colonies of *Myrmica lobicornis*, *M. rubra*, *M. ruginodis*, *M. scabrinodis*, and *M. sulcinodis* collected near Poyakonda (66° 33' N) at the end of June were maintained at 22.5 or 25°C and the day-lengths of 24, 17 and 12 h. All or almost all larvae pupated regardless of photoperiod and temperature. New larvae emerging from the eggs laid by queens developed up to the final instar and fell in diapause independently of the day-length and temperature. Thus, *Myrmica* colonies from the latitude of the Arctic Circle failed to produce rapid brood even under long days and optimal temperature.

In summary, our field and experimental data confirm a gradual decrease in the quantity of rapid brood in *Myrmica* along a latitudinal gradient from south to north, with this type of brood disappearing entirely at about the level of the Arctic Circle.

### Latitudinal variation in the seasonal cycle: Social constraints

The main consequence of the decreasing annual brood production as one proceeds northward is a diminished mature colony size and this may set the northern distribution limit of cold-climate ants. To show this let us consider the growth of a colony up to its mature, i.e. maximal size. As an incipient colony grows in size it passes through the three periods characterised by increasing, constant, and decreasing returns to scale (Oster and Wilson, 1978). The causes of this final decrease in growth rate have been considered by Oster and Wilson (1978) at greater length. Here it is most important that, ultimately, net colony growth should fall to zero. It means that the colony reaches its mature and maximal size, and is in a balanced state when the annual increase in worker number is approximately equal to their loss due to death, predation and other causes. A lot of factors, including queen's egg-laying capacity (for monogynous colonies), resource abundance, competition, and predation, are determinants of the mature colony size (Oster and Wilson, 1978). However, my purpose here is to consider the possible role of seasonal factors as determinants of colony size. Therefore, let us assume for a certain time that all other factors are fixed except seasonality.

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**Figure 5.** Field data on brood-rearing phenology in *Myrmica ruginodis* colonies living at four latitudes.

A. Near Kiev (50° 30' N); B. Near Vladimir (56° 15' N); C. Near St. Petersburg (59° 20' N); D. Poyakonda, near the Arctic Circle (66° 33' N). The vertical width of each zone denotes the proportion of the respective brood stage in the whole colony brood (except eggs) at the moment. Rapid brood is less numerous in St. Petersburg and completely absent in Poyakonda. However, even in Poyakonda all overwintered larvae pupate during the next growing season. Based on the results of unpublished study.

We should consider a mature colony in a balanced state. Let  $T_H$  be the half-life of adult workers, and  $P_W$  the annual production of new workers in a colony. The mean number of workers in a colony at equilibrium is therefore

$$N_W^* = 2T_H P_W \quad (3)$$

Evidently, if  $P_W$  decreases for some reason, then colony size would decrease as well, and vice versa, *other circumstances being unchanged*.

The annual production of workers is a part of the total production of new adults in a colony,

$$P_A = P_W + P_R \quad (4),$$

where  $P_A$  is total production of new adults and  $P_R$  is production of reproductives (queens and males). If  $q_W$  is the proportion of workers in the total annual production of new adults (i.e.  $q_W = P_W/P_A$ ), then

$$P_W = q_W P_A \quad (5)$$

If we know the annual production of new adults per nurse worker  $p_A$  and the proportion of nurses among all workers in a colony  $q_{NW}$ , we can calculate the total annual production of new adults as

$$P_A = q_{NW} N_W p_A \quad (6)$$

Then the substitution of  $P_A$  in 5 by equation 6 gives us

$$P_W = q_W q_{NW} N_W p_A \quad (7)$$

According to equation 2, the annual production of new adults per nurse worker  $p_A$  is equal to  $LS/D$ . Accordingly,

$$P_W = q_W q_{NW} N_W \frac{LS}{D} = \frac{q_W q_{NW} N_W LS}{D} \quad (8)$$

The main consequences of this equation are analysed in the next section. For now, let us note that when the length of the growing season  $S$  decreases, the annual production of new workers in a colony  $P_W$  should decline, which according to equation 3 should result in a reduction of the mean equilibrium number of workers in a colony  $N_W^*$  if all other parameters are held constant. This prediction needs to be tested in the field.

We have not found data in the literature on intraspecific variation in colony size according to latitude. However, our own studies of *M. ruginodis* show a significant decrease in the number of workers per nest between 56 and 69° N (Table 2). These are consistent with the prediction from the equations 8 and 3.

Kaspari and Vargo (1995) found a positive correlation between colony size and latitude by a broad comparison of ant species from tropical to cold-temperate region. These authors argued that Bergmann's rule holds true for social insects when colony size is regarded as the body size of a superorganism. They suggested that colony size in all social insects should be generally smaller in the tropics than in temperate regions and put forward the hypothesis that larger colony size can buffer harsh seasonal environments of colder regions.

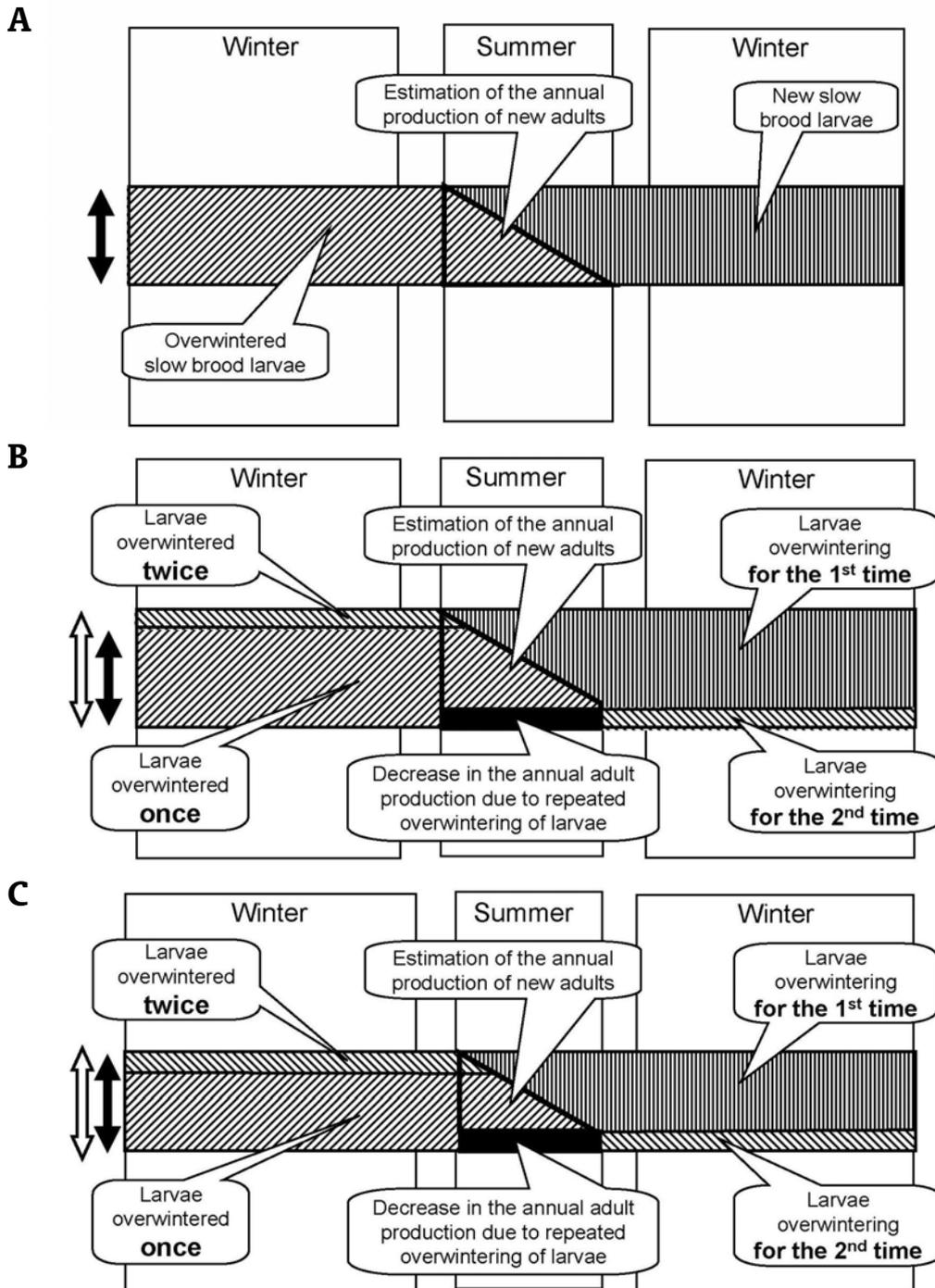
Table 2. *Latitudinal variation of worker number in Myrmica ruginodis colonies at different latitudes.*

Latitude	Region and Year	Sample size	Number of workers per colony			
			Min	Max	Mean	SE
56° 15' N	Vladimir, 1996	27	137	2333	613 <sup>a</sup>	86
59° 20' N	St. Petersburg, 1996	42	240	1961	799 <sup>b</sup>	63
	St. Petersburg, 1997	49	151	1830	798 <sup>c</sup>	58
66° 15' N	Chupa, 1997	53	41	4596	469 <sup>b,c</sup>	87
66° 33' N	Poyakonda, 1996	27	56	1844	565 <sup>b,c,d</sup>	76
68° 47' N	Murmansk (Fregat), 2001	32	135	867	398 <sup>a,b,c</sup>	46
69° 11' N	Murmansk (Polyarny), 2001	15	143	956	332 <sup>a,b,c,d</sup>	40

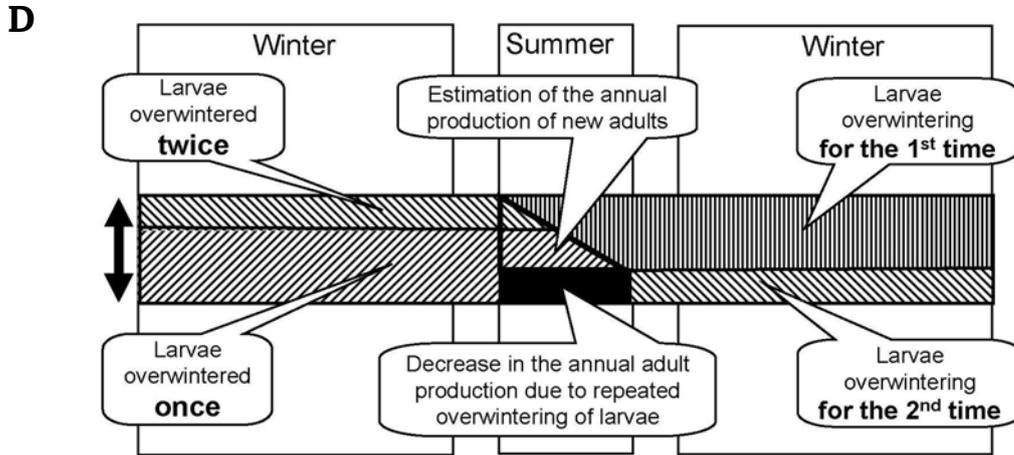
The mean numbers of workers per colony are significantly ( $p < 0.05$ ) different according to *t*-test between Vladimir (a), St. Petersburg 1996 (b), St. Petersburg 1997 (c) and the sites marked by the same letters. The means for Poyakonda and Polyarny are also significantly different (d). Based on the results of unpublished study.

This conclusion seems somewhat opposing to the prediction from the model and field observations discussed above. However, simple comparison between the two approaches might not be possible for two reasons. First, Kaspari and Vargo made interspecific comparison of colony size in relation to latitude. They did not consider intraspecific variation which was the subject of our study. However, the intraspecific variation may not obligatory follow the interspecific patterns and vice versa. Second, Kaspari and Vargo mainly compared between tropics and temperate regions, whereas our research was made in much colder regions, beyond 56° N. We suppose that in the warmer regions the duration of growing season may not be so limiting as in cold-temperate and boreal zones so that colony size mostly depends on other factors.

How is the seasonal cycle expected to evolve in any ant species that extend their range beyond the point at which rapid brood disappears entirely, so that the development of individual larvae continues into a second or even further growing seasons? Such life cycles are common among Arctic and Antarctic arthropods, which may continue growth and development over several years (e.g. Danks, 1981). Larvae of several ant species were experimentally shown to be capable of diapausing yet again after overwintering if faced with low temperature, food shortage and/or inadequate worker care (Kipyatkov *et al.*, 1996, 1997; Kipyatkov and Lopatina, 1999). However, do boreal and subarctic ants really use the opportunistic strategy of extending larval development for more than one year? It is our hypothesis that such a strategy is unavailable to them on account of social constraints, which therefore set a northern limit to the distribution of ants.



**Figure 6.** Graphic model of a seasonal cycle with repeated overwintering of some larvae.



**Figure 6.** Continued.

The width of the rectangle is proportional to the quantity of larvae in the colony at any moment. An arrow on the left denotes the maximum number of larvae in the colony where this is limited by the nurse workers' capacity to rear them.

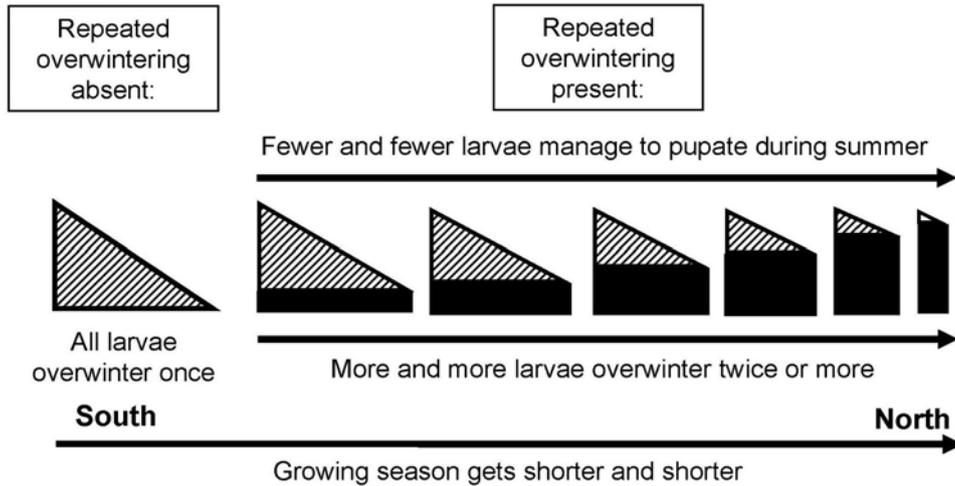
A. All larvae overwinter once. B. If some larvae overwinter a second time, this leads to an increase in the total number of larvae (white arrow). C. Repeated overwintering of some proportion of larvae is only possible at the expense of the total quantity of larvae that pupate during summer (a triangle), hence of the annual production of new adults. D. The decrease in annual production of new adults when the growing season shortens further.

This hypothesis, again, is illustrated by means of a graphic model (Fig. 6). The main assumption of this model is that the maximum quantity of larvae in a colony is limited by the nurse workers' capacity to rear them. Thus, the maximum quantity of larvae per worker is fixed (Fig. 6a). If the growing season is shortened, there comes a point where some overwintered larvae cannot complete their development during the second season. If they overwinter a second time, the total number of larvae in the colony is increased (Fig. 6b). Such an increase is maladaptive, however, as the workers are presumably already rearing as many larvae as they are able. A second or further diapause of some proportion of the larvae is only possible at the expense of a decrease in the total quantity of larvae that pupate each year, that is, in the annual production of new adults (Fig. 6c). In such a situation the annual production of new adults decreases not only because fewer larvae can complete their development during the shorter growing season but also due to the increase of the proportion of larvae that overwinter twice or more (Fig. 6d, 7).

Consequently, when an ant species extends into the far north the annual production of brood and new adults gradually decreases, leading to smaller colony size. Beyond the latitude at which some larvae are forced to hibernate twice or more, a much sharper decrease in the annual production of new adults and an abrupt decrease in the size of mature colonies are expected. This should result in a two-fold dependence of colony size on latitude in species using the strategy of prolonged brood-rearing (Fig. 8).

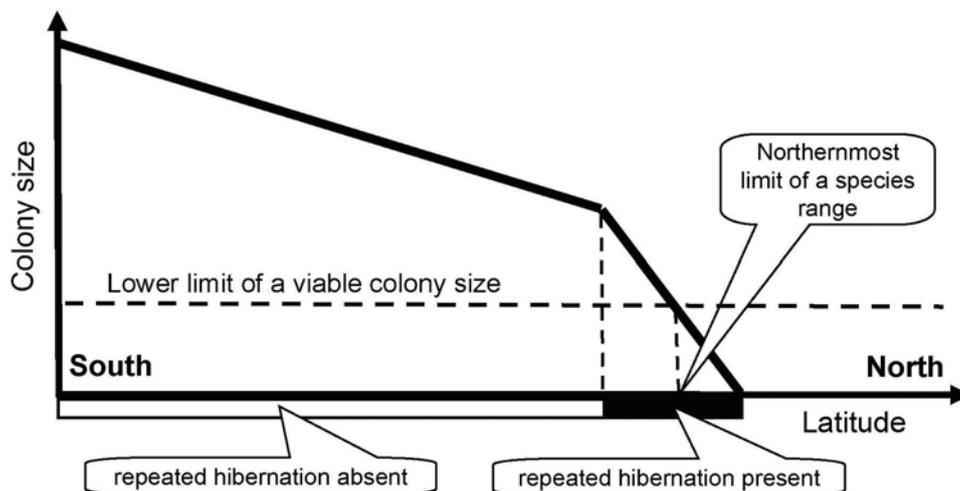
Since too small colonies seem to be unable to survive and reproduce, this will set a northern limit to distribution. In such a way, the social mode of life and the dependence of

brood on the worker care hinder the repeated hibernation of a noticeable proportion of larvae and thus make an opportunistic seasonal strategy unfeasible for ants.



**Figure 7.** Effects on the annual production of new adults of the proportion of larvae that overwinter more than once.

Here the annual production of new adults decreases not only because fewer larvae can complete their development during shorter growing season but also due to the increase of the proportion of larvae that overwinter twice or more.



**Figure 8.** Two-fold dependence of colony size on latitude under the strategy of prolonged brood-rearing.

As a species extends north of the latitude at which some larvae are forced to hibernate twice, the annual production of new adults is sharply decreased, leading to an abrupt decrease of the mature colony size. This is expected to set the northern distribution limit of cold-climate ants.

From this we can predict that most larvae should finish development and pupate during the second summer of their life even in the northernmost ant populations. Our field studies on *M. ruginodis* appear to uphold this prediction (Kipyatkov and Lopatina, 1997b; Kipyatkov *et al.*, 2003). In the Arctic Circle region all overwintered larvae in *M. ruginodis* colonies pupate during the growing season, as it is seen on Figure 5d. However, we have not yet examined more northern populations of this species, so that our hypothesis is only partly tested.

### Possible adaptations to overcome ecological and social constraints

What factors might buffer the decrease in mature colony size in far-northern ant populations? Returning to equations 8 and 3, a decrease in  $N_w^*$  due to a shortening of the growing season  $S$  could be compensated for by changing other parameters that we have held constant up to now:

1. Increase in the lifespan of workers, i.e. in their half-life ( $T_H$ ). Unfortunately, no data exist on the intraspecific latitudinal variation in worker lifespan in ants. An extension of worker lifespan might be possible if senescence happens mainly in summer due to the low metabolic load in winter. For example, honeybee workers live longer when they experience winter hibernation. It seems unlikely, however, that worker longevity would substantially increase under the harsh far-northern conditions of relatively cool summers and very long, cold winters. Much higher mortality due to the adverse abiotic environments might compensate for increased worker longevity in far northern habitats.

2. Increase in the proportion of workers in the annual production of new adults ( $q_w$ ). Colonies are certainly capable of altering this proportion. However, increasing worker production at the expense of alate production appears maladaptive, as it represents a decrease in the colony-level reproductive success.

3. Increase in the number of larvae that a nurse worker can care for simultaneously ( $L$ ). It is hard to see how this parameter could be increased, as one assumes that natural selection has already brought it to its maximum level.

4. Increase in the proportion of nurse workers in the colony ( $q_{NW}$ ). This is an unlikely candidate, as there is a necessary trade-off in the allocation of worker force to brood rearing and other social functions that are vital to the colony's survival and reproduction. For example, it seems hardly possible to increase the forager efficiency in order to reduce their number because the food resources are not more abundant and the foraging is more limited daily and seasonally by unfavourable climatic conditions in the far northern habitats.

5. Change from monogyny to polygyny and/or the increase of queen number in polygynous colonies in northern habitats. Simultaneously, colonies may become seasonally polydomous and experience the fission during summer and the fusion before the winter to make larger groups more capable of overwintering. This could really be an appropriate way of adaptation in some species. We found extremely polygynous and large colonies of *Leptothorax acervorum* near Poyakonda (66° 33' N) and *Myrmica rubra* near Uмба (Kola Peninsula, 66° 42' N). Some colonies included several thousands of workers and dozens or even hundreds of queens. Moreover, sometimes there were no distinct boundaries between numerous colonies of *L. acervorum* nesting in the wood under the bark along a long dead tree trunk, which is a sign of possible unicoloniality. However, this is not the case in *M. ruginodis*. According to our observations the colonies of this species are monogynous or weakly polygynous in all habitats studied from Belgorod and Kiev (50° 30' N) to Murmansk (68° 47' N).

6. Decrease in the development time from egg to adult ( $D$ ). Curiously enough, this seems like the only plausible adaptation to this end that is experimentally studied in far-northern ants. According to our data a decrease in the average development time from egg to adult could evolve through: (a) an increase in the development rate, (b) the preference for warmer nest sites, and/or (c) special design features of nests destined to concentrate incident sunlight.

The most surprising general result, perhaps, is that brood development in far-northern populations is more rapid over a rather broad temperature range than it is in more southern populations. In other words, given the same temperature conditions, northern ants are able to rear their brood in a shorter time (Elmes *et al.*, 1999; Kipyatkov and Lopatina, 2002; Lopatina *et al.*, 2002; Kipyatkov *et al.*, 2004). This is because brood development in northern populations is more temperature dependent, i.e. characterised by higher slopes of regression lines of development rate on temperature. The sum of effective temperatures decreased with the advance to North. The higher slopes were always associated with higher thermal thresholds for development. This is mainly due to latitudinal variation in the thermal reaction norm for brood development. Thermal reaction norms of ant colonies usually change according to the local climate in such a way that metabolism (Nielsen *et al.*, 1999), egg production, brood rearing, and the growth and development of individuals become more temperature-dependent in more severe environments. As a result, the physiological response increases at higher temperatures but decreases within lower temperature ranges (Kipyatkov and Lopatina, 2002; Kipyatkov *et al.*, 2004, 2005). It means that northern *Myrmica* colonies rear brood under lower temperatures evidently worse in comparison with ants from southern regions. In fact *Myrmica* colonies from northern populations need on average higher temperatures in their nests for successful production of new adults as compared to southern ants.

