Kin selection, social polymorphism, and reproductive allocation in ants

Katja Bargum

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Academic dissertation

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This thesis is based on the following articles, which are referred to in the text by their Roman numerals:


II. Bargum, K. & Sundström, L. Colony-level life history trade-offs and reproductive skew in the ant Formica fusca. – Manuscript.


IV. Bargum, K. & Sundström, L. Multiple breeders, breeder shifts and inclusive fitness returns in an ant. – Submitted manuscript.

Contributions

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Summary

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Introduction

Social groups are common across animal species. The reasons for grouping are straightforward when all individuals gain directly from cooperating. For example, in many cooperatively breeding species, larger group size may result in higher survival or foraging success for all members. Accordingly, individuals may help to rear offspring other than their own in order to increase group size (Kokko et al. 2001). However, the situation becomes more complex when helping entails costs to the personal reproduction of individuals. Moreover, such costs are often not equally shared by all individuals, but instead lead to some individuals reproducing less than others. Thus, in cooperatively breeding animals, the division of reproduction (reproductive skew) varies from each individual breeding equally to complete monopolisation by one or a few individuals, as is seen in the eusocial insects. This situation poses an evolutionary puzzle, since altruistic traits that make individuals reproduce less than others should disappear over evolutionary time.

The solution to the puzzle was offered by the realisation that individuals may spread their genes not only through their own reproduction, but also by helping related individuals reproduce (Hamilton 1964). Hamilton’s rule $br > c$ states that a costly behaviour such as helping can spread when the benefits $b$ to the recipient weighted by the relatedness $r$ outweighs the cost $c$ carried by the helper. In the wake of Hamilton’s seminal papers, kin selection theory has been widely and successfully applied to explain cooperation in animal groups, from collaborating microbes (West et al. 2006b) to the evolution of eusociality (Foster et al. 2006; Helanterä & Bargum 2006).

However, kin selection theory also implicitly predicts conflicts when groups consist of non-clonal individuals ($r<1$). Then, individual interests are not perfectly aligned, and each individual is predicted to favour the propagation over their own genome over others. Accordingly, conflicts have been studied at many levels of social complexity, from unicellular organisms to eusocial insect colonies. Emerging research into microbes shows how conflict can disrupt cooperation when genetically non-clonal strains come together (Rainey & Rainey 2003; Velicer 2003). In social insects, differing interests of colony members lead to conflict over reproduction, colony sex ratios, and caste fate (Ratnieks et al. 2006). Indeed, observations on
conflicts and conflict resolution in social insects have provided some of the strongest evidence for kin selection in action (Sundström 1994; Sundström et al. 1996, Ratnieks et al. 2006).

Intra-group relatedness varies from one, when organisms are clonal, through intermediate values where groups consist of extended families, to zero in e.g. male bottleneck dolphin male alliances (Möller et al. 2001). All other factors being equal, this variation is predicted to have implications for the extent of cooperation. For example, in many birds, parents collaborate to raise young. Multiple mating by the female lowers relatedness between the offspring, which some studies show leads to a reduction in cooperation, such as decreased offspring provision by the male (Burke et al. 1989; Neff 2003; Westneat & Stewart 2003). However, cooperation may be upheld if individuals can increase $\Gamma$ by preferentially interacting with their closer relatives in the group (nepotism) (Widdig et al. 2002; Griffin & West 2003; Wahaj et al. 2004). Alternatively, individuals may choose to harm non-siblings over siblings (Pfennig et al. 1994; Evans 1999). Thus, variation in relatedness may have dramatic effects on interactions between individuals.

On the other hand, cooperation will also be influenced by $b$ and $c$, i.e. benefits and costs of cooperation, which are in turn determined by environmental factors such as ecological constraints to leaving the group, and group productivity. For example, individuals may choose to cooperate when the cost for helping is low, as in the long-tailed tit, where individuals help only when their own dispersal is restricted by ecological constraints (Russell 2001). To incorporate all these factors and explain how reproductive inequality can be evolutionary stable across animal systems, an extensive modeling framework of optimal skew has been developed (reviewed in Reeve & Keller 2001). Recent studies have also stressed that helpers may stay in expectation of future fitness benefits, through resource inheritance (Kokko & Johnstone 1999; Ragsdale 1999; Blumstein & Armitage 1999; Michell 2005; Field et al. 2006). Since cooperation is frequently linked to the decision to disperse or not, variation in social structure will be reflected in patterns of population structure and gene flow.