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## **Life history, life types and caste evolution in termites**

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**Abstract** – *A relationship between life histories and caste patterns in termites has long been pointed out. Two crucial steps in termite evolution were (1) the onset of eusociality through the development of the soldier caste, and (2) the emergence of a caste of permanent workers. The evolutionary interpretation of these events is difficult because termite immatures have several developmental or behavioral options to choose from: helping, breeding at home, or growing wings and flying away. In addition, helping may often be a temporary strategy. The resulting picture of caste evolution and related selective pressures in termites is rather confused. Here I redefine the options open to individual immature termites and evaluate the associated genetic payoff, using a common currency for all options. Then I discuss previously proposed evolutionary relationships, (1) between inheritance opportunities, delayed dispersal and helping, (2) between available food resources and developmental decisions, and (3) between mutilations and caste evolution. I stress the role played by resource availability in directing the development and behaviour of individual termites, and ultimately in the complexification of caste patterns and the diversification of life history strategies.*

**Keywords:** Isoptera, caste differentiation, eusociality, helpers, reproductive strategies.

### **Introduction**

Up to now, very few studies have specifically addressed the life history of termite colonies. As revealed by the most recent synthesis on this topic (Lepage and Darlington, 2000), we have now a bunch of observations of life history traits in termites, which unfortunately remain mostly disconnected. The most consistent approach to termite life history was initiated by Abe (1987, 1991), through the definition of "life types", based on the relationship between the nest and the food sources. Abe (1987) recognized three major life types, the so-called "one-piece", "intermediate" and "separate type". One-piece termites live in a single piece of wood, which serves at the same time as shelter and food source. The intermediate type comprises wood-feeding species that nest in logs but reach other sources of wood through subterranean tunnels. Separate type species have a centralized nest, from which they exploit food items some distance away. These categories were called, respectively, "single-site", "multiple-site" and "central-site nesters" by Shellman-Reeve (1997), who added a fourth category, the "inquiline-site nesters".

Abe (1991), followed by Shellman-Reeve (1997), suggested a correspondence between life types and social organization patterns. In one-piece termites, tasks are done by unspecialized immatures which remain totipotent: they retain the possibility to proceed toward the alate, soldier or neotenic caste. This totipotency makes them analogous to vertebrate helpers-at-the-nest (Roisin, 1990a). It is convenient to call such totipotent immatures collectively "pseudergates" (Parmentier and Roisin, 2003), although the meaning of this term was originally more restrictive (see Grassé and Noirot, 1947; Noirot and Pasteels, 1987; Roisin, 2000). A caste of "true" workers, defined as permanently excluded from the alate developmental pathway, occurs in intermediate and separate type species. Further life history correlates of life type are colony size and life span, both smallest in one-piece termites (Abe, 1991; Lepage and Darlington, 2000), and mode of colony reproduction. Independent foundation by pairs of sexuals after a nuptial flight is the rule in the one-piece type, whereas new colonies may sometimes be founded by a cohort of secondary reproductives accompanied by workers and soldiers in intermediate and separate type species.

The originality of the Isoptera on the one hand, and the ecological success of intermediate and separate type termites on the other, emphasize the two major events in the evolution of the order: first the emergence of eusocial, soldier-defended societies, then the onset of a true worker caste. The evolution of the soldier caste presumably occurred once at the origin of the Isoptera. As to the true worker caste, whether it evolved once (to be lost in some lineages) or several times is still a controversial matter (Watson and Sewell, 1981; Noirot and Pasteels, 1987, 1988; Thompson *et al.*, 2000), but the most likely hypothesis involves at least three independent origins of workers: one in the Mastotermitidae, one at the origin of the Hodotermitidae, and at least one within the Rhinotermitidae plus Termitidae complex (Noirot and Pasteels, 1987, 1988; Parmentier and Roisin, 2003). Although true workers are characterized by their inability to pursue their development until the alate stage, they are not always permanently sterile: worker-derived (=ergatoid) reproductives are known from *Mastotermes* as well as from several Rhinotermitidae and Termitidae (review in Roisin, 2000). The loss of totipotency that marks the transition between pseudergates and workers is analogous to the transition between cooperative breeding and eusociality (Crespi and Yanega, 1995).

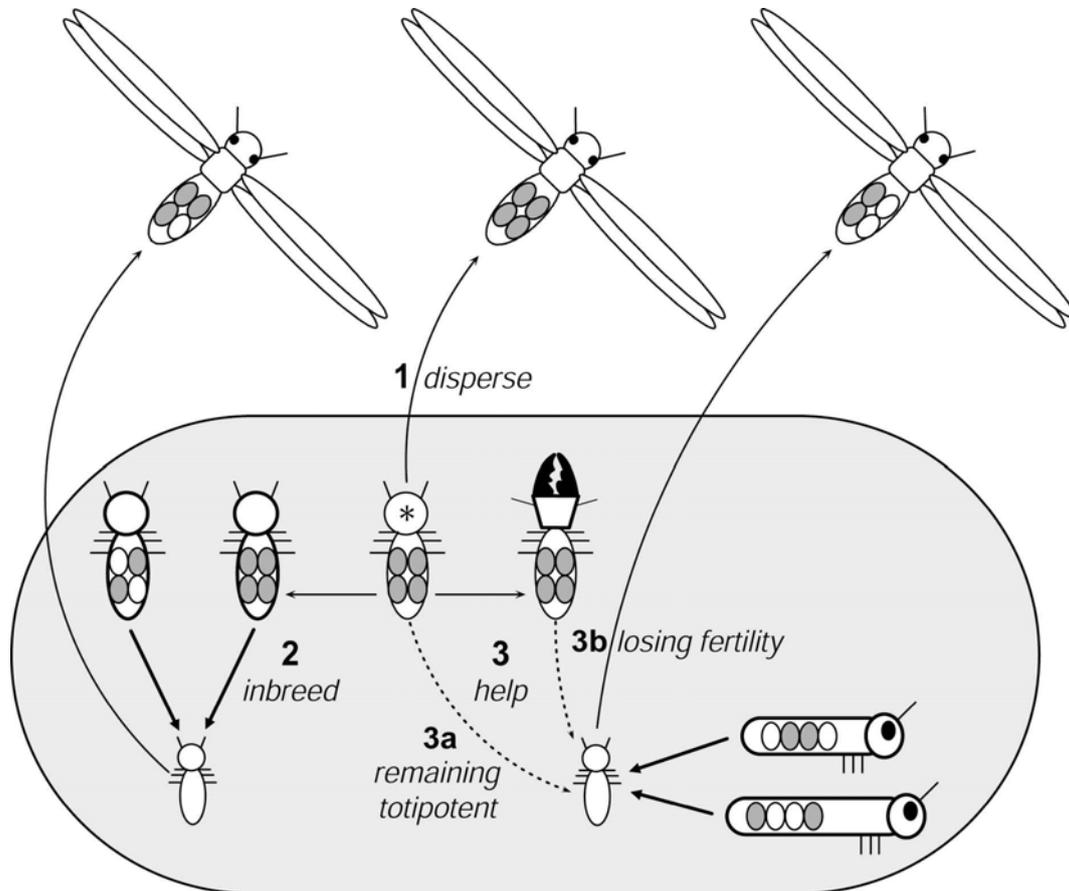
Several hypotheses have been proposed to account for these events (reviewed in Thorne, 1997). Analogies were sought among social Hymenoptera (relatedness patterns – e.g. Bartz, 1979; Lacy, 1980), among other wood-dwelling insects (onset of social life – e.g. Hamilton, 1978; Nalepa, 1988), among other "fortress defenders" (origin of soldier caste – e.g. Queller and Strassmann, 1998), and among cooperatively breeding vertebrates (evolution of helping-at-the-nest – e.g. Andersson, 1984). The resulting situation is a rather confused picture of caste evolution and related selective pressures in termites. Here 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. Then, on this basis, I will critically examine previously proposed roles for (1) inheritance opportunities in delaying dispersal and helping, (2) available food resources in developmental decisions, (3) wing pad mutilations in social regulation.

## Genetic payoff options open to a totipotent termite immature

Termite societies are simple in some respects and complex in others. Simplicity arises from a remarkable feature of the Isoptera, namely, that the winged morph (=alate) is presumably present in both sexes in all species, exhibiting similar swarming behavior followed by independent colony founding. There are species whose alates are unknown, but none for which the alate is presumed to be absent in either sex, or systematically skips the nuptial flight, or seeks readoption within an existing colony after this flight. This contrasts with other neopterous insect orders, including other Dictyoptera (cockroaches and mantids), among which apterous or brachypterous adults are commonplace (Hamilton, 1978; Zera and Denno, 1997). This also contrasts with ants, in which some species constantly found new colonies by mechanisms other than nuptial flights. Gynes or males may be apterous (review in Hölldobler and Wilson, 1990: 301–306; see also Heinze, this volume), and reproduction by colony fission may be the rule. In addition, social parasites are unknown in termites, but very diverse (although often rare) in ants and other social Hymenoptera. Some termites live asinquilines in other termites' nests, but their caste pattern is conventional and their interactions with their hosts remain mostly indirect, through the nest material (see Shellman-Reeve, 1997). It seems therefore that no termite species permanently circumvents the dispersal flight, which thus remains the most fundamental phase in the life cycle of termite colonies.

Contrary to most vertebrate juveniles, termite alates have almost no chance to assess opportunities offered by the environment before they initiate dispersal. They can only rely on meteorological cues, which help synchronize flights under favourable conditions, but do not provide any clue as to the actual availability of food or nesting sites. Therefore, it can reasonably be assumed that all termite alates depart from their colony for the nuptial flight with equal expectations: although actual chances of success may fluctuate, alates have no way to evaluate them before they actually take off. By contrast, immature birds or mammals often have the opportunity to wander out of their parental group to check for the availability of territories, resources, or mates before deciding whether to disperse or not. In view of these considerations, the dispersal phase appears as the best time to monitor genetic payoff in termites. Sooner or later, the colony will have to channel its reproductive investment into alate dispersers, which all have approximately equal (no matter how small) chances of future success. The inclusive fitness of any individual can thus be understood as the ability of this individual to enhance the representation of its genome in the alates released by the colony throughout its lifetime. I propose this representation (=genetic payoff) to be the common currency in which the effects of all behavioral or ontogenetic decisions should be evaluated.

The complex side of termite reproductive biology is the number of developmental and behavioral options that a totipotent termite immature may select to enhance its genetic payoff (Fig. 1). Firstly, it may proceed to the alate stage itself and disperse. According to our common currency, this is equivalent to producing one alate related to oneself by 1. This should be considered the baseline condition, because (1) the imago is the normal endpoint of development in hemimetabolous insects in general, and (2) this is a straightforward, selfish and terminal choice which does not allow for side benefits. A second option (hereafter called "home breeding") is to reproduce within the home colony. In a colony founded by a single pair of sexuals, the average relatedness between partners is 0.5, and relatedness to inbred offspring is 0.75. In all termites, this option requires forgoing future dispersal.



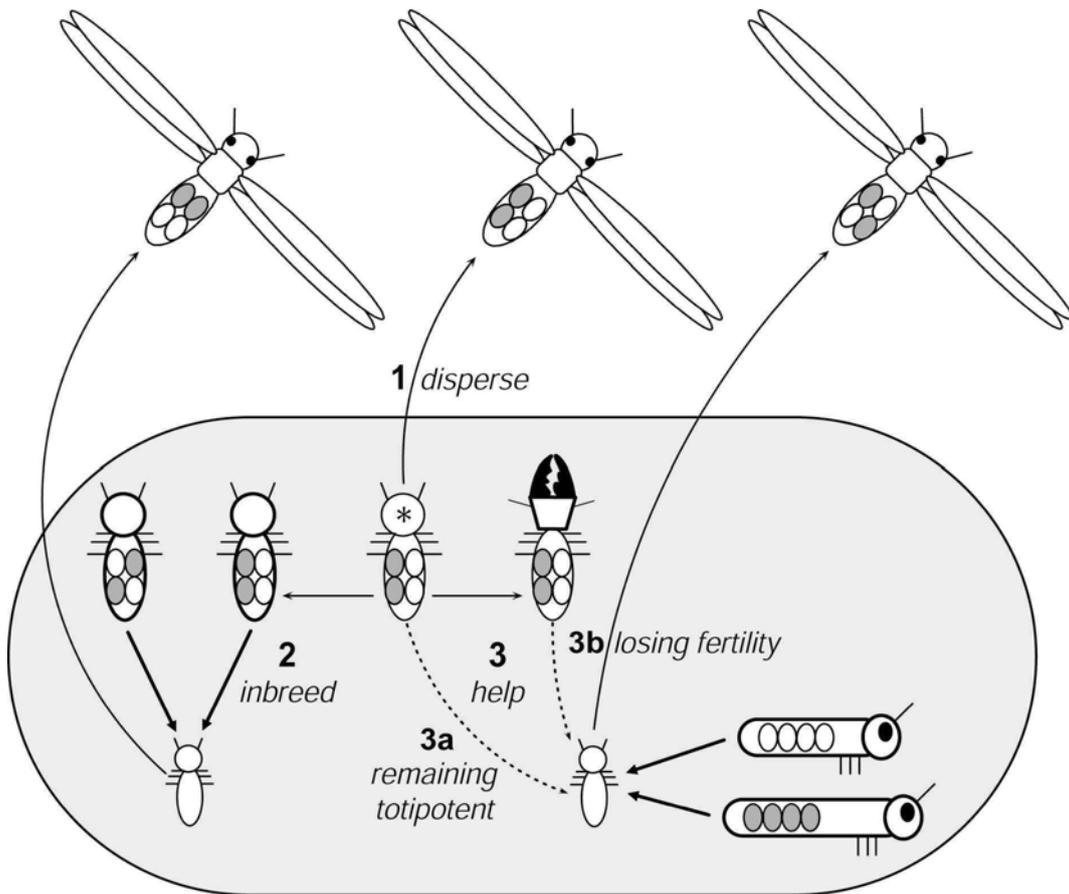
**Figure 1.** The various options open to a focal immature (asterisk) and their genetic payoff, in a termite colony without true workers.

Shaded area represents the home log. Grey ellipses represent the focal individual's genome and its representation in the individual's nestmates, including the alates released by the colony (flying out of the log). Thick arrows indicate reproduction. Thin arrows, transformation by molting. Dotted arrows, helping. Thickened integument of primary reproductives (lower right), soldier head (middle, with long mandibles), and neotenic reproductives (upper left) characterize terminal instars. Small white individuals are undifferentiated larvae. Option 1 is to proceed to the alate stage and disperse. Option 2 is to breed with a sibling within the home log. Option 3 is to help. Help can be provided while remaining totipotent (case of pseudergates, **3a**) or after losing fertility (case of soldiers, **3b**).

Compared to the dispersal option, there is thus a cost of one alate related by 1, but a benefit may result from enhancing one's genetical relatedness with the average alate (up to 0.75 instead of 0.5). In addition, the number of alates produced by the colony may be affected, either positively (e.g., if home breeding allows replacement of ailing founders and extends the life span of the colony), or negatively (e.g., because home breeders are distracted from working, they incur costs competing with each other, etc.). The third option is to help,

thereby increasing the total alate output of the colony, maintaining one's relatedness to the alates at the average value of 0.5 (basically, outbred siblings).

The personal cost of helping is highly variable. It reaches a maximum for individuals forgoing all possibilities of future reproduction (e.g., soldiers), but is likely to be low for individuals that remain totipotent and just help for some lapse of time, while intending to proceed to the alate stage later. In this case, the cost of postponing dispersal is merely a matter of increased risk of being unable to disperse in the future.



**Figure 2.** Same schema as in Fig. 1, but showing how the various options open to the focal immature (asterisk) may affect the queen's genetic payoff.  
Legend as in Fig. 1, except for grey ellipses, here representing the queen's genome.

The queen's viewpoint differs from that of her offspring. As shown in Fig. 2, all alates released from the colony have an equal value to the queen. In the absence of input of foreign genes, which is a reasonable assumption, her inbred grand offspring (neotenics' offspring) and her offspring are equally related to her. The founding queen's reproductive payoff can

therefore be equated with the lifetime reproductive output of the colony. This assumption equally applies to the founding king.

The costs and benefits of each option (see Table 1 in Roisin, 1994) can easily be calculated. It is obvious that the cost of forgoing the dispersal option cannot exceed the genome of a single individual, whereas the benefit of the other two options can raise as far as the colony's development allows. However, the dispersal option has the advantage of producing its genetic payoff (alates) within a short delay. Providing help to young dependent individuals cannot yield benefits until such young reach alatehood. Finally, benefits of home breeding cannot arise until the breeders' offspring reach maturity. Interestingly, according to the present model, the payoff of the selfish option (dispersal) arise sooner than that of the altruistic option (helping), thereby contrasting with Queller's (1989) "head-start of workers" hypothesis.

### **Inheritance opportunities**

Inheritance opportunities occupy a controversial place in termite social evolution. Several authors suggested that such opportunities provided the first impulse for postponing dispersal and engaging in temporary helping behaviour: "...the original payoff to temporary helpers is mainly delayed philopatric reproduction..." (Myles, 1988: 386). Shellman-Reeve (1997: 71) also suggests that "...choosing to stay in a functioning nest might be safer than initiating a new one, especially if the natal nest offers a stable, well-protected shelter." And according to Thorne *et al.* (2003: 12812), "Helping behavior by offspring that forgo or delay risky dispersal options, even if in a young family, results in their being profitably situated to become a reproductive upon the death of founding reproductives."

As discussed above, what matters is not so much the safeness of the home colony than the opportunities it offers. The inheritance option (=home breeding), at first seems highly profitable: among alates released by the colony, home breeders trade siblings ( $r=0.5$ ) for their own inbred offspring ( $r=0.75$ ). However, this hypothesis also faces a number of drawbacks (see Roisin, 1999). First, inbreeding depression may have been an important selective force against home breeding in the first place, although some large-colony termites have overcome this difficulty and heavily rely on inbreeding by neotenicis for colony expansion (e.g., Thorne *et al.*, 1999). Second, home breeders can obtain benefits only after a substantial time lag, necessary for their own progeny to reach maturity. Third, the magnitude of the benefits to the breeders depends on the actual fraction of the alates that result being their offspring, and this fraction varies in inverse proportion to the number of breeders. Competition among breeders is therefore likely to break out. The conditions worsen as the colony increases in size and age, because chances of emerging from intracolony competition decrease as well as colony life expectancy. It therefore appears that potential home breeders should attempt to breed as early as possible. However, as a rule, immatures do not proceed to sexual maturity and do not start breeding as long as the founding pair, or active secondary reproductives, are present in the colony. What, or who, prevents them from doing so? The old "parental manipulation" hypothesis (Michener and Brothers, 1974; Craig, 1979; Andersson, 1984) suggests that parents prevent their offspring from breeding in their presence. However, there seems to be no genetic advantage for the parents in doing so (Fig. 2), and the parents' ability to exert a direct control on offspring development is questionable, especially in populous colonies (Keller and Nonacs, 1993). Some

kind of sibling "policing" (analogous to "worker policing" of Ratnieks, 1988), or "sibling manipulation" (Zimmerman, 1983) can also be envisioned, but again, there is no genetic advantage for immatures to prevent inbred breeding by siblings, unless they vie for reproduction themselves. In *Kalotermes flavicollis*, severe elimination of neotenics primarily results from fights between the neotenics themselves (Ruppli, 1969).

For these reasons, the most likely hypothesis to explain why immatures postpone breeding and help remains deceptively simple: it just implies that the inclusive fitness benefits of helping outweigh the costs of delayed breeding. But if so, home breeding opportunities need not be invoked any more to justify delayed maturation. On the contrary, home breeding on the one hand and delaying maturation to help on the other should rather be perceived as competing options.

### Food resources and developmental decisions

It has long been suggested that remaining totipotent is important in "one-piece" colonies, which are likely to be short-lived (Roisin, 1990b; Lenz, 1994): immatures may so adjust their development to external conditions. Nymphs may undergo "regressive" molts, during which a shortening of their wing rudiments occur (Grassé and Noirot, 1947). Such regressed nymphs function as helpers, but retain the possibility to resume wing development (Roisin, 1990a). For instance, they can proceed to the alate stage and disperse when conditions deteriorate in the colony, e.g. when the log housing and feeding the colony approaches exhaustion. In *Cryptotermes* species, resource shortage was shown to stimulate selfish behaviour by nymphs, which preferentially pursue their development towards the alate stage (Lenz, 1994; Korb and Lenz, 2004; Korb and Katrantzis, 2004; Korb and Schmidinger, 2004).

By contrast, large-colony termites exploiting renewable resources display more rigid caste systems. Their workers are permanently excluded from the alate pathway, although they need not be permanently sterile: a few cases of "ergatoid" neotenics are known, resulting from the development of sex organs in workers, which can become active reproductives after one to three special differentiative molts (review in Roisin, 2000). In such termites, regressive molts seldom occur. Wing-padded nymphs usually follow a rigid developmental pathway to the alate, through a fixed number of molts. In some species, nymphs may become "nymphoid" neotenics in their colony of origin after a special molt. In other cases, nymphs have to proceed until the alate stage (although sometimes through a shortened sequence of molts, see Roisin and Pasteels, 1985) to start reproducing within their mother nest, as "adultoid" reproductives. Regressive molts, by which nymphs give rise to worker-like individuals, were mentioned in *Reticulitermes* (Buchli, 1958), but were until recently considered exceptional whenever true workers were present. However, reports of such events in various genera (*Coptotermes*, *Nasutitermes*, *Microcerotermes*) suggest that the potential for regressive molting is retained across many Rhinotermitidae and Termitidae. Observations of such regressed nymphs systematically occurred in orphaned colonies (review in Roisin, 2000).

For individual nymphs in "one-piece" colonies, approaching food exhaustion means that the costs of postponing dispersal increase, because the risk of being unable to complete the alate development increases. Simultaneously, perspectives offered by helping decrease, while those offered by within-nest maturation as neotenics worsen even more rapidly, due to the

additional delay needed for the neotenic's offspring to reach alatehood. Rushing toward alatehood therefore becomes the best option. For wing-padded nymphs in "separate-type" colonies, the normal developmental end point is the alate as well. Though rare, the occurrence of regressive molts after queen death therefore seems surprising. However, such molts may be an ultimate option for those nymphs that are unable to complete their development, due to insufficient attendance from a depleted worker population (Roisin and Pasteels, 1987).

### **Social role of wing pad mutilations**

A controversial matter is the role of mutilations on individual development in termites. Wing pad mutilations are commonplace in nymphs of several Kalotermitidae, such as *Pterotermes occidentis* (Zimmerman, 1983) and *Neotermes* species (Myles, 1986; Roisin, 1994). Such mutilations, which preclude the completion of the imaginal molt, were interpreted as evidence for sibling or parental manipulation: immatures or reproductives would mutilate nestmates to impede their dispersal and force them to stay as helpers (Zimmerman, 1983; Myles, 1986). Alternatively, Roisin (1994) suggested that mutilations might be the outcome of competition between nymphs for a limited number of places as alates. However, Korb (2005) was sceptical as to the significance of such mutilations: she found them only occasionally in *Cryptotermes secundus*, where they often result as artefacts of colony disturbance. Yet the frequency of mutilations in *Neotermes papua* and some other species (Roisin, 1994) is such that an accidental, artificial origin can be dismissed in those cases.

As outlined in the preceding section, our model easily permits the expression of helping by kalotermitid immatures, especially if such helping entails low personal costs to the helper but can yield large indirect benefits through enhanced colony survival and ultimate alate output. It is therefore easy to accept that helping can evolve without physical manipulation of potential helpers, and thus without mutilations. Then, why do mutilations occur in some species, and not in others? The "manipulation" hypothesis (Zimmerman, 1983; Myles, 1986) implies that immatures impede the development of nymphs into alates exclusively to increase the alate output of the colony through a reinforcement of its work force. However, such manipulations should only be expected in a narrow conflict window. If colony-level benefits of an additional worker are too low, manipulation should not be attempted, and if they are too high, nymphs should engage spontaneously in helping without being manipulated. A difficulty is to explain how colony members would be able to evaluate the colony's condition precisely enough to adjust their altruistic or manipulative behavior advantageously.

For an equal colony-level output, our model shows that there is a direct fitness benefit for an individual in being among the dispersers rather than among the left-behinds (see also Roisin, 1994). Mutilating the wing buds of nestmates could be the best way to eliminate them from competition for immediate dispersal, without jeopardizing the colony's lifetime success. This "competition" hypothesis (Roisin, 1994) however implies a restriction to the number of nymphs allowed to reach the alate stage during a given reproductive episode. Such restrictions may result from increased nutritional requirements to build up reserves for colony founding: nymphs might have to compete for direct access to the best feeding sites (e.g., nitrogen-rich cambium – see Shellman-Reeve, 1994) or for attendance by other immatures.

The "sibling manipulation" and "competition" hypotheses result in different predictions as to who should act as manipulators: colony members not involved in wing development in the former case, wing-padded nymphs in the latter. However, both hypotheses imply that the future prospects for the colony are good enough to make the build up of a populous group of helpers profitable. It may be significant that *Pterotermes* and *Neotermes* colonies, in which mutilations are frequent, are rather populous for kalotermitids and presumably long-lived (Nutting, 1970; Zimmerman, 1983; Roisin, personal observations). A comparative analysis of individual development and colony dynamics across kalotermitids with and without frequent wing pad mutilations might help resolve this question.

## Conclusions

In view of the presumed importance of ecological constraints on dispersal for the evolution of helping behavior in most social animals (Hatchwell and Komdeur, 2000; Kokko and Ekman, 2002), considering them as irrelevant to the evolution of helpers in termites appears iconoclastic. This is however justified by the omnipresence of alate flights, which presumably remain as an obligatory step in the life cycle of all termite species. To evaluate the adaptive value of a behavioral or developmental trait, focussing on how the expression of this trait influences the number and genetical endowment of alates leaving the colony appears as the most logical and practical procedure. Adopting this point of view allows to express the payoff of all options in a common currency. According to this view, the availability of resources within the colony is essential to determine the behavior of individual termites and direct their development. It is also likely that resource availability played a pivotal role in the concerted evolution of increasingly complex caste patterns on the one hand, and increasingly diversified life history strategies on the other.

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## **Division of labour and its regulation in a primitively eusocial wasp**

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### **1. Eusociality**

Social insects, such as termites, ants, bees and wasps have long intrigued biologists and laymen alike both because of the intricate organization and complexity of their colonies and also because of the extreme forms of cooperation and altruism they display. To the particular delight of biologists aiming to unravel the evolution of social life, social hymenopterans display varying degrees of sociality ranging from the solitary all the way to large, complex societies, with thousands and even millions of individuals, functioning as a coordinated unit, aided by organized division of labour and communication, that invite comparison with human societies.

To focus attention on species with the highest accomplishments of social evolution, a category of “truly social” or “eusocial” species has been created. To qualify for the status of eusocial, any species must exhibit all three traits: (1) reproductive caste differentiation of colony members into fertile reproductives (queens, and also kings in the case of termites) and sterile workers, (2) cooperative brood care and (3) an overlap of at least two generations of adults in the same colony (Michener, 1969; Wilson, 1971).

It is customary to recognize two sub-divisions of the eusocial, the primitively eusocial and the highly eusocial. Primitively eusocial species generally have small colonies, queens and workers are not morphologically differentiated, caste determination is generally post-imaginal and queens suppress worker reproduction by physical aggression. On the other hand, highly eusocial species generally have large colonies, queens and workers and sometimes even different groups of workers are morphologically differentiated, caste differentiation is generally pre-imaginal and queens suppress worker reproduction (or, as is now more fashionable to say, queens honestly signal their reproductive superiority to workers) by means of pheromones (Wilson, 1971; Michener, 1974; Hölldobler and Wilson, 1990; Bourke and Franks, 1995; Crozier and Pamilo, 1996; Gadagkar, 2001b).

## 2. Division of labour

Social insects have achieved spectacular ecological success, exceeding even vertebrates in biomass in some tropical habitats (Wilson, 1990). Division of labour is primary to colony organization in social insects. Division of labour and the consequent increase in ergonomic efficiency due to parallel processing of tasks is considered a major factor in the ecological success of social insects. The most fundamental division of labour within the colony is between the reproductive queen and sterile workers. The workers are either completely or partially sterile. In many species workers have lost the ability to mate and in some species workers have lost their ovaries altogether. Workers perform all tasks related to colony maintenance and growth such as building the nest, brood care, foraging, and nest defence (Wilson, 1971). Further division of non-reproductive labour among the workers may be based on physical or temporal castes. In physically differentiated castes, behaviour is primarily morphology-correlated and in temporally differentiated castes behaviour is age-correlated.

Division of non-reproductive labour increases the work efficiency of the colony by making it possible for workers to acquire special skills. A set of individuals specializing in performing a particular task is said to compose a particular caste. In some castes individuals are morphologically differentiated and consequently specialized for performing certain tasks. Therefore the allocation of workers to different castes is permanent. Colonies of most ants and termites include workers of two or more different sizes. Workers of a particular size class specialize in the tasks for which they are more suited owing to their size. Small ant workers typically labour in the nest while bigger individuals defend and forage. Sometimes this form of division of labour involves elaborate morphological adaptations that go beyond simple differences in relative sizes, such as allometric growth of powerful jaws in castes specialized for defence. Such morphological polymorphism however, is not usually seen in bee and wasp societies (Oster and Wilson, 1978). Alternatively, individual allocation to a caste can be temporary and temporal, wherein morphologically identical individuals successively specialize to perform different tasks, each for limited period of their life. This is known as age polyethism and is one of the more common forms of division of labour observed in species with no morphological differences among the workers (reviewed by Jeanne, 1991; Robinson, 1992).

## 3. The juvenile hormones

In spite of their relatively small brains, insects exhibit a rich diversity of behaviours. They have the capacity to respond to diverse environmental stimuli with great efficiency and flexibility. Much insect behaviour is stimulated, modified or inhibited by hormones. The juvenile hormones are the most versatile hormones in the insect world. They play a role in almost every aspect of insect life – development and reproduction, metamorphosis, caste determination, regulation of behaviour, polyphenism, vitellogenin synthesis, ovarian development. Structurally most similar to retinoic acid, a morphogen in vertebrates, the juvenile hormones are unusual sesquiterpenoids with an epoxide group near one end and a methyl ester on the other. There are seven naturally occurring juvenile hormones, differing in the lengths of their side chains. Juvenile hormone-III, a 16-Carbon molecule, is the only form found in the Hymenoptera (reviewed by Nijhout, 1994).

As a developmental hormone, juvenile hormone controls switches between alternative pathways of development at several points in the insect life cycle. If juvenile hormone is absent during the critical period, gene expression changes and new processes begin and launch the insect on a new developmental pathway. The continuation of the current developmental state in the presence of juvenile hormone led Williams (1952) to refer to juvenile hormone as the “status quo” hormone. Developing larvae moult to another larval stage if they have high juvenile hormone titers during a critical period prior to each ecdysis. A drop in juvenile hormone titre is again required to achieve the transformation to pupa and then to adult. In adult insects, juvenile hormone serves as a gonadotropin. An increase in juvenile hormone titer either causes or hastens the onset of reproductive maturation. Juvenile hormone controls oocyte development by regulating both vitellogenesis in the fat body and vitellogenin uptake by developing oocytes. Juvenile hormone has been implicated in the control of many behaviours in different species, including receptivity and mating behaviour, oviposition behaviour, maternal behaviour, flight activity, and feeding (Nijhout 1994 and the references therein).

#### 4. Post-imaginal regulation of reproductive division of labour

Eusocial insects display many interesting phenomena that merit investigation. Here we focus on two such interesting phenomena namely post-imaginal regulation of reproductive division of labour and, (in the next section), age polyethism (Tab. 1). As described above, reproductive caste differentiation means that only one or a small number of individuals in the colony reproduce. How does this come about? In most species studied, the difference between queens and workers is not a genetic one; any egg can potentially develop into a queen or a worker depending on the environment it encounters. In highly eusocial species such reproductive caste determination occurs in the pre-imaginal stage so that adults eclose with their fates (as queens or workers) fixed. It is such pre-imaginal caste determination that permits queens and workers to be morphologically distinct. Despite some pre-imaginal caste-bias (Gadagkar *et al.*, 1988), many or all females in primitively eusocial species are totipotent at eclosion with respect to queen and worker roles. How then do they differentiate into queens and workers? Post-imaginal caste determination or post-imaginal regulation of reproductive division of labour is brought about by aggressive interactions among the adult females, which may result from and/or influence their nutritional and hormonal status. It is the absence of pre-imaginal caste determination and the totipotency of the adults at eclosion that result in morphologically identical queens and workers.

There is growing evidence that juvenile hormone modulates post-imaginal regulation of reproductive division of labour in primitively eusocial species (Tab. 1). For e.g., juvenile hormone acts as a gonadotropin in the bumble bee, *Bombus terrestris*. In the absence of a queen, the onset of ovarian development in worker bumble bees is preceded by a sharp elevation in rates of juvenile hormone biosynthesis and circulating titers (Röseler and Röseler, 1978; Bloch *et al.*, 1996, 2000). Egg-laying individuals have high titers, while reproductively inactive individuals have low titers of juvenile hormone (Bloch *et al.*, 2000). Treatment with juvenile hormone also promotes ovarian development in the primitively eusocial sweat bee, *Lasioglossum zephyrum* (Bell, 1973). Several investigations in the primitively eusocial wasp genus *Polistes* also demonstrate the role of juvenile hormone as a gonadotropin. During nest foundation, female wasps establish a linear dominance hierarchy

and the most dominant female becomes the functional queen of the colony (Röseler *et al.*, 1985). The probability that a female will be dominant in the colony is strongly correlated with the size of her corpora allata, the source of juvenile hormone (Röseler *et al.*, 1984, 1985). Treatment with juvenile hormone significantly increases the aggressiveness of females in *Polistes annularis* (Barth *et al.*, 1975).

**Table 1.** Two interesting phenomena in eusocial insects.

Phenomenon	Primitively Eusocial	Highly Eusocial	<i>Ropalidia marginata</i>
Post-imaginal regulation of reproductive division of labour	Present	Absent	Present
Age polyethism	Absent, poorly developed or poorly studied	Present	Present

## 5. Age polyethism

Age polyethism or the systematic change in task specialization of workers as they grow older, is the best known mechanism of division of labour, especially in those species where task specialization is not based on morphological sub-castes among the workers. The honey bee is a prime example of age polyethism where worker bees perform different tasks as they grow older, always beginning with intranidal tasks and ending with extranidal tasks (Wilson, 1971). There is good evidence that age polyethism is regulated by juvenile hormone (Tab. 1). Titters of juvenile hormone gradually increase during adult life so that high titters are correlated with foraging behaviour. Application of juvenile hormone to young adult worker bees causes them to shift their behaviour from nursing and to become precocious foragers (reviewed in Robinson, 1992). Juvenile hormone titters are low in bees that work in the hive performing brood care ("nursing") and other activities, and high in foragers (Robinson, 1987b; Robinson *et al.*, 1989; Huang *et al.*, 1991, 1994; Huang and Robinson, 1995). Experiments designed to understand the role of juvenile hormone in age-related division of labour suggest that treatment with juvenile hormone-III (or its analogue methoprene) on the first day of adult life could induce a worker bee to forage precociously (Jaycox, 1976; Robinson, 1985, 1987a; Robinson and Ratnieks, 1987; Sasagawa *et al.*, 1989). Results of the juvenile hormone treatment experiments as well as the juvenile hormone measurements suggest that an elevated juvenile hormone titre is required for bees to mature into foragers.

Juvenile hormone has also been shown to be involved in the regulation of age-related division of labour in other highly eusocial social insects. O'Donnell and Jeanne (1993) report that treatment with juvenile hormone analogues affect division of labour in colonies of the highly eusocial tropical wasp, *Polybia occidentalis*. Wasps treated on day 1 of adulthood began foraging at younger ages, just as in honey bees.

## 6. The conundrum of juvenile hormone action

As described above, a phenomenon of particular interest in primitively eusocial species is the post-imaginal regulation of reproductive division of labour, which permits queens to maintain reproductive monopoly, in spite of the workers being potentially capable of reproduction. Similarly a phenomenon of special interest in highly eusocial species is age polyethism, which permits colonies to adaptively allocate workers to different tasks even though all workers are morphologically identical. The evidence available so far suggests that juvenile hormone modulates reproductive division of labour in primitively eusocial species and promotes the production of queens while it modulates age polyethism and promotes the production of foragers in highly eusocial species. To the extent that queens and foragers represent opposite ends of the spectrum of division of labour in social insects, these two effects of juvenile hormone appear to be in “opposite” directions and that is the conundrum of juvenile hormone action (Tab. 1).

## 7. Possible solutions to the conundrum of juvenile hormone action

Since juvenile hormone was hitherto known only to modulate ovarian development in primitively eusocial species and age polyethism in highly eusocial species, there was not such a serious conceptual problem in reconciling its two functions. It was argued that juvenile hormone might have acquired a novel function (regulation of age polyethism), and one that is probably incompatible with its original function (regulation of ovarian development), in the course of evolution from the primitively eusocial to the highly eusocial state (Robinson *et al.*, 1992). This has been referred to as the novel function hypothesis by West-Eberhard (1996). Because the essence of hypothesis proposed by Robinson *et al.* (1992) is that juvenile hormone can have only one of the two functions in any species it should perhaps be referred to as the “single function” hypothesis rather than the novel function hypothesis (Agrahari and Gadagkar 2003). Alternatively, it has also been suggested that juvenile hormone can modulate age polyethism without losing the ability to modulate ovarian development. This, it has been argued, may be possible because the function of modulating ovarian development is performed in one set of individuals (queen-destined individuals) while the function of modulating age polyethism is performed in a different set of individuals (worker-destined individuals). This has been termed as the “split function” hypothesis (West-Eberhard, 1996). In order to distinguish between the novel function or the single function hypothesis and the split function hypothesis, we need a species that simultaneously exhibits both phenomena, post-imaginal regulation of reproductive division of labour and age polyethism, and therein lies the importance of *R. marginata*.

## 8. *Ropalidia marginata*

*Ropalidia marginata* is an Old World, tropical, primitively eusocial polistine wasp abundantly distributed in South India (Fig. 1; see in colours on the cover of this book). New colonies are founded throughout the year by a single foundress or a group of foundresses. In a single foundress nest, the lone female builds the nest, cares for the larvae, forages and feeds the developing brood, guards the nest, and, like any solitary wasp mother, she brings her offspring to adulthood, all by herself. In multiple foundress nests there is division of labour. One and only one individual functions as the sole egg layer or queen, who begins her

career as a very aggressive individual attacking and biting her nestmates. Once she begins to lay eggs however, she becomes a strikingly docile individual who nevertheless maintains her reproductive monopoly, very likely through the use of pheromones (Gadagkar 2001b). At any given time only one individual monopolizes all egg laying; the rest of the individuals, in all colonies studied, do not lay eggs while the queen is present.



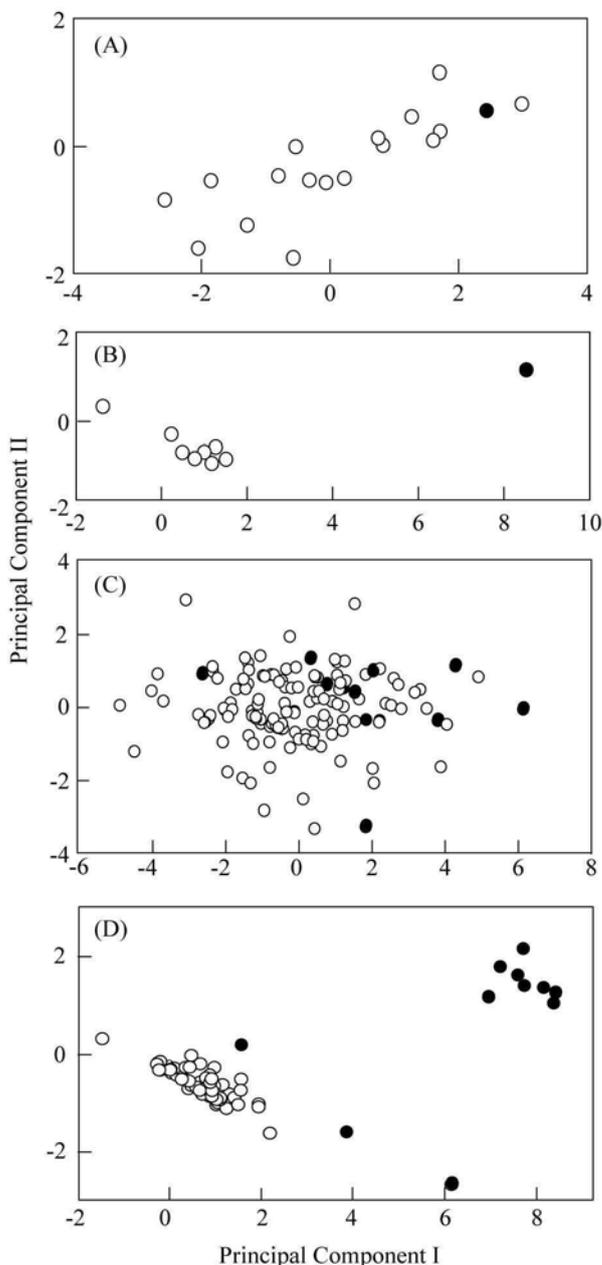
**Figure 1.** A typical nest of *Ropalidia marginata* (Photo: R. Gadagkar)

## **9. Post-imaginal regulation of reproductive division of labour in *Ropalidia marginata***

Dissection of all the female wasps in a colony of *R. marginata* and examination of their ovaries confirms the behavioural observation of monogyny. Most colonies have three kinds of individuals: a queen with well-developed ovaries and at least one mature oocyte in each of the six ovarioles; a subset of individuals with partially developed ovaries containing several developing oocytes; but usually no fully mature oocytes and another subset of individuals with completely undeveloped ovaries containing thread like ovarioles without any discernible oocytes. In Figure 2 data on several measures of body size as well as several measures of ovarian development have been subjected to principal components analysis and the relative positions of the members of a colony have been plotted in the space of the first two principal components. We see clearly that the queen, though among the largest individuals in her colony, is not distinguished in any qualitative way from her nestmates (Fig. 2A). The situation with ovarian development is quite different the unique position of the

queen is obvious (Fig. 2B). Figures 2C and 2D depict the results of a similar analysis except that data from 11 different colonies are analysed simultaneously. When variation across colonies is thus taken into consideration, a new result comes to the fore – while most workers in most colonies have poorly developed ovaries compared to the queens of most colonies (Fig. 2D), many workers in many colonies are larger in body size compared to the queens of many other colonies (Fig. 2C). Even if the queen of a colony is sometimes larger in

body size than all her nestmates, the fact that workers of some colonies can be larger in body size than queens of other colonies is striking proof of the lack of morphological caste differentiation between queens and workers. If queens and workers are morphologically distinct, the process of caste differentiation must necessarily take place in one of the pre-imaginal stages because no morphological changes are possible in the adult stage. But, in the absence of morphological differentiation between queens and workers the process of caste differentiation can also take place in the adult stage.

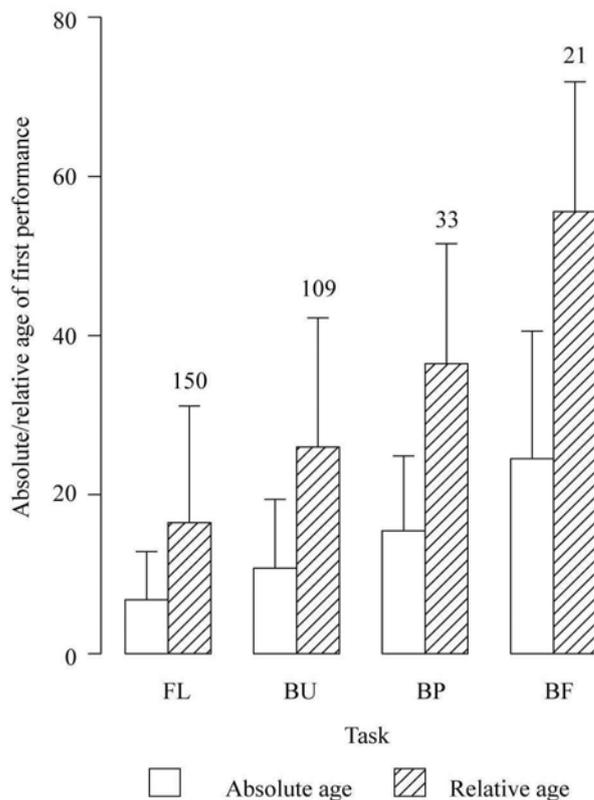


**Figure 2.** A and B. Relative positions of queen and workers, with reference to their body size (A) and ovarian condition (B) in a typical colony. Data on body size and ovarian condition are subjected to principal components analysis and the relative positions of the queens and workers are plotted in the space of the first two principal components.

C and D. The relative positions of queens and workers from 11 colonies, derived from a similar analysis. Note that in body size (C) queens and workers are not separated from each other, but that in their ovarian condition (D) queens and workers are well separated from each other.

(Reprinted from Gadagkar, 2001b).

Another line of evidence for post-imaginal regulation of reproductive caste differentiation in *R. marginata* comes from experiments in which hundreds of female wasps were isolated at eclosion and provided suitable conditions for them to build nests and lay eggs, much as single foundresses do in nature (Gadagkar *et al.*, 1988, 1990).



**Figure 3.** Age polyethism in *Ropalidia marginata*. Mean ( $\pm$ SD) age of first performance for each task in terms of absolute age (open bars) and relative age (hashed bars). FL – feed larvae; BU – build; BP – bring pulp; BF – bring food. The sample size for each task is given above each bar. Multiple comparisons of mean ages of first performance using the Tukey-Kramer method indicated significant differences across tasks ( $p < 0.05$ ). The first performance of task was significantly influenced by absolute age (one-way ANOVA;  $F = 33.4$ ,  $p < 0.0001$ ) and relative age ( $F = 49.12$ ,  $p < 0.001$ ). Mean ages for successive tasks were also significantly different ( $p < 0.05$ ) when subjected to a Mann-Whitney *U* test. (Reprinted from Naug and Gadagkar, 1998a).

The clear-cut results of several replicate experiments was that about 50% of the wasps under these conditions built nests and laid eggs while the remaining 50% died without doing so, in spite of living longer on average than the time taken by those laying eggs to begin to do so. At the time these experiments were performed, the exciting result was that 50% of the wasps did not build nests and lay eggs. In the present context however, the fact that 50% of the wasps in a population can potentially build nests and lay eggs is the relevant result. Since there is always one and only one individual per colony who lays eggs, only a small fraction of out of the wasps who are potentially capable of laying eggs actually end up having the opportunity to do so and this is what we mean by post-imaginal regulation of reproductive caste differentiation.

The final and most compelling evidence of post-imaginal regulation of reproductive caste differentiation comes from repeated queen-removal experiments. Experimental removal of the queen always results in the emergence of a new queen; one of the workers becomes extremely aggressive and takes over as the colony's next queen. When she starts laying eggs she, in turn, will become a behaviourally docile queen who nevertheless maintains her reproductive monopoly.

We have had the opportunity to witness such queen replacements during experiments designed to understand the nature of future queens (Chandrashekara and Gadagkar 1992), to compare queens with their successors (Sumana and Gadagkar 2003), to understand the role of queens in regulating worker activity (Premnath *et al.*, 1995) as well as during studies of natural queen replacements conducted with the aim of constructing pedigrees of queens (Gadagkar *et al.*, 1993). Every observation of queen replacement by a worker wasps proves that individuals potentially capable of functioning as queens are forced to function as workers by processes that bring about reproductive caste differentiation among totipotent adult wasps.

### **10. Age polyethism in *Ropalidia marginata***

Given the primitively eusocial status of *R. marginata*, there is a surprisingly well-developed, remarkably honey bee like- age polyethism (Fig. 3). Feeding larvae, building the nest, bringing pulp, and bringing food are four tasks performed sequentially by successively older wasps. More than the absolute age of the wasps, their relative position in the age distribution of the colony appears to strongly influence the task profile of an individual (Naug and Gadagkar 1998a). As in the case of honey bees, age polyethism in *R. marginata* is flexible. Loss of older individuals results in precocious foragers who forage at abnormally young ages (Naug and Gadagkar 1998b). Similarly, the reduction in nursing caused by the loss of young individuals is compensated by hard working nurses (Agrahari and Gadagkar 2004).

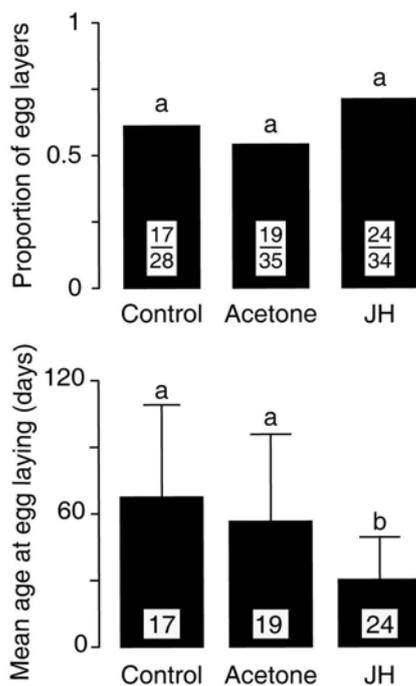
*Ropalidia marginata* thus appears to be a unique primitively eusocial species which has both, *Polistes* like reproductive division of labour and honey bee like non-reproductive division of labour, making it an ideal model system to investigate the conundrum of juvenile hormone action and thus understand the evolution of the modulatory function/s of juvenile hormone.

### **11. Role of juvenile hormone in post-imaginal regulation of reproductive division of labour in *Ropalidia marginata***

To investigate the role of juvenile hormone in post-imaginal regulation of reproductive division of labour, two large *R. marginata* nests (containing 75 and 135 pupae respectively) were collected from their natural nesting sites, brought to the laboratory, cleared of eggs, larvae and all adult wasps, and were checked daily for eclosion of wasps. Female wasps eclosing from these nests were randomly assigned to one of three treatments (see below) and isolated into well ventilated transparent plastic jars (22cm x 11cm x 11cm) and provided with *ad libitum* food, water and building material. The plastic jars were monitored daily until the wasps in them built a nest and laid an egg or died without doing so. Treatment 1 (juvenile hormone treated): 100 mg of juvenile hormone-III (Sigma Inc. USA) in 2ml of acetone, applied on the abdomen on the day of eclosion (sample size = 34 wasps). Treatment 2 (Acetone treated): 2 ml of acetone applied on the abdomen on the day of eclosion (sample size = 35 wasps). Treatment 3 (Control): Isolated without application of either juvenile hormone or acetone (sample size = 28 wasps).

There was no significant difference between the juvenile hormone treated, acetone treated and control wasps, in the proportion of individuals that built nests and laid eggs

(Pair-wise G test,  $p > 0.05$ ; Fig. 4, upper panel). However juvenile hormone treated wasps began laying eggs significantly sooner than acetone treated or control wasps (Pair-wise t-test,  $p < 0.05$ ; Fig. 4, lower panel). Figure 5 shows the scatter in age of wasps of each group at the time egg laying and clearly brings out the difference between juvenile hormone treated individuals and the acetone treated and control wasps. Thus topical application of juvenile hormone did not alter the proportion of egg layers and non-egg layers among freshly eclosed wasps isolated and tested, as described above.



This does not however mean that juvenile hormone did not affect ovarian development in these wasps. There was a significant reduction in the age at egg laying of juvenile hormone treated wasps as compared to acetone treated and control wasps. We conclude therefore that in *R. marginata*, juvenile hormone modulates post-imaginal reproductive division of labour and promotes the production of queens as has been observed in *Polistes* and *Bombus*.

**Figure 4.** Upper panel: Effect of juvenile hormone on egg laying in isolated wasps. The proportion of isolated wasps that lay eggs in the three treatments are not significantly different from each other as indicated by same letter on each bar (Pair-wise G test,  $p > 0.05$ ). The number of egg layers and total number of wasps tested is indicated inside the bars.

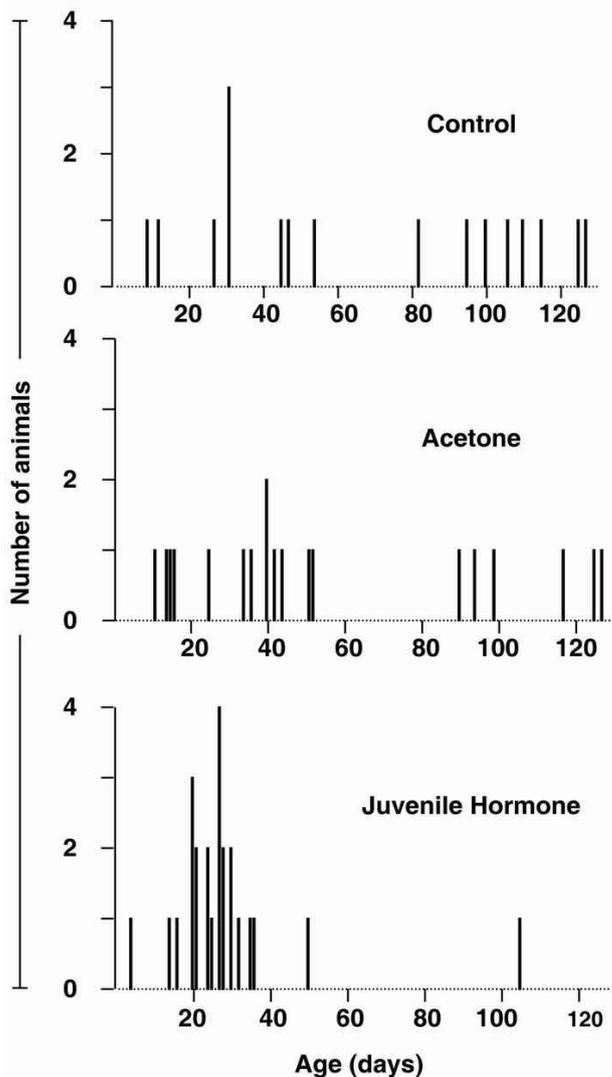
Lower panel: The mean age at egg laying of juvenile hormone treated wasps is significantly less than control and acetone treated wasps, as indicated by letters on the bars (Pair-wise t-test,  $p < 0.05$ ). The number of wasps tested is indicated inside the bars. (Reprinted from Agrahari and Gadagkar, 2003, Copyright: Elsevier).

### 13. Role of juvenile hormone in age polyethism in *Ropalidia marginata*

To investigate the possible role of juvenile hormone in regulating age polyethism in *R. marginata*, behavioural observations were conducted on 3 naturally occurring *R. marginata* nests. Observations consisted of, recording every occurrence of feed larva, build, bring pulp and bring food (see Gadagkar, 2001b, for methods of observation). Adults were uniquely marked and randomly assigned to one of two treatments viz. juvenile hormone or acetone within 24 hours after eclosion. Subsequently the treated individuals were returned to their natal nests. Because there was no difference between acetone treated wasps and control wasps in the isolation experiments described above, here we did not have control wasps with neither treatment (Fig. 5).

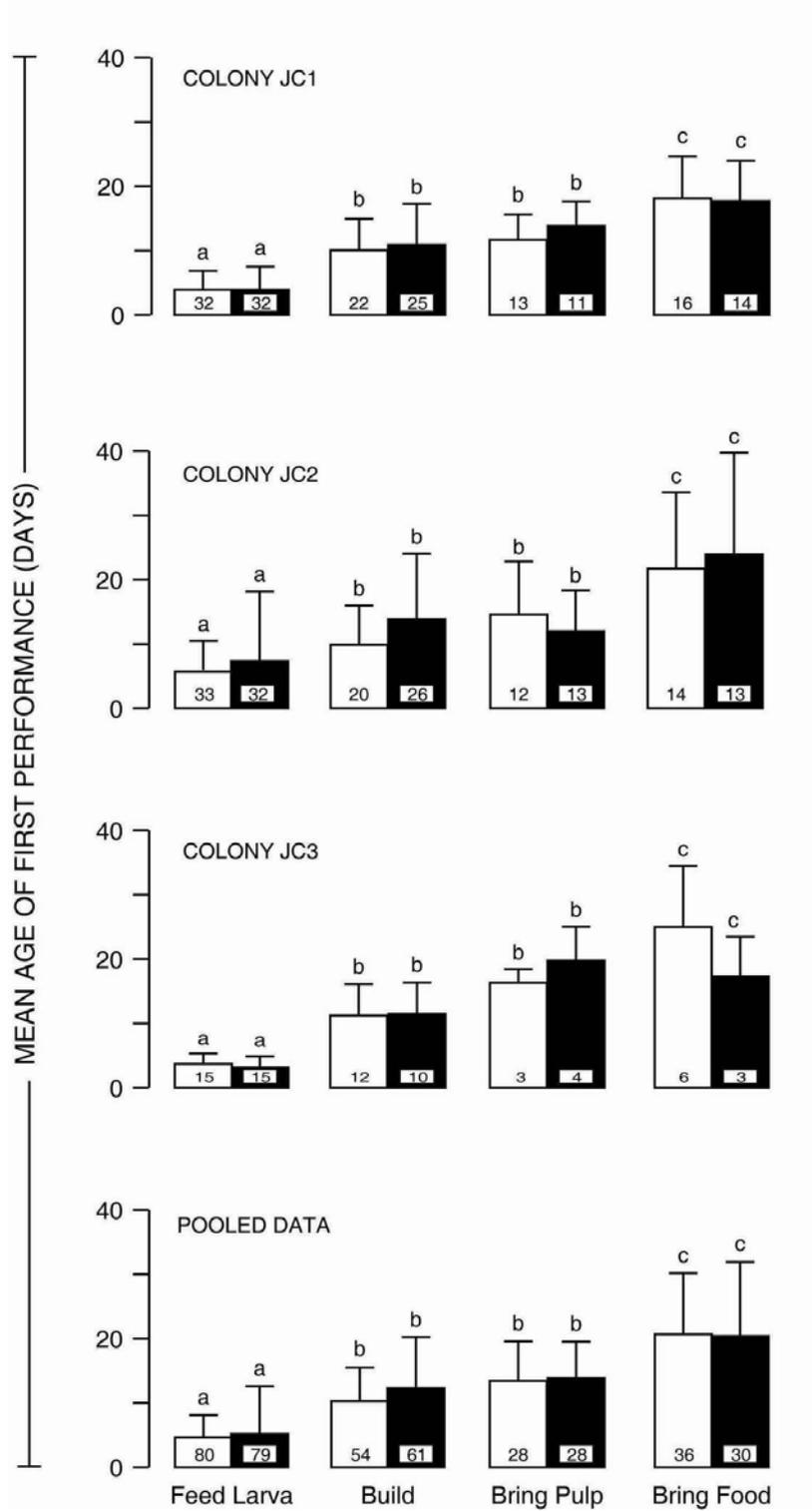
We found no detectable influence of juvenile hormone on age polyethism. The ages of first performance of feed larva, build, bring pulp and bring food did not significantly differ between the juvenile hormone treated and acetone treated wasps. The same result was obtained for data from each of the three nests as well as for the data pooled from all the

three nests (2-way ANOVA followed by Tukey-Kramer test,  $p > 0.05$ ; Fig. 6). While there was no effect of juvenile hormone treatment on age polyethism, there was clear evidence of age polyethism itself in both the juvenile hormone treated wasps as well as the control wasps; the age of first performance of feed larva was significantly lower than the age of first performance of build/bring pulp, which in turn was significantly lower than the age of first performance of bring food. And yet there was no difference in this regard between the juvenile hormone treated and control wasps. It should also be noted that the age of first performance of different tasks observed in this study are nearly identical to those observed in the previous study that demonstrated age polyethism in *R. marginata* (Naug and Gadagkar, 1998a).



Of all the primitively eusocial species studied so far, *R. marginata* has the best developed, honey bee-like, age polyethism (Naug and Gadagkar, 1998a,b). And yet we find no effect of similar topical application of juvenile hormone on age polyethism. Unlike what has been observed in the honey bees, juvenile hormone did not significantly affect the age of first performance of any task examined and certainly did not produce precocious foragers. We conclude therefore that in *R. marginata*, which exhibits both post-imaginal regulation of reproductive division of labour as well as age polyethism, juvenile hormone modulates the former but not the latter.

**Figure 5.** Number of wasps that initiated egg laying at different ages in the three treatments.



## 14. Conclusions

Juvenile hormone was hitherto known only to modulate ovarian development in primitively eusocial species and age polyethism in highly eusocial species, it was proposed that juvenile hormone might have acquired a novel function, and one that is probably incompatible with its original function, in the course of evolution from the primitively eusocial to the highly eusocial state (Robinson *et al.*, 1992). Neither primitively eusocial species such as *P. dominulus*, where there is a clear evidence for post-imaginal regulation of reproductive division of labour but no evidence of age polyethism, nor species such as honey bees where there is no post-imaginal regulation of reproductive division of labour but there is clear age polyethism, can be used to distinguish between the novel or single function hypothesis and the split function hypothesis. Species such as *R. marginata*, which appear to be intermediate between primitively and highly eusocial stages, and exhibit both post-imaginal regulation of reproductive division of labour as well as age polyethism, are suitable for discriminating between the two hypotheses. In such a species, if juvenile hormone regulates any one, but only one of the two phenomena, the novel or single function hypothesis may be said to be supported. On the other hand if juvenile hormone regulates both the phenomenon, then the split function hypothesis may be said to be supported.

There appears to be some recent evidence that juvenile hormone may influence both age polyethism as well as ovarian development in the primitively eusocial wasp *Polistes canadensis* (Giray *et al.*, 2005). To the extent that juvenile hormone modulates ovarian development and does not affect age polyethism in *R. marginata*, the split function hypothesis is not supported in our study. Since only one of the two phenomena, namely, reproductive division of labour is modulated by juvenile hormone in *R. marginata*, we conclude that the novel or single function hypothesis is supported in the present study. Why has juvenile hormone not acquired a “split function” of modulating both ovarian development and age polyethism? This may be because, in spite of evidence for pre-imaginal caste bias (Gadagkar *et al.*, 1988), many adult wasps can become either queens or workers depending on the social environment they find themselves in, i.e., there are no clear-cut, queen destined and worker destined individuals in natural colonies of *R. marginata* (Gadagkar, 2001b).

## 15. Summary

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,

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**Figure 6.** Mean and standard deviation of age at first performance of different behaviours in three colonies and in the pooled data. In each panel, bars carrying the same letter are not significantly different from each other. There is no significant difference between juvenile hormone treated wasps (open bars) and acetone treated wasps (filled bars) in all cases (2-Way ANOVA followed by Tukey-Kramer test  $p > 0.05$ ). Number of wasps tested is indicated inside the bars. (Reprinted from Agrahari and Gadagkar, 2003, Copyright: Elsevier)

caste differentiation is often post-imaginal. The processes by which some individuals in primitively eusocial species, succeed in becoming reproductive queens while others end up as sterile workers 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 (Naug and Gadagkar, 1998a). Like in the honey bees, 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, 2004).

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 *R. 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).

## Acknowledgements

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## Evolution of fighting ability in soldiers of Australian gall thrips

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**Abstract** – At least six species of Australian gall-inducing thrips on *Acacia* have eusocial colonies. That is, they exhibit alloparental care; in these cases it is defence of the colony brood by a morphologically and behaviourally distinct sub-fertile caste (eusociality as defined by Crespi and Yanega, 1994). Members of this defensive group, soldiers, are morphologically identifiable by having reduced wings and antennae, but most importantly for defence of the gall soldiers possess greatly enlarged pronotums and fore femora useful when seizing and applying a crushing force to arthropod invaders.

Previous studies have shown that between species the soldier level of sub-fertility is negatively correlated with their ability to kill their primary threat, members of the thrips species within the genus *Koptothrips* (Perry et al., 2002; Perry et al., 2004). Although, these studies refer to the phylogenetic relationship of the species involved they do not formally include the phylogeny within the analysis, and, as they acknowledge, may thereby have violated the statistical assumption of independence within the data set.

In this paper, we revisit the proposed correlation between two measures of soldier ability with soldier reproduction by females relative to their foundress mothers. Using Felsenstein's (1985) method of independent contrast to control for phylogenetic non-independence a correlation between relative reproductive outputs by female soldiers was found with a soldier's proclivity to attack (proclivity,  $r = -0.30$ ), and with soldier ability to kill an invader (efficacy,  $r = -0.84$ ). However, these results were not statistically significant ( $p = 0.559$ ,  $p = 0.076$ , respectively). We discuss these implications for future work on this system.

**Keywords:** Evolution, soldiers, eusociality, gall inducers, colony defence.

## Introduction

Insects within the Order Thysanoptera are small (0.5–2 mm long) and possess a set of fringed wings and arolia (bladder) footed tarsi (Mound, 1971; Mound and Heming, 1991; Ananthakrishnan, 1992). There are over 6000 described species in the world, and they are

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found mainly in tropical climates with widely varying life histories, ranging from herbivores that feed on plant and fungal tissues to carnivores feeding on other smaller arthropods (Mound, 1971; Lewis, 1973; Mound and Heming, 1991; Ananthkrishnan, 1992). However, the majority of galling thrips are phytophagous, feeding on rapidly growing plant tissues such as, flowers, fruits, pollen and leaves (Ananthkrishnan, 1992). The thrips of interest here (Thysanoptera: Phlaeothripinae) are associated with various native Australian *Acacia* trees and shrubs throughout Australia's arid and semi-arid interior. These thrips feed on the contents of plant cells within an induced gall in which the thrips are enclosed (Mound, 1971; Crespi and Mound, 1997; Mound and Crespi, 1995).

A solitary female, the foundress, punctures a developing phyllode (adapted petioles functioning as leaves) with her "mouth cone" (proboscis) that comprises three grooved slender stylets that form a feeding tube (Ananthkrishnan, 1992). She stimulates the growing phyllodes to roll, evaginate or pinch into an enclosed chamber. Once the foundress is interred inside a completely closed gall she lays and attaches eggs to the gall's substrate from which larvae then emerge and develop within the protected confines of the gall (Mound and Heming, 1991). In social species the first cohort to eclose comprise a morphologically distinct soldier morph (micropterous) with reduced wings and antennae, reduced cuticular melanisation and pronounced forelimbs (Crespi, 1992a). The second cohort to eclose is a dispersing morph (future foundresses and their mates) that possess fully developed wings, that for the exception of one species (*K. intermedius*) are thought not to eclose within the gall (Morris *et al.*, 2001). Soldiers, along with the foundress produce the dispersers (Crespi and Mound, 1997; Chapman and Crespi, 1998; Chapman *et al.*, 2002). Foundresses remain alive within the gall at least until the soldiers have eclosed. While the soldiers remain within the gall for the duration of their lifespan.

Gall usurpers belonging to the genus *Koptothrips* invade the galls of solitary and social species. These kleptoparasites cannot induce their own galls. *Koptothrips* invade a gall and drive out or kill the host inhabitants, the foundress will then produce a single brood of male and female dispersers who eclose and leave the galls as adults (Crespi, 1992a; Crespi and Mound, 1997). *Koptothrips* are considered to be the main evolutionary force driving the evolution of a defensive specialist in the gall inducers (Crespi and Abbot, 1999).

The study of altruism has had a long history as one of the outstanding questions in evolutionary biology (Hamilton, 1964 and 1972; Wilson, 1971 and 1975; Trivers and Hare, 1976; Lin and Michener, 1972; Evans, 1977; Stubblefield and Charnov, 1986; Wcislo, 1998). The gall-forming thrips of Australia are one of the more newly discovered species systems that have evolved a self-sacrificing caste and provide an important addition to the comparative database available for studying the evolution of eusociality (Crespi, 1992a; Crespi and Mound, 1997; Crespi and Choe, 1997; Kranz *et al.*, 2001). This addition has been made more significant by the inference of a phylogeny of the social and solitary *Acacia* thrips from DNA sequence data (Crespi *et al.*, 2004). The resulting phylogenetic pattern, and the mapping of character traits onto this phylogeny has led to several major insights into the evolution of a caste in the gall-inducing thrips.

Australian gall-inducing thrips appear to have evolved soldiers only once and have lost soldiers along two lineages (Crespi *et al.*, 2004). This ancestral population that gave rise to soldiers may have been highly inbred (Chapman *et al.*, 2000; McLeish *et al.*, in review). In this ancestral population the proto-soldiers may have been non-dispersing, but highly fecund individuals that produced a significant number of dispersing offspring via incestuous mating

within their natal gall (Chapman *et al.*, 2002). After the development of specialised soldier morphology and behaviour this group has evolved to vary greatly in female reproductive output, ranging from equal fecundity to the gall foundress to very diminished or even absent egg production (Chapman *et al.*, 2002). Potentially linked to reduced soldier-fecundity was the corresponding evolution of a reduced galls that may have limited the space available for soldier-produced dispersers (Wills *et al.*, 2001; Wills *et al.*, 2004). Perry and colleagues (2002) suggested that, as galls evolved to be smaller, soldiers were making an evolutionary trade-off between offspring production and the ability to defend the gall. They reported that the soldier ability to kill an invader increased across species as reproductive output decreased. This correlation was shown using a Pearson's correlative analysis on a multi-species data set. However, with closely related species the independence of data points assumed in such an analysis may have been violated. An association between these two traits may have formed in a common ancestor and therefore the use of tip data, data on extent species, may represent pseudoreplication (Felsenstein, 1985). In this paper we revisit the work of Perry and colleagues (in press) and investigate an association of soldier ability, measured as proclivity to attack and effectiveness or killing rate of attacks, and reproduction, but this time we incorporate the phylogenetic relationship of the species investigated.

## Methods

Measures of female soldier per capita reproduction relative to the foundress were taken from Wills and colleagues (2001). Results of trials designed to assess the willingness and effectiveness of soldiers were taken from Perry and colleagues (2002, 2004). Female and male soldiers from bisected galls were randomly chosen for either the proclivity or efficacy assays (described below). Kleptoparasitic *Koptothrips flavicornis* adults were found within the galls of *Kladothrips intermedius*, *Kladothrips habrus*, *Kladothrips waterhousei*, and *Kladothrips hamiltoni*, while in the collections of *Kladothrips morrisi* *Koptothrips dyskritis* were found. The *Koptothrips* used had been collected from the same localities and host plants as the gall-inducers.

*Koptothrips* were clasped with fine forceps by the abdomen and introduced head first to soldiers, such that a *Koptothrips* pronotum, forelimbs and head moved freely. Interactions had two possible outcomes. Either an attack resulted, which involved a soldier attempting to grasp the presented *Koptothrips*, or the soldier was seen to turn away from the *Koptothrips*, or no response was shown at all. Assays lasted until either an attack had transpired or 4 minutes had elapsed. The likelihood that soldiers attacked under this provocation was referred to at the species level as 'soldier proclivity'.

The response to the proclivity assay was found to be generally quite low (Perry *et al.*, 2002), so an assay was developed that allowed the soldiers and *Koptothrips* to interact more naturally and to determine the final outcome of these interactions and this determined what was called 'soldier efficacy' in defence (Perry *et al.*, 2004). One soldier was placed into a PCR tube to face a single *Koptothrips*. The "cage matches" were allowed to proceed over a period of 40 hours. The outcome of the trial was recorded as either an outright victory or defeat (i. e. *Koptothrips* died or the soldier succumbed).

The correlation between reproductive skew versus propensity and efficacy was examined using the phylogenetic comparative program COMPARE (v. 4.5) (E. Martins, Indiana University: <http://compare.bio.indiana.edu>). Felsenstein's (1985) method of independent

contrast was used to control for phylogenetic non-independence. Data obtained here was combined with demographic measurements of reproductive skew (measured as female soldier per capita reproduction relative to the foundress) obtained from Wills *et al.*, (2001). Two tree topologies (one each for the efficacy and proclivity data) based on those inferred by Morris *et al.*, (2001) were used for the analysis since efficacy data was not obtained for *K. kincheha*. Standardised contrast values were analysed with a linear regression forced through the origin with efficacy and propensity in separate analyses regressed on reproductive skew.

Independent contrast methods have been considered by some to be an overly conservative approach when addressing phylogenetic non-independence therefore we explored the outcomes of relaxing phylogenetic constraint imposed upon the coevolution of efficacy and reproductive skew. Phylogenetic generalised least squares analysis was conducted on standardised contrast values and the resulting regression parameters were examined at different levels of a parameter known as *alpha*, which represents three types of models. The definition of *alpha* is associated with the degree of phylogenetic constraint or inertia inflicted upon the evolution of the characters expressed in the terminal taxa (Grafen, 1989; Martins and Hansen, 1997; Hansen, 1997). Three main levels of *alpha* are considered (1) *alpha* is small and approximates the results of (FIC), (2) a maximum likely *alpha* which reflects the recent evolution of characters (i.e. less historical influence) and is determined based upon a generalised least squares statistical method. (3) *Alpha* is large and approaches the results that would be obtained if the tips were analysed independently of the phylogeny (~ raw data analysis). The regression slope for each level of *alpha* was tested statistically using a two-tail t-test.

## Results

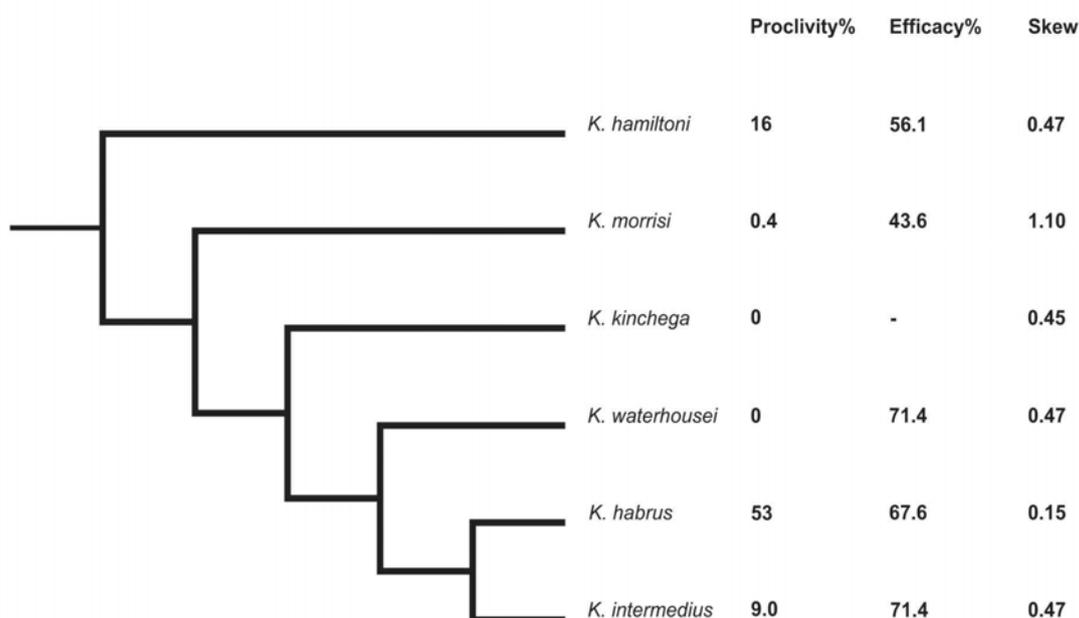
The resulting regression of the independent contrast analysis revealed that there was not a significant correlation between propensity and reproductive skew [ $F(4,1) r = -0.30$ , two tail  $P = 0.559$ ]. Also there was no significant correlation between efficacy and reproductive skew [ $F(3,1) r = -0.84$ , two tail  $P = 0.076$ ]. Proclivity, efficacy and skew estimates are mapped along side the phylogeny depicted in figure 1.

Analysis for proclivity for all three models (refers to method section) did not alter significantly the outcome of the original independent contrast results. For models 1 and 2 there was no significant correlation between efficacy and skew, but the correlation between efficacy and skew was significant for the third model. When the value of *alpha* in this model was very large (approaching infinity) [ $r = -0.88$ ,  $t_{0.05(2), 3} = 3.128 > 2.776_{(crit)}$ ].

## Discussion

Following the development of a defensive specialist in the gall-inducers female soldiers appear to have decreased their production of eggs until the soldiers of the two most derived species produce only a few offspring (Chapman *et al.*, 2002). Perry and colleagues (2004) suggest that soldiers over evolutionary time must be redirecting resources from reproduction to defensive morphology, physiology or vigilance. Crespi (1992b) showed that in one species, *Oncothrips tepperi* (renamed *K. intermedius*), there is an inverse relationship between wing development and limb armature. This observation is consistent with a developmental trade-off between defence and dispersal, but the relationship of these traits with

reproductive output is not known. In contrast to Crespi's observations, the existence of the species *K. morrisi* challenges the assertion that soldiers are energy limited. Soldiers of this species are the most reproductive yet they have the robust forelimbs of typical soldiers (Chapman *et al.*, 2002; Kranz *et al.*, 2001). The galls of *K. morrisi* are the largest in volume and wall thickness of the species with soldiers, and perhaps they provide higher levels of nutrients compared to the galls of other species. The trade-off proposed by Perry and colleagues (2004), needs to be investigated in more detail. We are currently examining the relationship of wing, oocyte and fore-femora development across species of the gall-inducers with soldiers. However, is there even statistical support for this proposed trade-off in the gall-inducers?



**Figure 1.** A pruned phylogeny from Morris *et al.* 2001 showing only social species within our study. All branch lengths are assumed equal and set to 1.0. Mapped onto the phylogeny are proclivity estimates taken from Perry *et al.* (2002), efficacy estimates from Perry *et al.* (2004) and skew estimates taken from Chapman *et al.* (2002).

In our reassessment of Perry and colleagues paper (2004) we also found a large negative correlation between the effectiveness of the soldiers and the reproductive output of soldiers, but the slope of this regression was not now statistically different from zero ( $P=0.076$ ). The comparative approach that we have taken here is widely employed (eg. Diaz-Uriarte and Garland, 1996; Martins, 1996; Pagel, 1998; Diaz-Uriarte and Garland, 1998). However, independent contrast methods are considered to be a statistically conservative approach in fact some argue too conservative (eg. Harvey and Rambaut, 2000). Other biologists have chosen to ignore phylogenetic relationships and simply assume that the lability of the

characters under investigation evolve so quickly that common ancestry plays no role in the association between two traits (eg. Westoby *et al.*, 1995; Mayhew and Hardy, 1998). Martins (1996) asserts that unless you can show that the phylogenetic relationship of the species studied plays no role than it must be taken into account. In reaction to these polarized views a number of authors have begun developing methods that make the promise of determining which microevolutionary model (eg. Brownian motion) is appropriate for the data in question and even formal methods for determining when removing phylogenetic constraint altogether is appropriate (Grafen, 1989; Pagel, 1994; Pagel, 1998; Harvey and Rambaut, 2000). These methods generally propose some transformation of branch lengths that when combined with information contained within the data set would give an indication as to how likely and to what degree phylogenetic inertia is impacting the relationship between two continuous traits. These methods remain largely theoretical and are not currently practical to apply. However, we did evaluate our correlation and the role of the phylogeny as well as alternate models of evolution using PGLS relationships analysis (a component of the program Compare 4.5). Our results using this approach indicate that if the phylogenetic effects were reduced greatly we would obtain a significant result.

However, our conclusion is that the phylogeny has some effect on the strength of the correlation found between soldier efficacy and reproduction and in the absence of information regarding the lability of these characters it would not be prudent to ignore this effect. On the other hand, we are not willing to conclude yet that there is no association evident here. Analyses of simulated data indicate that with less than 10 independent contrasts (there are 4 in this current example) type II errors are inflated (Harvey and Rambaut, 2000). Additional species or host-plant races with soldiers have recently been discovered, but not yet described. There are at least a dozen species within what is now called the *Kladothrips waterhousei* complex (Crespi *et al.*, 1997a,b; Crespi *et al.*, 2004). The determination of the phylogenetic relationships and life history details of this complex would potentially triple the number of species available for analysis and potentially would enable stronger conclusions regarding the strength of the association between fighting ability and reproductive output.

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## **Abscending, migration and swarming in honeybees: An ecological and evolutionary perspective**

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**Abstract** – Abscending, migration and swarming in honeybees are strategies correlated with climate, hence flowering, in temperate and tropical regions. Reproductive swarming usually coincides with the ascendant phase of a pollen/nectar flow. Migration is a resource-related, seasonal movement of tropical honeybee colonies without the production of queens and drones. It maximizes the colonization of new areas, serves as a spatial re-fuelling cycle and an evolutionary alternative to the hoarding characteristic of temperate bees. There are two kinds of absconding: “prepared” and “simple”. The former results from chronic disturbance/predation, declining nest quality, and sustained resource depletion. Simple absconding is a response to disasters: fire, floods, and severe predation. Prepared absconding is essentially migration on a smaller scale. The primary stimuli for prepared absconding or migration are resource depletion, deterioration of the microclimate of the nest and chronic disturbance by pests and predators.

To migrate/abscond, bees must have sufficient flight fuel and energy reserves to construct new combs at a new site. Abscending colonies typically engorge honey, accelerate wax production, reduce oviposition and consume eggs and young larvae to conserve protein. Small colonies of tropical honeybees may also merge into polygynous swarms of several to hundreds of queens but when such swarms settle supernumerary queens are usually killed. Amalgamation may favour the genes of a colony better at invasion than stockpiling its own resources and provides a solution for colony build-up, reducing pro rata costs of survival. Evolutionarily, it also directs the energies of non-viable units towards survival of a large social unit as the greater the diversity of patriline, the greater the averaging effect on phenotypic behaviour of the whole colony.

**Keywords:** absconding, migration, swarming, honeybees, *Apis*.

### **Introduction**

Striking differences among honeybees include the extent of resource investment in reproductive swarming and absconding and migration, differences ascribable to climate and the seasonality of flowering in tropical and temperate regions (cf. Koeniger and Koeniger, 1980; Seeley, 1985; Ruttner, 1988; Nakamura, 1993, 1995; Hepburn and Radloff, 1995, 1998).

These are the essential prerequisites that both allow and drive honeybees to abandon their maternal nests and to establish new ones. The phenomenon of nest abandonment by absconding/migration is ubiquitous in all species of honeybees except that it occurs at a very low level in the Eurasian, but not African, subspecies of *A. mellifera*.

Temperate zone honeybees have only brief periods of weather favourable for swarming and establishing new colonies and nests and conserve large stores to survive winter; few abscond or migrate (Martin, 1963). In sharp contrast, tropical climates with perennial flowering facilitates swarming, absconding and migration (cf. Seeley, 1985; Nakamura, 1993, 1995; Hepburn and Radloff 1995; 1998). However, predation pressure is severe in many tropical areas and must also select for greater colony mobility through absconding and migration. Honeybees that construct a single comb in the open are subject to constraints different in kind and quality from those that affect the multiple-comb, cavity-dwelling species. Thus, thermal homeostasis is also a continuous selective pressure affecting the distribution and seasonal cycles of colonies.

Absconding/migration may be beneficial to the survival, dispersal and propagation of some honeybee species, but imposes serious difficulties in beekeeping in the tropics (Smith, 1961; Crane, 1990; Soares and De Jong, 1992; Verma, 1992). This has stimulated observations and experiments over the last two centuries that are beginning to provide a biological basis for absconding, migration and reproductive swarming in the context of insect sociality. This review synthesizes the relevant literature and seeks underlying principles for these behaviours as life history phenomena. The terminology related to swarming, absconding and migration is historically conflated because it covers a spectrum of phenomena without definite boundaries (Nakamura, 1993, 1995; Hepburn and Radloff, 1998).

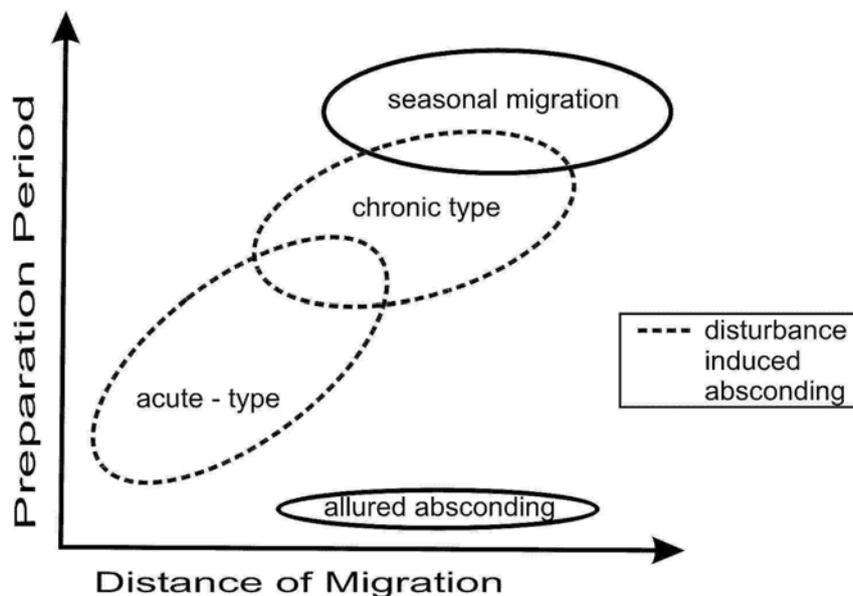
## Terminology

Reproductive swarming is the movement of a queen and part of a honeybee colony from the maternal nest to an entirely new site for colony reproduction. Migration is distinguishable from swarming because in the former there are no queen cells or drones on the combs (Woyke, 1978). It is the seasonally predictable movement of a colony from one region to another and a return journey is not prerequisite. Absconding is also the movement of a whole colony away from its maternal nest site to another place either as “prepared” or “simple” absconding. The inferred causes of prepared absconding (functionally synonymous with migration) are often intertwined, but resolve into severe, chronic disturbance and/or predation, declining quality of the nest site and resource depletion.

Migration/prepared absconding is reflected in the behaviour of a colony preparing to abandon its combs. In this context, the terms “nomadic absconding” (Crane, 1990), “prepared absconding” (Woyke, 1978; Nakamura, 1993, 1995), “undisturbed absconding” (Mutsaers, 1991), and “chronic disturbance absconding” (Nakamura, 1993, 1995) are synonymous with “migration” because all involve preparations for the departure of colonies. Simple absconding, also “acute disturbance”, is the reaction to disaster. “Chronic disturbance absconding” is an example of prepared absconding of longer duration and for some weeks prior to absconding such colonies have little honey or brood and foraging is reduced (Nakamura, 1993, 1995).

## Seasonality of prepared absconding and migration

Seasonal migration is characteristic of tropical *A. cerana*, *A. mellifera*, *A. florea*, *A. andreniformis*, *A. dorsata* and *A. laboriosa* (information for other species is lacking). The migrations are seasonally predictable consequences of resource depletion or dearth, a widespread decline in available pollen and nectar usually associated with high temperatures, extreme aridity; or, conversely, extended rains or cold. Changes in microclimatic conditions of the nest and the increased advent of pests/predators are very often coincident with and even amplify the effects of resource depletion. Resource depletion as a stimulus for prepared absconding and migration is a conspicuous and recurrent theme in the literature for all species of honeybees (except Eurasian races of *A. mellifera*). The essential differences in the relationships between distance of colony movement (migration) and the length of preparation time before movement and nest abandonment can be visualized diagrammatically (Fig. 1).



**Figure 1.** Relationship between the preparation period for prepared absconding or migration and distance eventually moved for four types of colony movement (after Nakamura, 1993).

The climatic conditions that lead to seasonal dearth and then to migration obviously vary. *A. cerana* migrates during periods of high temperatures and again during the dearth of the dry season (Dulta *et al.*, 1988), or follows the abatement of the heavy rains (Olsson, 1989). A complex pattern occurs in the mountains in Sichuan Province, China where most colonies migrate/abscond every year. The region is a highly convoluted landscape where subtropical and temperate climatic regimes converge. So, some species of flowers are in bloom for a long time but in different places so that *A. cerana* migrates continually (Chen, 1995).

Large-scale seasonal migrations occur in several African races of *A. mellifera* as well. In Tanzania, the majority of *A. m. scutellata* colonies migrate annually during the long dry

season. In Kenya, by the middle of the dry season colonies of *A. m. scutellata* move into the forests and return six months later to the more open savanna; but movements are facultatively related to available forage and water (cf. Hepburn and Radloff, 1998). Further south, in the Okavango delta migrations of *A. m. scutellata* are protracted during the dry season (Schneider and McNally, 1994).

Amongst mountain honeybees, *A. m. monticola* and *A. m. scutellata* migrate up and down the slopes of Mt Kilimanjaro when their stores are depleted and dearth prevails (Smith, 1961). Similarly, *A. m. scutellata* also migrate vertically in the Drakensberg mountains (Fletcher and Tribe, 1977). In the lowlands of Tanzania *A. m. litorea* migrates during the dearth, apparently driven to move because it fails to co-ordinate brood-rearing with diminishing stores, and because of the arrival of bee pirates at the same time (Ntenga, 1976). In the fynbos of South Africa, *A. m. capensis* migrations occur in autumn and winter and results from fluctuations in forage coupled to warm days and berg winds between winter cold fronts (Hepburn and Radloff, 1998).

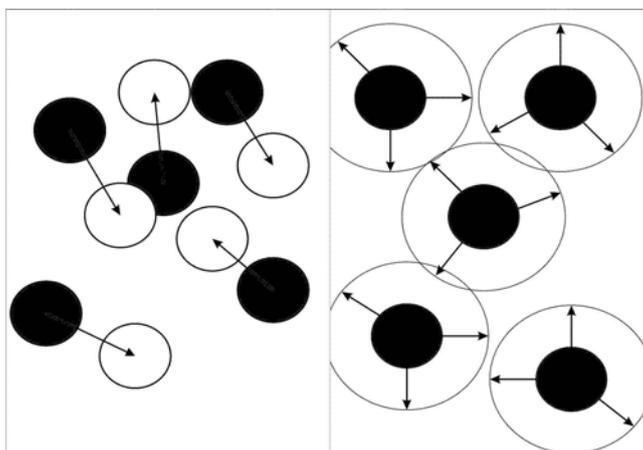
Cycles of absconding/migration and swarming by *A. florea* are also linked to forage availability and high temperatures, seasonal changes in flowering, dearth and the depletion of resources (Thakar and Tonapi, 1962). In a general summary of the biology of these little bees, Deowanish *et al.* (2001) reported that both *A. florea* and *A. andreniformis* in Thailand abscond in response to increased exposure to heat/sunlight and during dearth. Tirgari (1971) noted that *A. florea* migrated to sites with maximum exposure to sunshine in late autumn and in spring returned to dense foliage where the combs were not directly exposed to sun.

In an analysis of hundreds of colonies of *A. dorsata*, Deodikar *et al.* (1977) reported that they migrate to the hills in summer and to the plains during the monsoon in response to declining forage or resource depletion, interpretations endorsed by Venkatesh and Reddy (1989) and Ahmad (1989). *A. dorsata* colonies migrate annually in response to resource depletion, allowing them to track seasonally varying sources of forage in different areas (Dyer and Seeley, 1994). Colonies arrived at their study site at the end of the dry season, swarmed but stayed in the area until the onset of the rains. Absconding/migrations by thousands of colonies of *A. dorsata* coincides with the monsoon, which determines the dry and rainy seasons, hence onset of resource depletion (Deodikar *et al.*, 1977; Koeniger and Koeniger, 1980; Thapa, 1998). Ahmad (1989) showed that migration in *A. dorsata* is facultative and he delayed absconding/migration by re-queening colonies and then providing supplemental feeding.

In the case of *A. laboriosa*, Underwood (1990) concluded that the effects of altitude are rather marked because these bees are apparently unable to survive the cold of winter on cliffs above 1675m but return to higher altitudes with warmer weather. This species is unique in that these bees do not build comb nor rear brood during winter. In spring the bees migrate back to their traditional cliff sites and begin the annual cycle again.

Absconding and migration under tropical conditions would be advantageous to small, weak colonies, which may not be able to effectively expand their forage areas or to scout for new but patchily distributed resources. Resource-related absconding, often termed "seasonal migration", is a tropical strategy to survive relatively long periods of dearth or the distribution of forage resources at very wide distances apart. When resources deteriorate, the weaker absconding colonies abandon depleted areas and move on. The stronger stationary colonies simply expand the area in which they forage, small incremental increases

in radius resulting in very large area gains for little additional foraging distance incurred (Fig. 2).



**Figure 2.** Foraging strategies of absconding (left) and stationary (right) honeybee colonies.

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. Under tropical and subtropical conditions where vegetative resources occur in larger patches

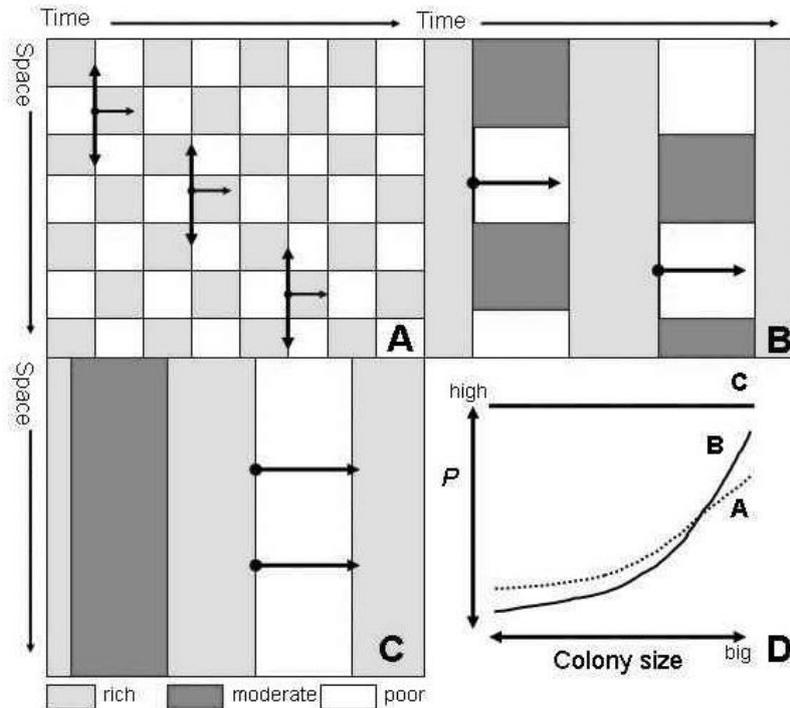
and where seasonal conditions alternate between wet and dry phases, a direction strategy similar to the tropics is preferred, but distance will be greater. In the final scenario of temperate conditions with seasonality and a cold winter, direction of movements is more limited and distances all the greater (Fig. 3).

These three strategies can be combined into a probability plot (Fig. 4). Differences in the relationships between distance of colony movement (migration) and length of preparation time before movement and nest abandonment can be visualized diagrammatically (Fig. 1). The relationship between disturbance and the potential for absconding is illustrated in (Fig. 5). The literature for *A. florea* also reflects considerable argument as to primary or secondary causes of nest abandonment. It is abundantly clear that there are several sources of stimuli that drive absconding and migration and that no specific one need be unique; nor, need the several stimuli be mutually exclusive. It appears quite improbable as well as unnecessary that a single factor could explain the observed movements of honeybees when there is preparation before such a move.

The obvious effects of resource depletion can be directly measured as changes in honeybee colonies. Dulta *et al.* (1988) fortnightly recorded the demographic changes in 10 strong and 10 weak colonies of *A. cerana*. In all of the weaker colonies which absconded/migrated, honey and pollen stores, eggs, open and sealed brood decreased by nearly 90%. In contrast, the 10 stronger colonies, which did not abscond had increased honey stores and had only small decreases in pollen stores and brood area.

Turning to *A. florea*, Akratanakul (1977) reported from Thailand that about a fortnight before two colonies absconded, they also stopped brood rearing, but waited for capped brood to emerge before departure. These colonies were presumed to have absconded owing to resource depletion. These accord by with the observations of Woyke (1978) in India.

Another consequential aspect of brood as a stimulus is that its presence apparently inhibits/delays the actual onset of absconding by *A. florea* (Dutton and Free, 1977).

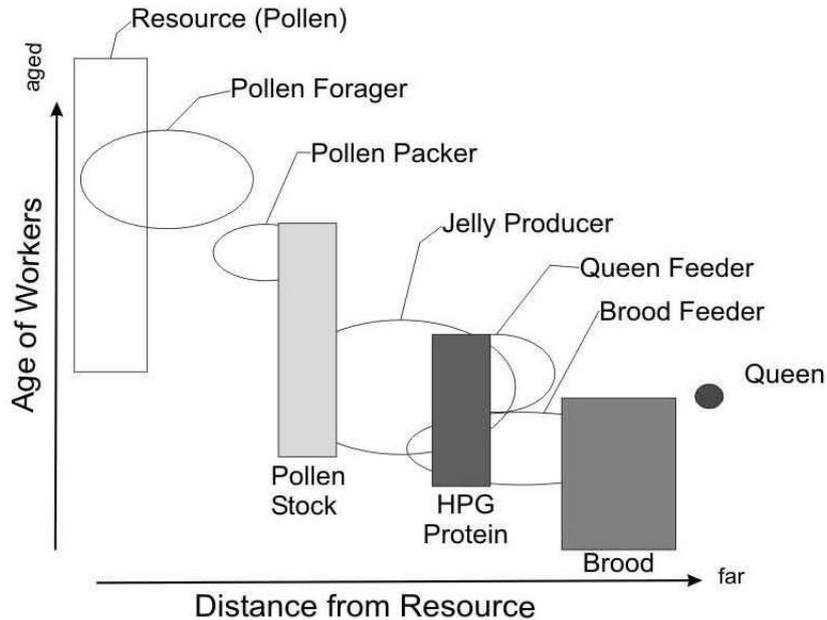


**Figure 3.** Direction of colony movements during dearth under different resource distribution patterns. A – Patchy resource distribution under aseasonal tropical conditions; B – Large patch distribution of resources under seasonal conditions; C – temperate, seasonal resource distribution; D – Probability of colony movement in relation to colony size, where low  $p$  is migratory, high  $p$  stable and stationary with A, B and C as above (after Nakamura, 1993).

The interpretations as to causes of absconding/migrating are supported by experiments to avert it. Woyke (1978) gave brood and pollen to a colony of *A. cerana* and over the next two days the bees ate all of the brood but did not forage for pollen. When additional combs of brood of all ages were supplied, they began to forage, rear brood and absconding was averted. During a poor pollen flow, the queens continue to lay resulting in more larvae than nurse bees can feed. The workers eat older larvae to produce bee milk to feed the queen and other larvae. Other attempts to prevent absconding/migration by supplementary feeding and manipulation of the combs were also successful (Olsson, 1989; Wei, 1994; Lin, 1977).

Resource-related absconding/migration is a strategy to overcome long periods of dearth while cannibalism is adapted to overcome shorter periods of dearth or small fluctuations in forage resources (Nakamura, 1993, 1995). The rationale is that a honeybee colony has several metabolic buffers to reduce the effects of fluctuation in the normal field resources: pollen stocks, the secretions of the hypopharyngeal glands of the workers and brood which can be

recycled through cannibalism. The spatial relationships of protein sources as buffer zones within the colony are shown diagrammatically in Figure 4.



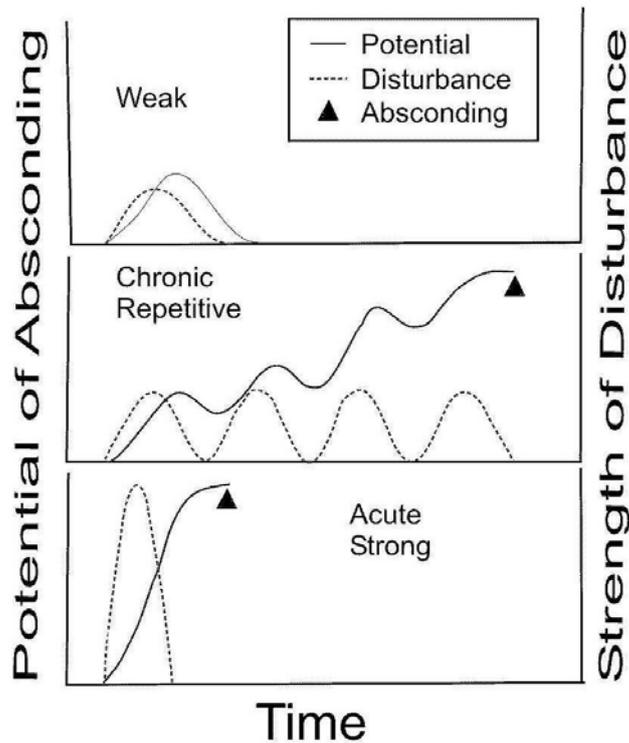
**Figure 4.** Distance from resources in relation to worker polyethism, solid bars indicate functional buffers within the colony (after Nakamura, 1993).

The role of pollen in prepared absconding or migration by *A. cerana* was quantitatively investigated by Punchihewa *et al.* (1990) in field studies in Sri Lanka. They noted, like Woyke (1978), that one of the distinct characteristics of a colony preparing to abscond is a decline in the numbers of returning foragers carrying pollen. The preparative stages are phasic and gradually build up and can be measured as the progressive reduction in pollen foragers over time. Punchihewa *et al.* (1990) developed what they termed a “colony performance index” defined as the total number of returning foragers bearing pollen loads divided by the periods of observations (in seconds) multiplied by the total number of returning foragers. In the course of preparative absconding the index gradually falls to 0.00 on the actual day of absconding. These authors also noted that once the absconding impulse is activated the bees no longer defend the nest against intruders such as wax moths and ants and cease to rear brood.

### Predation pressure

Pests and predators as well as robbing amongst colonies of *A. cerana* are generally regarded as major contributory factors for prepared absconding throughout China (Wei, 1994; Chen, 1995). Olsson (1989) demonstrated the impact of pests and predators by narrowing hive entrances to restrict the entry of wasps and beetles. Reduction in the numbers of combs and replacement of old with new combs also reduces the chance of wax moths gaining a

deleterious foothold in the nest. Likewise, uniting all weak colonies greatly reduced absconding, in part, by providing a stronger defense force against natural enemies.



**Figure 5.** Relationship between intensity of disturbance and absconding potential (after Nakamura, 1993).

While the pests and predators of *A. dorsata* are numerous, there are actually fewer reported links between them and absconding/migration in these bees than might be expected. On the one hand both Ahmad (1989) and Viraktamath (1989) reported that infestations of wax moths lead to absconding in *A. dorsata*; on the other Mahindre (1997) thought that a wax moth infestation is not a sufficient stimulus to induce prepared absconding in *A. dorsata* colonies. Nonetheless, Viraktamath (1989) reported that some 34/56 combs were infested with wax moths before absconding/migrating and, after abandonment all 56 nests were infested with wax moths, which he regarded as a contributory cause of absconding.

A reasonable compromise interpretation would be that colonies of honeybees preparing to abscond generally reduce their defensiveness against intruders at which time any wax moths present in the nests might begin to expand their activities and numbers and by the time the colony actually abandons the nest the wax moth population flourishes and is regarded as a cause of absconding on a post hoc basis. Kastberger *et al.* (1999) have elegantly documented the behaviour of honey buzzard attacks on *A. dorsata* colonies and while these

The full extent of predatory forces acting against the subspecies of *A. mellifera* in Africa is not quantifiable but its impact is striking (cf. Hepburn and Radloff, 1998). Often interactive effects leading to migratory absconding include gradually deteriorating field resources which lead to reduced brood production, hence colony size, providing sufficient imbalance to allow the takeover and total nest destruction by wax moth or small hive beetles (cf. Hepburn and Radloff, 1998). Akratanakul (1977) concluded that absconding/migration in *A. florea* is driven by two main stimuli: resource depletion and serious disturbances by various pests and predators (man, ants, wax moths). When he continuously provided supplementary feeding and pollen was still abundant, a combination of weaver ant and wax moth infestations apparently precipitated their absconding. Moreover, Seeley (1983) thought that nest site selection was largely driven by predator avoidance criteria.

birds certainly evoke a massive defense attack against these predators they are not induced to abscond. In the case of *A. laboriosa*, the broodless winter cluster remains close to ground and the bees are often attacked by drongos and thrushes, which induce some absconding; otherwise migration is temperature and resource related (Underwood, 1990).

### Microenvironmental effects

The interrelationships between variables that may lead to prepared absconding/migration are often inter-twined, especially in the case of climatic factors which drive dearth as well as more directly affect the microclimatic conditions of the open-air or cavity-nesting species. Absconding intensity by *A. cerana* is closely related to ecological/climatological conditions: it is most intense in dry lowland areas and becomes less acute in wetter areas and with increasing altitude in Sri Lanka (Punchihewa *et al.*, 1990). Environmental effects are particularly evident where different climatic systems converge. So, in Sichuan, China where very weak colonies cannot effectively thermoregulate, they normally abscond and often amalgamate with others (Chen, 1995).

More direct effects of microclimate on the absconding impulse is seen in colonies of *A. cerana* kept in hives or natural nest cavities. All of the hived colonies attempted to abscond while none in natural nest cavities did so (Punchihewa *et al.*, 1990). The difference was attributed to micro-climatic conditions in the hives. The evidence for this conclusion was that a reduced "colony performance index" in hived bees could be experimentally increased by control of temperature and humidity regulation in hives. This has the effect of averting a low index, which activates the absconding impulse. Moreover, Punchihewa *et al.* (1990) were able to artificially reduce the index of a colony by constant disturbance, smoke and high temperatures.

Depreciation of nest quality may result from inundation by rain, overheating, too small a cavity size and fire. Overheating of exposed nests of *A. m. adansonii* may be caused by direct sun penetrating the bare branches of deciduous trees during hot dry seasons; conversely, bees hanging beneath the branches of trees may be dislodged by rain. *A. m. scutellata* readily absconds over the wetter parts of its range but considerably less so in drier areas such as the Kalahari (Fletcher and Tribe, 1977). Presumably the efficacy of absconding has had a marked effect on the probability of colony survival in the drier areas, thus selecting against absconding.

Nest site selection is of fundamental importance from a microclimatic and thermoregulatory point of view, especially those stimuli which perturb the microclimatic environment of the nest. For example, *A. florea* moves to sites providing maximum sunshine in autumn and in spring move to sites with reduced insolation (Tirgari, 1971; Mossadegh, 1990). *A. florea* that dwell in caves move more deeply into them at the beginning of the hot season and, when cooler conditions return, move closer to the opening again (Free, 1977). Similar movements have been noted for nest positions in bushes. Moreover, Seeley (1983) thought that nest site selection was largely driven by predator avoidance criteria.

## Absconding/migration behaviour

Subsequent to absconding, colonies of *A. florea* may cluster for several days at an interim site near the old nest and over the next few days scout bees search for new nest sites (Akratanakul, 1977). There are few data for the distances travelled by such colonies, but Soman and Chawda (1996) reported that in one year many colonies were found about 20–25 km from where bees normally occur. Targari (1971) observed that colonies of *A. florea* moved only 5 to 400 m and Whitcombe (1984) observed that absconding colonies only moved short distances of 4 to 65 m while reproductive swarms moved 25 to 800 m.

*Apis dorsata* very evidently moves considerable distances in the course of migration; but, as noted by Koeniger and Koeniger (1980) it is extremely difficult to follow migrating swarms in dense jungle or to estimate distance travelled. Nevertheless, they observed that swarms may take as much as a month to reach their final destinations and that they stop frequently along the way and speculated that the bees move as far as 100–200 km.

Observations on amalgamations of colonies range from the merger of two queenright dwarf swarms in *A. m. capensis* to an extraordinary mega-swarm of *A. m. adansonii* containing in excess of 500 queens (Silberrad, 1976). Amalgamation of colonies is a rare phenomenon in temperate *A. mellifera* but commonly occurs in *A. cerana* (Nakamura, 1993, 1995) and in subspecies of African *A. mellifera* (cf Hepburn and Radloff, 1988). Frequent reference is made to the smallness of merging colonies of *A. cerana* (Nakamura, 1993, 1995), *A. m. adansonii*, *A. m. capensis*, and *A. m. scutellata* (cf. Hepburn and Radloff, 1998) Such colonies often amalgamate with other colonies on the move (“allured absconding” of Nakamura, 1993, 1994, 1995) or enter the nests of other colonies.

Amalgamation of small swarms (migratory colonies and/or reproductive swarms) into conglomerates provides an immediate solution to building up colony population and reducing pro rata costs of survival (Chandler, 1976; Hepburn and Radloff, 1998). Inclusive fitness notwithstanding, it also has the effect of directing the energies of non-viable units towards survival of a large social unit. Significant differences in colony behaviour are associated with the degree of genotypic diversity: the greater the diversity, the greater the averaging effect on phenotypic behaviour (Page *et al.*, 1995) Amalgamation increases the patriline of the new conglomerates.

That a modified dance language is associated with absconding/migrating was demonstrated by Koeniger and Koeniger (1980). They recorded the migration dances of *A. dorsata*, which entail only waggle dances of very long duration. The bees do not return to their starting point at the end of a run but begin anew elsewhere. They do not complete the total cycle of the usual waggle dance, thus separating a migration dance from the waggle dance associated with foraging. Essentially the same observations were made for absconding colonies of *A. florea* (Free, 1977; Dyer & Seeley, 1994) and *A. m. scutellata* (Schneider and McNally, 1994) and *A. cerana* (Sasaki, 1990).

Desertion of the nest and successful re-establishment elsewhere requires that the bees have sufficient flight fuel and reserves of energy to construct new combs when they have settled. Engorgement is a normal step in preparing to abscond/migrate in *A. m. scutellata* (Otis *et al.*, 1981) as well as for *A. cerana* in China (Chen, 1995). Reduction in egg-laying commonly precedes migration and so conserves protein. Likewise the worker bees commonly eat even sealed brood in the colony before leaving the nest. Thus full preparation for

migration includes elevated wax production, increased protein uptake and massive fuel intake.

Because colonies kept in flight rooms at Oberursel, Germany exhibited the usual preparations for migration, declining brood rearing a few times a year, Koeniger and Koeniger (1980) concluded that seasonal migration in *A. dorsata* might be genetically fixed. This is reminiscent of sheltered migratory birds exhibiting zugenruhe. It has also been mooted that there is a genetic basis for absconding/migration in *A. florea* (Koeniger *et al.*, 1982; Whitcombe, 1984) but there is not much experimental evidence to assess this hypothesis. In a breeding programme using recurrent selection the tendency for both swarming and absconding could be reduced in *A. cerana* (Deodikar and Thakar, 1966) and in *A. mellifera* (Foti, 1980). Nonetheless, it is extremely noteworthy that *A. mellifera* honeybees of temperate European origin have not acquired the absconding/migratory traits even four centuries after their introduction to the neotropics

The genetic variability for the “prepared absconding” trait is evidenced by honeybee reaction to the seasonal nature of pollen income cycles, which start and stop during any particular season. Parallel observations were that some colonies preparing to abscond did not collect pollen or rear brood even if pollen flow conditions improved in the area. Yet, other colonies in the same apiary quickly responded to available pollen and reached peak development. So, after such a pollen flow diminished, some colonies immediately ceased brood rearing and prepared to abscond, others not. These constitute significant and probably genetically based differences among *A. cerana* colonies exposed to the same environmental conditions in the same apiary (Woyke, 1976; Nakamura, 1993, 1994, 1995).

## Reproductive swarming

Reproductive swarming in temperate zone honeybees varies with climate and season and more particularly with weather and the availability of forage. When adverse circumstances arise, swarming may be either postponed or aborted entirely. Reproductive swarming in the honeybees of tropical and subtropical Asia and Africa is just as seasonal as in temperate zones, but “season” acquires different meaning. The sharply defined categories “spring-summer-autumn-winter” of the temperate regions usually resolve into alternating wet and dry periods; but mountainous areas are often more temperate. It is evident that climatic regime greatly influences swarming behaviour irrespective of the species.

The propensity for and frequency of swarming varies among colonies on a regional and often very local level, almost always associated with the sequence rainfall > flowering > swarming. If the usual season for swarming is preceded by drought and dearth, swarming may be reduced or even totally inhibited. At the opposite end of the spectrum unseasonably heavy rains may provide the insertion of an atypical “extra” swarming period as noted for *A. m. scutellata* and *A. m. adansonii* in arid regions (cf. Hepburn and Radloff, 1998).

In several other regions reproductive swarming is regularly biphasic and corresponds to separated major flowering periods *A. m. scutellata* (Silberrad, 1976). In the more tropical areas of its distribution, *A. cerana* may swarm virtually continuously throughout the year as in southern China (Yang and Xu, 1982); or, biphasic without any obvious seasonal rhythms as occurs in Sumatra (Inoue *et al.*, 1990) and southern India (Venkatesh and Reddy, 1989). By contrast, in very temperate areas such as Japan swarming is very clearly related to a single well-defined season, spring (Yoshida, 1997) or summer in northern India (Goyal, 1978). In an

extensive study of nearly 350 colonies of *A. dorsata* at five sites in India, Venkatesh and Reddy (1989) showed that reproductive swarming is biphasic. The subtropical *A. laboriosa* of Nepal has a single swarming period during April and May (Underwood, 1990). Swarming in *A. florea* is often biphasic in (Free, 1977) but may also occur in a single spring season (Soman and Chawda, 1996; Akratanakul, 1977). Yet in very tropical Sri Lanka, swarming is continuous throughout the year (Lindauer, 1956).

The apicultural literature is heavily dominated in volume by studies of temperate races of *A. mellifera* and among the fundamental tenets of this literature is that crowding of the nest is a major stimulus for reproductive swarming. While this may well correlate with the issue of the so-called prime swarm it cannot apply to subsequent swarms from the same colony when population pressure has become considerably reduced. This idea does not hold up too myriad observations on Asian and African species and races of honeybees (Takuno, 1994; Sharma, 1960) Kellogg (1941) noted that in Fukien Province in the southeast of China that *A. cerana* is prone to swarming irrespective of colony size, congestion or food supply. A major conclusion is that small *A. cerana* colonies swarm, broodnest congestion and colony size do not provide convincing answers as to cause (Hadiseosilo 1990).

## Swarming and migration

There are several examples of migration being closely linked to reproduction. In Zambia, *A. m. adansonii* colonies build up rapidly in spring and undergo both reproductive swarming and migration. Brood-rearing declines in the rainy season and then, there is another cycle of brood-rearing, reproductive swarming and subsequent migration (Silberrad, 1976). When the searing harmattan blows down from the Sahara resulting in dearth, extensive migrations are coupled with reproductive swarming (Sawadogo, 1993). Alternatively, in *A. m. scutellata*, reproductive swarming occurs immediately after migration (Fletcher and Tribe, 1977). The distribution and frequency of absconding and migration in Africa must serve as prima facie evidence that this strategy of moving enhances the probability of survival, otherwise it would have been dampened or eliminated by selection (Hepburn and Radloff, 1998).

As has been previously noted, the phenology of reproductive swarming in Africa closely corresponds with local climate and the availability of forage. Very simply, rainfall ultimately drives flowering, the intensity of which is related to rainfall intensity. Flowering is a resource dispensing mechanism that drives brood rearing and swarming and leads to a well defined sequence of relationships: peak rainfall > peak flowering > maximum brood rearing > reproductive swarming (Hepburn and Radloff, 1998).

Nonetheless, an intimate temporal relationship between swarming and migration occurs in other regions of Africa. While reproductive swarming is obviously ubiquitous, migratory movements are clearly associated with tropical honeybees; and, indeed the situation for the subspecies of *A. mellifera* in the Horn of Africa exhibits patterns similar to those found elsewhere. In the case of *A. dorsata*, the most conspicuous of migratory honeybees, it is well established that migration is driven by resource depletion, which is tied to alternating rainy and dry seasons ultimately determined by the monsoon (Ahmad, 1989; Mardan, 1989; Dyer & Seeley, 1994).

The significance of resource depletion as the general driving force for large-scale migratory movements is also reflected in *A. cerana* (Ahmad, 1989; Nakamura, 1993). The situation in *A. florea* is somewhat different: in some regions migration is apparently driven

by resource depletion (Thakar and Tonapi, 1962) and in others as a response to micro-environmental changes in ambient temperature (Tirgari, 1971). It would appear that migration is a reasonably clearly defined phenomenon among tropical honeybees where resource depletion is the immediate stimulus for movement; it is not directly tied to swarming as such even though the movements deliver colonies to more favourable localities where reproductive swarming may eventually occur.

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## **Castes in neotropical swarm-founding wasps (Hymenoptera: Vespidae: Epiponini). The influence of colony cycle**

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**Abstract** – *In neotropical swarm-founding wasps, caste differences are multi-faceted. Typical queen-worker differences found in highly eusocial Hymenoptera are found in some species simultaneously with the absence of fairly distinct caste attributes. In addition, caste differences may become accentuated as the colony ages. An updated verification of these traits suggests that social regulation in epiponines is not a unique, and caste determination may occur prior to or subsequent to the adult stage. At least five recognizable patterns of caste distinction are reported here, some of which are influenced by colony cycle. Only one caste pattern is clearly determined during the larval stage, indicating caste flexibility in several epiponines.*

**Keywords:** Polistinae, Epiponini, caste differences, colony cycle, caste determination.

### **Introduction**

#### **Castes, complexity, and neotropical swam-founding wasps**

In social insects, the origin and the maintenance of a sterile caste have been one of the main problems to the theory of natural selection (*Darwin's dilemma*, in West-Eberhard, 1996). With few exceptions, workers are not completely sterile, and they combine behaviors typical of the sterile caste (like food collection, brood care, defense and nest construction) with some type of reproduction, giving rise to the various patterns found in the Hymenoptera (Bourke, 1988). In fact, as previously predicted by the kin selection theory, worker sterility is conditionally expressed and reveals the variations of genetic interests of the colony (Queller and Strassmann, 1998).

Even though population size of mature colonies can be probably determined at least partially by ecological factors, changes in the number of individuals in a colony can hold very important social consequences (Jeanne, 1991; Alexander *et al.*, 1991; Bourke, 1999). Among them, the most important may be the predicted change in the reproductive potential of the workers. As suggested by Bourke (1999), as the colony size increases, workers experience a decrease in their chances of becoming reproductive substitutes so that they increase mutual

reproductive inhibition (*worker policing*, Ratnieks, 1988). As the reproductive potential of workers decreases, the level of reproductive dimorphism between castes increases (Wilson, 1971; Michener, 1974; Oster and Wilson, 1978; Hölldobler and Wilson, 1990; Alexander *et al.*, 1991; Wheeler, 1991). This sort of *morphological skew* (Bourke, 1999) would help to explain why societies composed of a few individuals have small differences between castes, and those with many individuals present a more pronounced differentiation. For these reasons, small societies would be characterized by a direct conflict towards reproduction and caste determination. In contrast, conflicts in larger societies should be predominantly on brood composition and the members of these societies should be relatively more “resigned” with the manipulation of their castes (Bourke, 1999). In this way, colony size deserves greater consideration as a determinant of caste differentiation, just as kin structure, social complexity, workers reproductive potential, levels of caste differentiation, and the nature of social conflicts in a society (Bourke, 1999).

Neotropical swarm-founding wasps, the Epiponini (Carpenter 1993), represent an ideal model for studying morphological caste evolution, because differentiation in these wasps varies from null to complete dimorphism. All species are polygynic and reproduce by swarms, an indisputable evidence of a complex society (Jeanne, in press) compared with independent founding Polistinae (Tab. 1). Initially, Richards (1978) documented three forms of caste discrimination, and recent research builds upon these: (A) Queens larger than workers: In some species caste differences are so pronounced that they must be determined by nutritional differences during larval development (Evans and West-Eberhard, 1970; Jeanne and Fagen, 1974; Sakagami *et al.*, 1996; Noll *et al.*, 1997). (B) Allometric differences: with queens smaller than workers in some body parts, but larger in others, which may result from ontogenetic reprogramming in growth parameters (Jeanne *et al.*, 1995), assuming that the body plans represent fundamentally different end products, not different points along a continuum. Sometimes, such castes are barely detectable (Jeanne, 1996). (C) Slight or indistinct morphological differences: with castes absent or manifested weakly, based on only a few traits (Richards, 1978; Jeanne, 1980).

**Table 1.** *Contrasting independent and swam-founding Polistinae*

<b>Polistinae</b>	
<b>Independent founders</b>	<b>Swarm-founders</b>
Behavioral castes	Behavioral and morphological castes
Monogyny	Polygyny
Univoltine colonies	Multivoltine colonies

As we will see below, in several cases caste syndromes cannot be determined exclusively by looking at single colonies. It is necessary to visualize some of the changes that occur in the colony cycle. We have been working with these aspects, integrating caste differentiation and colony cycle. Even though several authors have also been working on caste issues on epiponines (reviewed in O’Donnell, 1998), we will focus exclusively on those comparable works for the purpose of understanding castes and possible variations according to colony cycle.

## Castes and colony cycle

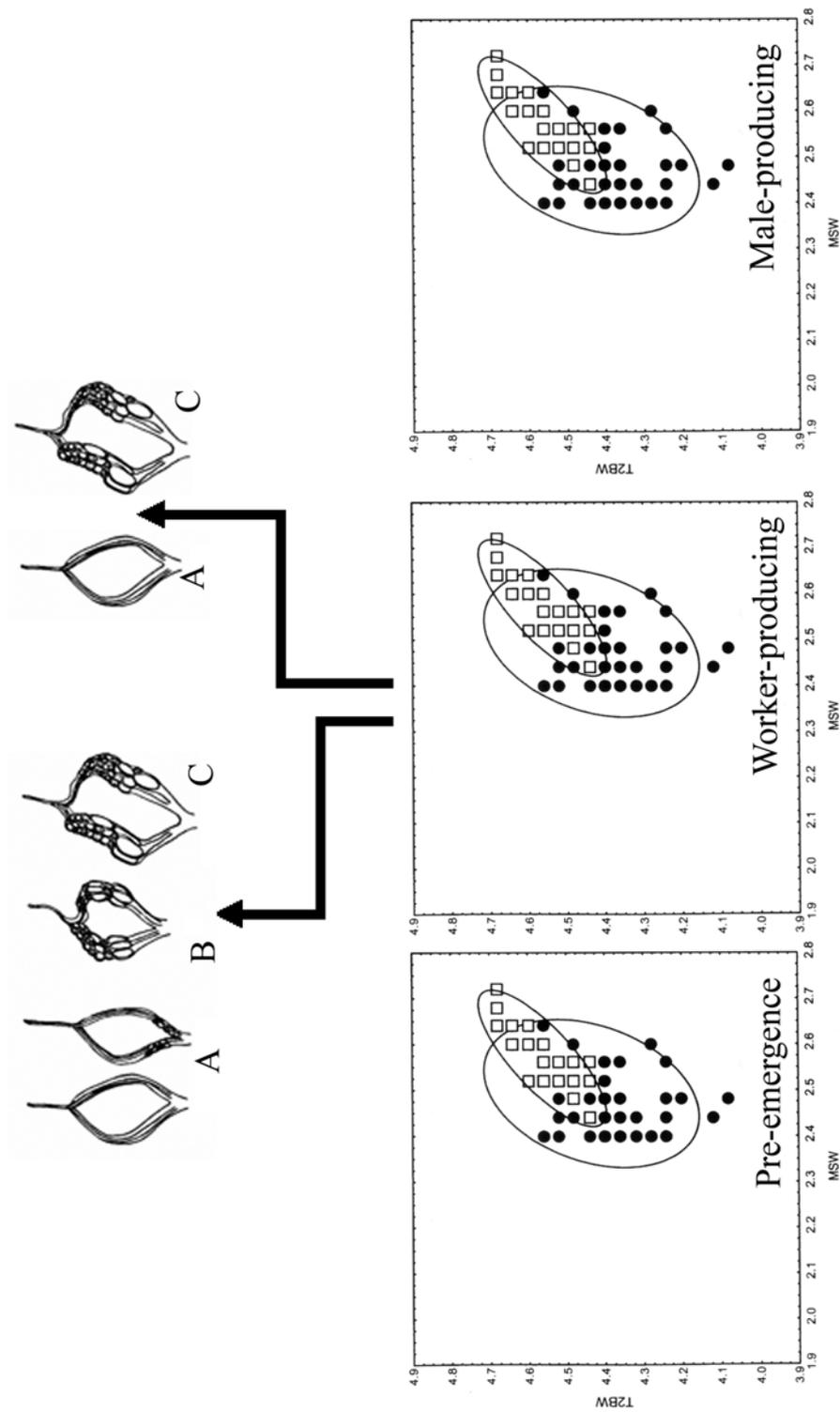
Colony cycle is apparently an important factor in the social organization in several epiponines, because queen number decreases as the colony ages. The number of queens can decrease until monogyny occurs, when new queens are produced (cyclical oligogyny; West-Eberhard, 1978). Along with decreases in queen numbers, morphological and physiological discontinuity seem to increase in some species (Noll and Zucchi, 2000, 2002). This sort of increase in caste differences is probably due to the exclusion of smaller queens (Noll and Zucchi, 2000). Such a phenomenon has also been reported in *Polistes* (West-Eberhard, 1969) and some Ropalidiini (Fukuda *et al.*, 2003a,b).

The number of studies on the biology of swarm-founding neotropical wasps is so few that generalizations are difficult to make. However, different types of caste differences can be clearly delimited. It is obvious that there is not only one pattern involving caste differences and ovarian development for epiponines. Below is given an update and a description of each recognized pattern.

**1. Morphological and physiological caste inception.** In this first case, which unexpectedly differs from other highly eusocial insects, morphological differences between queens and workers are lacking and such a pattern is kept during the whole colony cycle (Fig 1.1). It was observed in *Chartergellus communis* (Mateus *et al.*, 1999), *Parachartergus fraternus* (Mateus *et al.*, in press) and *Angiopolybia pallens* (Noll, in prep.). Because queen-worker differences are practically absent, it is possible to assume that castes are probably determined in the adult stage. A strong indication that this is true is the constant presence of non-inseminated laying females in the colonies, suggesting that workers develop their ovaries throughout their lives without restriction, and young females could probably reach queen status (West-Eberhard, 1978; 1981; Forsyth, 1978). As suggested by Noll and Wenzel (2003) and Noll *et al.* (submitted), this is the basal condition for castes in epiponines.

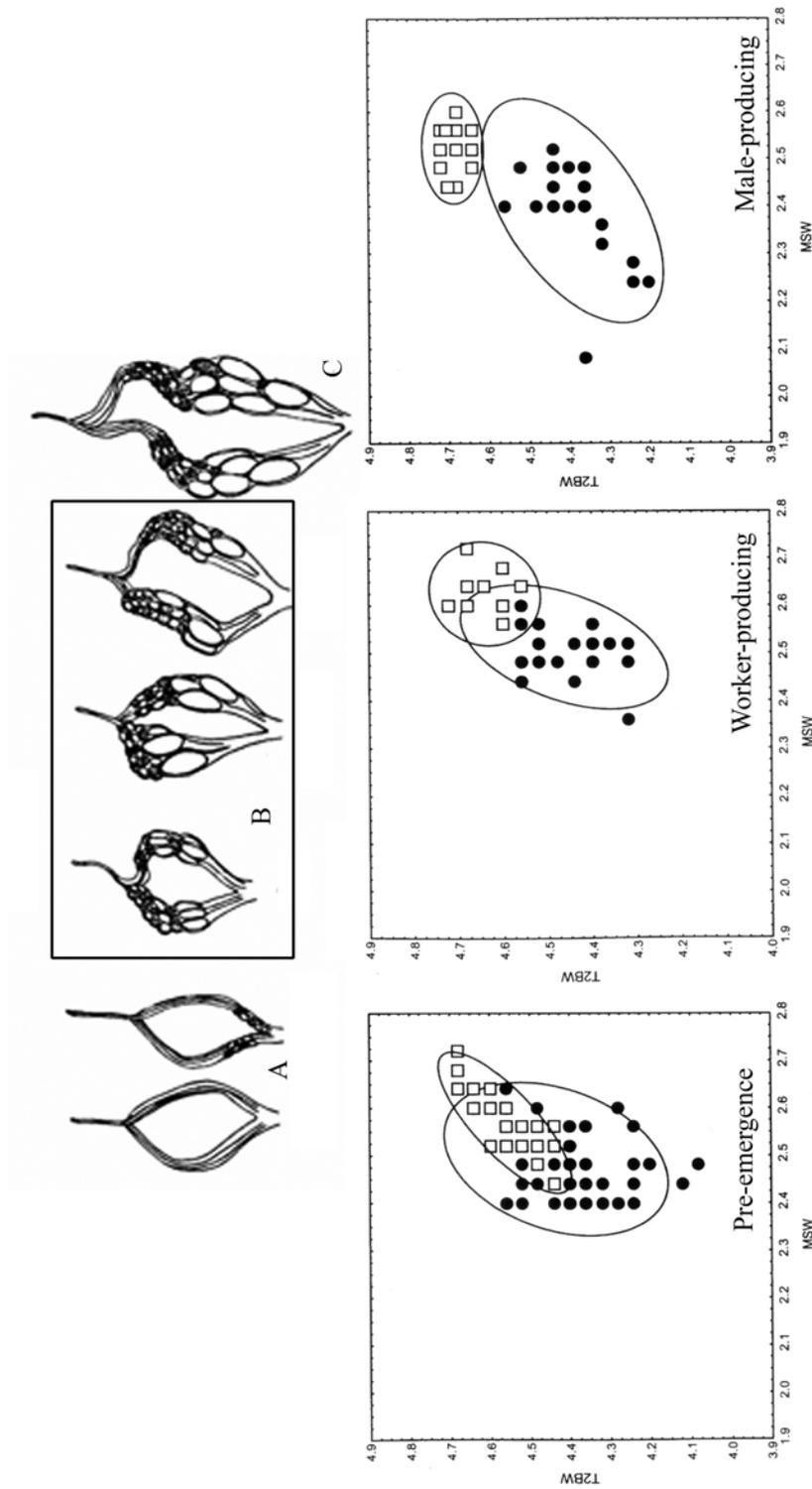
**2. Morphological caste inception.** This condition is probably derived from 1 (Noll and Wenzel, 2003; Noll *et al.*, submitted). Here, as seen in 1, morphological differences between queens and workers are absent throughout the whole colony cycle, however, young females would develop ovaries only in some phases of the colony cycle. For epiponines, this is the first pattern, detected by West-Eberhard (1978) and used as a general rule for the whole tribe. It was observed in *Metapolybia aztecoides* (West-Eberhard, 1978), but also in *M. docilis* (Baio *et al.*, 2003a), *Synoeca cyanea* (Noda *et al.*, 2003) and *S. surinamensis* (West-Eberhard, 1981) (Fig. 1.2). Even though caste differentiation not involving size could be related to this syndrome (Baio *et al.*, 2003a), physiological castration seems the more reasonable cause (West-Eberhard, 1978), once queen loss occurs and would be the switching point for the attainment of reproductive status (West-Eberhard, 1981).

**3. Morphological cycle dependent caste with permissively physiological development.** This is the first indication of morphological discontinuities between castes, in epiponines and these differences increase according to colony cycle. Queens have a variable size when the colony starts and, as the colony ages, queens tend to be among the larger individuals during worker production phase, and finally, at the end of the colony cycle, queens are the largest individuals (Fig. 2; Noll and Zucchi, 2000). In *Protopolybia exigua* (Noll and Zucchi, 2002), *P. sedula* (Baio, 1997) and *Brachygastra augusti* (Baio *et al.*, 2003b), non-inseminated laying females are always present during the colony cycle. Here, queens seem to be more clearly determined during the larval stage, which means that non-inseminated laying females are



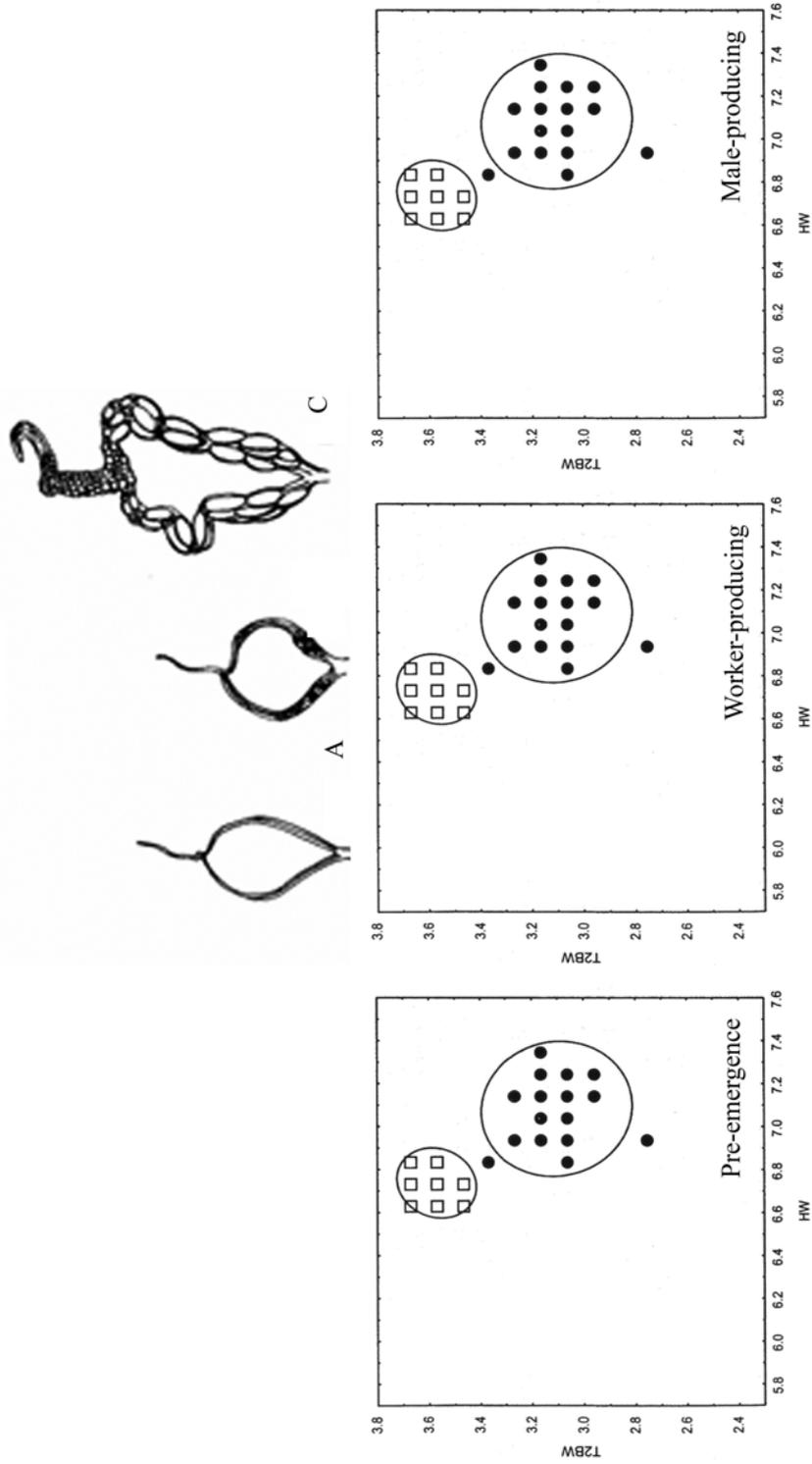
**Figure 1.** Caste discrimination (in three different stages of the colony cycle) found in some epiponines in which size is not an important characteristic for separating castes.

The lack of difference is maintained even when queen number decreases. 1. Corresponds to syndrome 1 (see text) in which non-inseminated females (A and B) develop ovaries along the colony cycle permissively. 2. Corresponds to syndrome 2 (see text) in which non-inseminated females remain sterile (A). C represents queen ovaries.



**Figure 2.** Caste discrimination increase in three different stages of the colony cycle. This increase is related to queen number reduction.

In syndrome 3 (see text), ovarian types A and B are present in non-inseminated females, suggesting ovarian development along the colony cycle. In syndrome 4 (see text), however, non-inseminated females remain sterile in most part of the colony cycle, once ovary type B is hardly found. C represents queen ovaries.



**Figure 3.** Typical pre-imaginal caste discrimination found in species bearing syndrome 5 (see text). In this syndrome morphological distinction is accompanied by physiological differences (ovary type A belongs to workers and C type to queens), without variation according to three different stages of the colony cycle.

only a worker phase. Apparently, queens being larger, giving rise to morphologically distinct castes, is a derived trait from pattern 1 (Noll and Wenzel, 2003; Noll *et al.*, submitted). In this case, even though queens might be determined in the larval stage, flexibility might be kept in this syndrome (see Concluding Remarks).

**4. Morphological and physiological cycle dependent castes.** As a derivation of 3, caste differences also increase during the course of the colony cycle. However, physiological distinctions between queens and workers approach the “highly eusocial” status, with queens fully fertile and workers sterile. Non-inseminated laying females, however, may appear in some phases of the colony cycle (Fig. 2), as in some *Polybia* (Noll and Zucchi, 2000), *Chartergus globiventris* (Noll and Zucchi, 2002), and *Protonectarina sylveirae* (Shima *et al.*, 2003). Ovarian development in other females, rather than queens, could reflect the loss of dominance in the colony (Noll and Zucchi, 2002), so that young females would find a more flexible way to decide their way (but, see Concluding Remarks).

**5. Morphological and physiological cycle independent castes.** In this condition, morphological differences between castes are constant and queens are always distinct from workers during the colony cycle. Non-inseminated laying females are absent throughout the whole colony cycle, suggesting that workers do not develop their ovaries adequately to become layers (Fig. 3). This pattern is recognized in some *Apoica* (*Apoica flavissima*, Shima *et al.*, 1994; Noll and Zucchi, 2002; *Ap. pallens*, Jeanne *et al.* 1995) and *Agelaia* (*Ag. flavipennis*, Evans and West-Eberhard, 1970; *Ag. areata*, Jeanne and Fagen, 1974; *Ag. pallipes* and *Ag. multipicta*, Noll *et al.* 1997; *Ag. vicina*, Sakagami *et al.* 1996; Baio *et al.* 1998) and would fit the definition of caste differences for higher eusociality: queens differ from workers in both morphology and physiology. An interesting aspect, however, is the origin of this syndrome. It would be reasonable to expect that this syndrome would be derived from 4. However, phylogenetic studies revealed that it is probably derived from 1 (Noll and Wenzel, 2003; Noll *et al.*, submitted).

## Concluding remarks

The cases illustrated here indicate that there is not an exclusive caste system that may encompass all epiponines. In addition, these schemes of queen selection may include size dependence or not. Among the five recognized patterns stated above, it is obvious that only number 5 bears undisputable caste determination during the larval stage.

The other four schemes may indicate that even though the colony might invest in the production of larger individuals, size differences may not be important. There are two clear subdivisions, in this case. In the first, schemes 1 and 2 are very alike and, based on morphology; they might be a good indication of post-imaginal caste determination. In scheme 1, all individuals are able to reach queen status, as observed in *Parachartergus colobopterus* (Strassmann *et al.*, 2002). In scheme 2, the absence of free ovarian development along the colony cycle would represent a stronger control under recently emerged individuals, inhibiting them from developing ovaries, but caste flexibility is still conserved.

Schemes 3 and 4 might be interpreted as a logical sequence of scheme 1. However, it is clear that being large is a very important trait for those individuals trying to become new queens, because only these sorts of females are found in later stages of the colony cycle. However, the presence of non-inseminated ovarian-developed females in all stages (scheme 3) or limited to a certain stage (scheme 4) might suggest that young individuals, (even not

bearing desirable traits) may become potential queens and join the next swarm. However, in these cases workers seem very selective in choosing their future queens, so that they would remove “fake” queens.

Finally, it is obvious that a lot of work has to be done until we come to a more robust approach of how caste systems are organized in epiponines. However, it is obvious that any species studied so far can be considered as a model for the whole tribe. Future studies integrating detailed morphological structure, physiology of glands associated to social, ovarian development, and especially the social behavior on site of these wasps will surely come with more well-supported conclusions.

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## **Phylogenetic analyses of life history traits in allodapine bees and social evolution**

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**Abstract** – *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 sister clade to the remainder of the allodapine clade, is apomorphic. Although allodapines have traditionally been regarded as displaying recent origins of sociality, so that they 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 perhaps the 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.*

**Keywords:** Allodapine bees, life history, DNA sequences, evolution, alloparental care, eusociality, phylogenetic patterns, evolutionary transitions.

## Connections between life history and social traits

Allodapine bees (family Apidae, tribe Allodapini) are useful for comparative approaches to social evolution because of the wide range in forms of sociality among species and genera. They differ from all other bees in that they rear their brood in an unsealed and undivided communal burrow and this aspect of their nesting biology creates very different social environments from mass provisioning species. Because offspring are not enclosed within sealed cells, they have no physical barriers protecting them from parasites and predators except for the presence of parents or alloparents. Nearly all species rear their brood progressively in a communal area and, combined with lack of cells, this means that survival and development of offspring is completely dependent on the continued presence of parents or alloparents. Communal rearing of larvae means that, when more than one female shares a nest, adults have few or no opportunities to direct care to only their direct offspring – parental or alloparental care is spread across all brood within the spatially limited and linear burrow.

All allodapine species show at least some signs of sociality. In *Halterapis nigrinervis* this seems to be restricted to brief periods after eclosion of the brood, when mothers and their recently emerged daughters share the nest prior to dispersal (Michener, 1971). However, in most species, sociality involves more protracted cooperation among nestmates. Colony sizes can vary from as little as two females to as many as 40+ during brood rearing. Reproductive skew can be very low, such that all females reproduce to more or less the same extent (eg. Tierney *et al.*, 2002; Langer *et al.*, 2004), through to species where some females are effectively sterile (eg. Schwarz, 1986; Schwarz *et al.*, 2005). There is only one known species that exhibits morphologically distinct castes, although size-based reproductive roles can be very marked in some other species (eg. Tierney *et al.*, 1997; Schwarz *et al.*, 2005).

In allodapines, life cycle traits have the potential to impact very strongly on the kinds of sociality that can evolve, and we now briefly outline some of the major ways in which this can happen.

**Brood provisioning methods.** Most allodapines progressively rear their young, feeding them on a day-by-day basis. This means that a large number of brood can be produced at any one time and the burden of having to provision those brood can be spread out over a long period; if colony sizes are large, then it is possible that a large number of feeding brood can be supported as happens in *Exoneura robusta* (Schwarz, 1986) and *Exoneurella tridentata* (Hurst, 2001). Progressive provisioning in a communal tunnel may be important for understanding incentives for alloparental care: the existence of many brood requiring continual feeding could mean that alloparental opportunities are not as limited as they would be for species that provision only one cell at a time such as all ceratinines and many *Xylocopa*. Interestingly, the African species *Halterapis nigrinervis* sequentially mass provisions each egg after it is laid and this seems to be the only allodapine that is exclusively subsocial (Michener, 1971).

**Egg production schedules.** Allodapine species vary in the rate at which eggs are produced – some produce one large batch and oviposition is completed at about the time that larval eclosion occurs (eg. Michener, 1971; Schwarz, 1986). In other species, eggs are produced slowly and more or less continuously (e.g. Michener, 1971; Tierney *et al.*, 1997). In some others, foundresses rear a clutch of offspring to maturity, after which oviposition becomes

more gradual and protracted. The former schedule often results in a situation where brood reach post-feeding stages at more or less the same time, limiting opportunities for older brood to engage in alloparental feeding of their younger siblings. In species where oviposition is gradual and protracted, the different developmental stages of brood within a colony mean that opportunities for alloparental care will be frequent and protracted.

**Voltinism.** A major proposed benefit in Queller's (1989) "headstart advantage" and Gadagkar's (1990) "assured fitness returns" models is the ability of alloparents to complete the development of younger, partially reared siblings, and this benefit becomes greater if potential alloparents have to wait for long periods of time before becoming reproductive themselves. Latency to reproduction is likely to be higher in univoltine species, where females eclosing in summer need to wait until the following spring before commencing their own reproduction (eg. Schwarz, 1986). In multivoltine species, or tropical species, latency to reproduction is likely to be smaller or even negligible (e.g. Neville *et al.*, 1998; Tierney *et al.*, 2001; Thompson and Schwarz in press), limiting the opportunities and magnitudes of headstart advantages.

**Adult longevity.** Allodapines generally have long adult lifespans, though precise data are limited. Maeta *et al.* (1985) found that females of *Braunsapis hewitti* could live as adults for at least 18 months and in the Australian allodapine *Exoneura robusta*, some females can attain reproductive dominance in their nests 18 months after adult eclosion (Hurst, 1993). Adult longevity is potentially very important for social evolution, since it allows extended windows of opportunity for reproduction, as well allowing adult daughters to aid their still reproductive mother. Extended adult longevity could facilitate flexibility in reproductive strategies because of the greater possibility that the dynamics of dominance contests will change over time.

## Phylogenetics and the comparative approach

The large variation in both life history and social traits among allodapine species creates enormous potential for comparative approaches to social evolution, but such approaches need to be informed by phylogenetic information. Up until recently, phylogenies of allodapines were based on relatively small sets of morphological and life history characters. Use of life history traits in phylogenetic reconstruction can create difficulties if the phylogeny is also used to infer evolutionary transitions in the trait itself, especially when the total number of characters is small. Indeed, inclusion of mass/progressive provisioning as a character in earlier phylogenetic studies of allodapine bees (Michener, 1977; Reyes, 1998) contributed to the notion that mass provisioning was plesiomorphic for allodapines (Schwarz *et al.*, 2003). More generally, morphological characters in allodapines entail a variety of problems: (i) female morphology is relatively constant; (ii) male genitalic characters are highly variable but difficult to codify, and physical constraints can potentially involve forced correlations leading to non-independence of characters; (iii) larval characters are highly variable but present problems of convergent evolution, where homoplasies may be difficult to detect. Homoplastic changes in allodapines are already well known through the multiple instances of convergent evolution among independent origins of social parasitism (Michener, 1970).

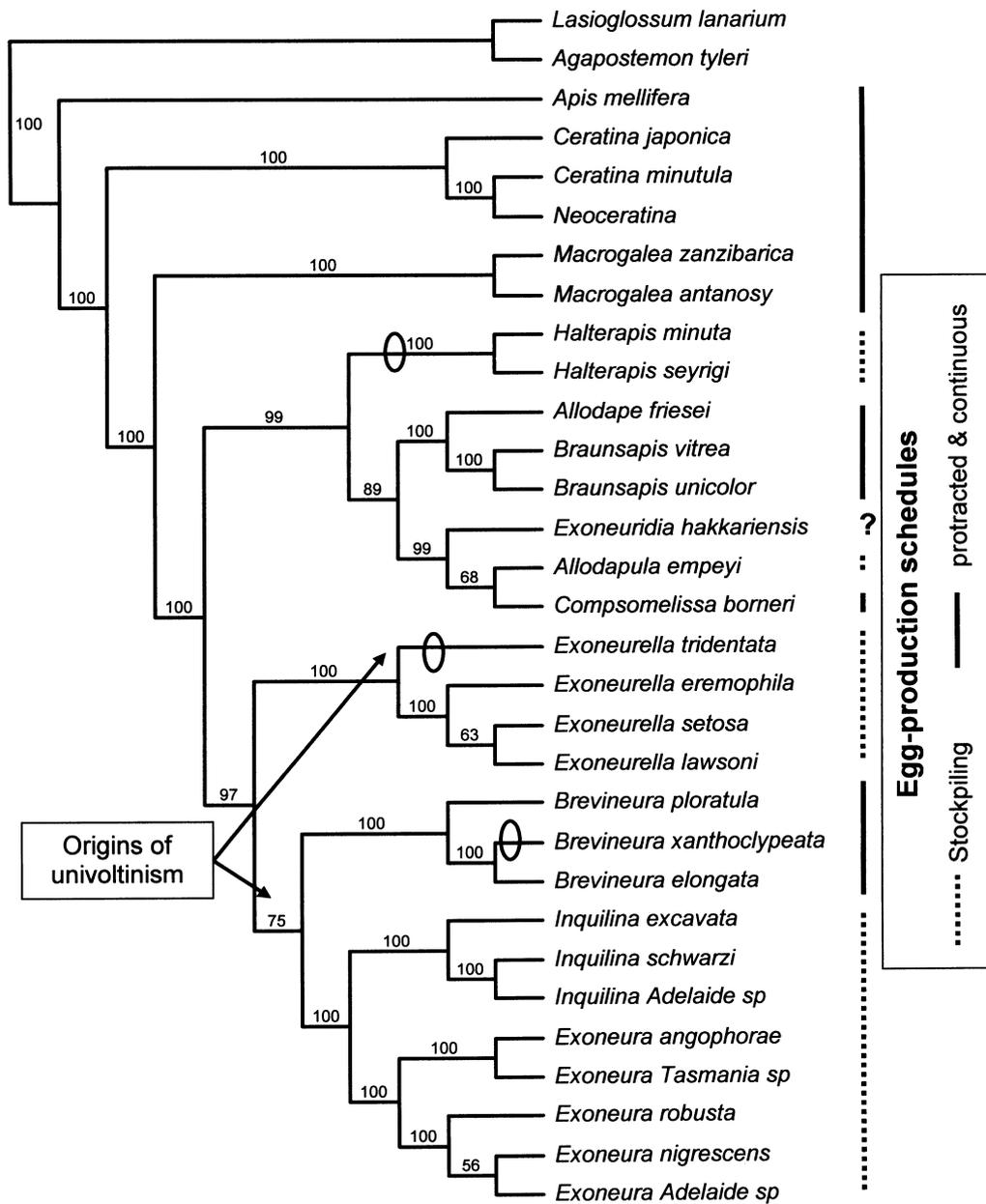
Very recently we have begun investigating allodapine phylogenetics using DNA sequence data and this is leading to major insights into the relationships between life history traits and social evolution. In the following section we outline recent DNA-based phylogenetic hypotheses and use these to infer relationships, or lack thereof, between life history and social traits.

## DNA sequence-based phylogeny of the Allodapini

Analyses below are based on nucleotide data from two mitochondrial genes, COI and Cyt b, and one nuclear gene, EF-1a. Gene regions were amplified and sequenced using bi-directional sequencing. Primers used for PCR amplification are given in Schwarz *et al.* (2003) and Schwarz *et al.* (2004). The mitochondrial regions were from the protein coding genes cytochrome oxidase b (Cyt b; 427 bp sequenced) and cytochrome oxidase subunit I (COI; 1282 bp), and the nuclear region was from the F2 copy of elongation factor-1alpha (EF-1a; 774 bp). We used two halictid species as the outgroup and included *Apis mellifera* and three *Ceratina* species in the in group to help root the ancestral allodapine node.

Extreme AT bias at 3<sup>rd</sup> mtDNA positions leads to very substantial problems for phylogenetic analyses because of the high rates of homoplastic changes (Schwarz *et al.*, 2004). Furthermore, heterogeneity in base composition and evolutionary rates between partitions (1<sup>st</sup>, 2<sup>nd</sup> and 3<sup>rd</sup> codon positions for both mitochondrial and nuclear regions respectively, Schwarz *et al.*, 2004), means that fitting single models to a combined data set is not valid. Maximum parsimony and maximum likelihood analyses are unable to deal with this heterogeneity and we therefore analysed our data using Bayesian analyses (MrBayes, version 3.0b4, Huelsenbeck and Ronquist, 2001). We used the same protocol as Schwarz *et al.* (2004), with a general time reversible model (Nst=6) applied to each of the six partitions. We assumed a gamma shaped distribution with a proportion of invariant sites and allowed partition models to vary by unlinking gamma shapes, transition matrices, the proportions of invariable sites, and base compositions. MrBayes default priors were otherwise used. MCMC chains were run for  $3 \times 10^6$  generations and trees were sampled every 500<sup>th</sup> generation. The number of burnin generations (1.5 million) was much greater than when stationarity was reached (assessed by graphing likelihood scores against generation number). To check that Bayesian runs were converging on similar parameters we carried out three runs and compared parameter estimates for consistency.

The resulting consensus cladogram is given in Figure 1 with posterior probability support indicated for each node. *Macrogalea* is resolved as the sister group to all other Allodapini, which form three main clades comprising the Australian exoneurines (*Exoneura*, *Inquilina*, *Exoneurella*, *Brevineura*), the Madagascan *Halterapis* species, and the remaining largely African taxa (*Allodape*, *Braunsapis*, *Halterapis*, *Compsomelissa*, *Allodapula*). Like Schwarz *et al.* (2005) we found no evidence to indicate that the African and Madagascan *Halterapis* species form a monophyletic group. This topology is concordant with very recent DNA-based studies (Schwarz *et al.*, 2003, 2004; Bull *et al.*, 2003) but very different from previous studies based on morphological and behavioural evidence (Michener, 1977; Reyes, 1998), which implied that the African clade *Halterapis* + *Compsomelissa* represented the sister group to all other allodapines and that *Macrogalea* formed a monophyletic clade with the exoneurine genera.



**Figure 1.** Consensus cladogram from partitioned Bayesian analysis with posterior probability node support indicated for each node.

Ellipses indicate origins of sociality where small colony members are effectively sterile. Vertical lines indicate taxa that produce eggs slowly over a protracted period of time (solid lines) or taxa that stockpile eggs (dotted lines) such that clutches of eggs accumulate within the nest. The arrows indicate the origins of univoltinism and all other clades are bivoltine or multivoltine.

## Inferences from the molecular phylogeny Origins of sociality and provisioning methods

African members of the allodapine genus *Halterapis* (traditionally regarded as a subgenus of *Compsomelissa*, Michener, 2001) are mass provisioners, and were thought to be entirely sub-social (Michener, 1971). Although African representatives of *Halterapis* are not included in our analysis here (summarised in Fig. 1), other studies (Schwarz *et al.*, 2003; Bull *et al.*, 2003) provide strong support that this group forms a monophyletic clade with *Compsomelissa* and *Allodapula*. The *Halterapis* + *Compsomelissa* clade was thought to form the sister group to the remaining allodapine genera (Michener, 1977; Reyes, 1998). The trait of mass provisioning in *Halterapis nigrinervis* and closely related African congeners (Michener, 1971) is shared with the sister tribe Ceratinini, which is a largely solitary tribe, and it was therefore thought that subsocial behaviour was plesiomorphic for allodapines. Furthermore, the evolution of true sociality in the remaining allodapine genera was assumed to be linked to the transition from mass to progressive provisioning. However, Schwarz *et al.* (2003) showed that the tropical African genus *Macrogalea* is in fact the sister lineage to the remainder of the allodapines, and Tierney *et al.* (2002) showed that *Macrogalea zanzibarica* displays relatively complex forms of sociality and highly female biased sex allocation patterns. A recent study by Thompson and Schwarz (in press) on an undescribed *Macrogalea* species from Malawi has demonstrated very complex social behaviour in that species, and sociality is recorded for species of all other non-parasitic allodapine genera for which data are available. It is therefore apparent that if *Halterapis nigrinervis* is indeed exclusively subsocial, this trait represents an apomorphy in the allodapines.

The coincidence of subsociality and mass provisioning in *Halterapis* may suggest that progressive provisioning is linked to sociality in allodapines. However, a recent study of the Malagasy species *Halterapis minuta* shows that this species also mass provisions clutches of eggs (Schwarz *et al.*, 2005). Up to 11 eggs can be provided with a single, long, cylindrical-shaped pollen mass before larval eclosion commences, cutting off contact between the adults and their young brood. *H. minuta* also shows well-developed sociality, with very strong size-based reproductive differentiation, where helpers belong to a smaller size class than the dominant reproductives. This study therefore suggests that the loss of sociality in *Halterapis nigrinervis* is not linked to mass provisioning *per se*, although it is possible that it could be linked to mass provisioning of individual eggs. In *H. nigrinervis* only one egg is provisioned at a time, and then the next egg is laid before provisioning can begin again, and this may act to limit the size of indirect fitness benefits from alloparental provisioning.

In the mass provisioning *Halterapis minuta*, and in progressive provisioning allodapines, a large number of brood are present at any one time and the rate of food delivery to larvae is not limited by having access to only one brood member at a time. This raises the possibility that the critical evolutionary transition, which allowed sociality to proliferate in the allodapines, was not the evolution of progressive provisioning, but instead the loss of cell partitions. Once cell structure had been lost, prior to divergence of the extant allodapine clades, adult females were able to provision more than one brood at a time and this may have increased the size of benefits available to alloparents.

### Phylogenetic conservatism in voltinism

Tierney *et al.* (2000) showed that there was a high degree of phylogenetic conservatism in key life-history traits within the three Australian non-parasitic exoneurine genera. *Exoneura* species are all univoltine, co-found new nests, and exhibit winter-egg-stockpiling with subsequent synchronized brood development. *Brevineura* species are also univoltine, but do not co-found nests and egg production and brood development are continuous and protracted. Three of the four *Exoneurella* species are bivoltine, with solitary nesting in spring, social nesting in summer, and with two pulses of egg production corresponding to spring and early summer. The remaining *Exoneurella* species, *E. tridentata*, has very large, perennial colonies and is highly eusocial. Tierney *et al.* (2000) argued that, with the exception of *E. tridentata*, these generic patterns in voltinism and brood production schedules could not be explained by habitat differences because of their broad overlap in ecological and climatic distributions, and that some phylogenetic constraints might instead be operating. Using a molecular phylogenetic approach, Bull *et al.* (2003) were unable to resolve bifurcation order of the exoneurines, and argued that it was likely that the three non-parasitic genera diverged very rapidly after a single colonization event of the Australian continent. Results presented above, using Bayesian analyses of a larger nucleotide data set than was available to Bull *et al.* (2003) also show that these clades are not well resolved and probably diverged rapidly after initially colonizing the Australian continent. Such rapid divergence is not unexpected following colonisation of a new and large landmass, but intra-generic uniformity in life-history features for all three groups suggest that initial and rapid divergence of these features has been followed by relative stasis.

Phylogenetic conservatism in life history traits such as voltinism and brood production schedules is important because these features have the potential to impact strongly on social evolution. Synchronised brood development combined with univoltinism leads to a situation where opportunities for alloparental care are limited, whereas staggered and continual brood development is likely to provide extended opportunities for sib-rearing.

### Evolution of size-based castes

The origin of morphological castes is one of the most critical transitions in social evolution. However, facultative and behavioural castes allow species and individuals capacity to respond to changing circumstances (such as varying resource levels, effects of mortality in small colonies, etc.), whereas pre-imaginal determination of caste membership reduces this flexibility. The evolutionary importance of pre-imaginal caste determination is reflected in recent proposals to restrict the definition of 'eusociality' to only those species exhibiting this trait (Crespi and Yanega, 1995). Pre-imaginal caste determination is usually associated with large colony size, and this may be due to the more predictable conditions that are expected for larger colonies (Wenzel and Pickering, 1991). On the bases of these kinds of arguments, pre-imaginal caste determination may be relatively unexpected in allodapines, which have very small colony sizes compared to many other social insect taxa. Nevertheless, size-based reproductive differentiation occurs in allodapines and this can be quite marked (eg. Schwarz *et al.*, 2005).

For some allodapines, there are no clear relationships between reproductive dominance and body size (eg. Schwarz, 1986; Michener, 1971; Aenmey, 2002) and in many other species

the relationships are very weak and could reflect the advantage that larger body size gives to winning contests for dominance within a colony (Thompson and Schwarz in press). However, there are some species where absolute body size appears to strongly determine reproductive roles. The most clear-cut example is *Exoneurella tridentata* which has morphologically distinct castes (Houston, 1977; Hurst, 2001). However, strong body-size effects have been reported for other species as well. In another Australian allodapine bee, *Brevineura xanthoclypeata*, Tierney *et al.* (1997) found that females below a certain body size never reproduced, leading to effective pre-imaginal determination of caste for at least some females. In a recent study of the Malagasy species *Halterapis minuta*, Schwarz *et al.* (2005) found that reproductively dominant females comprised a distinctly larger size class than non-reproductive females, and that this difference also involved generation membership, whereby older and larger mothers comprised a reproductively active caste while their younger and smaller daughters were likely to be non-reproductive workers. The species above exhibiting clear size-based reproductive differentiation have almost no life history features in common that jointly distinguish them from other allodapines. For example, *Exoneurella tridentata*, *Brevineura xanthoclypeata* and *Halterapis minuta* differ strongly in terms of egg production schedules, colony sizes, and brood provisioning traits. We are unable to identify any clear life-history factors underlying the evolution of size-based reproductive castes. This mirrors developments in the broader field of insect social evolution, where there has not been a clear identification of factors that can explain, by themselves, the evolution of eusociality (Crespi, 1996). If mosaics of selective factors underlay sociality and if these mosaics involve many different factors it might be difficult to identify themes in such mosaics without studies on a very large numbers of taxa.

In summary, we can rule out some life-history factors that were thought to be critical for the evolution of sociality in allodapines, and we can tentatively suggest others that may be important. But it seems that at least the evolution of size-based castes seems to be capricious and not strongly linked to any one set of major life history traits.

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