Social insects have proven one of the most successful fields to study kin selection in a variety of social settings. Breeding systems in Hymenoptera (i.e. wasps, bees and ants) range from solitary breeding and temporary associations of cobreeders to eusocial colonies displaying complete division of reproduction between the fertile queen and the permanently sterile worker caste (Sherman et al. 1995). Within eusocial colonies, additional variation is provided by the presence of several reproductive individuals. In many species, the queen mates multiply, which causes the colony to consist of half-sib instead of full-sib workers. Furthermore, in many species colonies contain multiple breeding queens, which further dilutes relatedness between colony members, resulting in lower inclusive fitness paybacks from helping. Evolutionary biology is thus faced with the challenge to answer why such variation in social structure, or social polymorphism, exists, and what the consequences are on the individual and population level.

The main part of this thesis (Chapters I-IV; Fig. 1) takes on this challenge by investigating the dynamics of socially polymorphic ant colonies. The four chapters
investigate the causes and consequences of different social structures. The thesis ends with a theoretical chapter (V) focusing on different social interactions (altruism and spite), and the evolution of harming traits (Fig 1).

In this summary, I will start by introducing the reader to the concept of social polymorphism in ants. Using a kin selection framework, I will point out the potential costs and benefits of different social systems, and define predictions that were tested in this thesis. I will then describe the key results of this thesis as they pertain to the topics discussed. I will end by considering methodological issues raised by this work, as well as future directions towards answering unresolved questions.

1. Social polymorphism in ants: causes and life history consequences

All ants are eusocial and most species contain strictly defined queen and worker castes. Social polymorphism is generated by differences in the number of breeders. In many species, colonies are headed by one singly mated queen. Such a system ensures high fitness payoffs for all individuals in the colony. The queen reproduces to her full potential, without competition from other queens. Additionally, all workers are full sisters and receive high inclusive fitness returns from raising their full siblings.

However, not all ant colonies consist of such simple family units. In many species of ants,

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Box 1. List of terms used in the introduction

<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
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<tbody>
<tr>
<td>Gynes</td>
<td>female sexual offspring (i.e. future queens)</td>
</tr>
<tr>
<td>Monogyny</td>
<td>colonies contain only one queen</td>
</tr>
<tr>
<td>Polygyny</td>
<td>colonies contain several queens</td>
</tr>
<tr>
<td>Monandry</td>
<td>single mating by the queen</td>
</tr>
<tr>
<td>Polyandry</td>
<td>multiple mating by the queen</td>
</tr>
<tr>
<td>Queen turnover</td>
<td>the rate of replacement of queens within a colony</td>
</tr>
<tr>
<td>Reproductive skew</td>
<td>the extent to which reproduction is unevenly shared between queens.</td>
</tr>
<tr>
<td></td>
<td>The more unequal the sharing, the higher the skew</td>
</tr>
<tr>
<td>Sexual offspring</td>
<td>offspring who, in contrast to worker offspring, will mate and reproduce</td>
</tr>
<tr>
<td></td>
<td>(i.e. future queens and males)</td>
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queens are multiply mated (polyandry), or the colony encompasses multiple queens (polygyny) (Hölldobler & Wilson 1977, 1990; Keller 1993b). The degree of polyandry varies between species, from single mating in fire ants to tens of matings in leafcutter and harvester ants (Strassmann 2001; Kronauer et al. 2004; Denny et al. 2004; Rheint et al. 2004), and, albeit less dramatically, within species as well (reviewed in Boomsma & Ratnieks 1996). Similarly, polygyny is often facultative, with queen number varying from one to several hundred either within species and between populations, or even within populations (Hölldobler & Wilson 1977, 1990; Keller 1993b; Sundström et al. 2005). Indeed, in many species, facultative polygyny appears to be the rule, rather than the exception (Bourke & Heinze 1994; Keller 1995; Sundström et al. 2005). We may therefore ask what factors promote and maintain social polymorphism in ants.

Polyandry and polygyny have been suggested to entail several costs and benefits for the parties involved (see Table 1). Both polyandry and polygyny pose a cost to workers because the

**Figure 1.** Main themes of this thesis
increased number of patri- and/or matrilines dilutes relatedness among colony members, and thus reduces inclusive fitness returns for workers. For queens, polyandry may be costly when multiple mating increases energy consumption or predation risk of queens (i.e. Bourke & Franks 1995). Similarly, polygyny poses a cost to resident and joining queens alike, because the per capita reproductive output per queen is usually lower than in monogyne colonies where the queen reproduces to her full potential without competition from other queens (Elmes 1973; Herbers 1984; Keller 1988; Sundström 1995b; but see Walin et al. 2001). However, there may be several benefits to polyandry and polygyny which potentially make up for these costs, and maintain social polymorphism in ant species.

Table 1. Some costs and benefits associated with a) a polyandrous colony structure relative to a monandrous one, and b) a polygyne colony structure relative to a monogyne one, and predictions drawn from these (e.g. Keller 1995; Crozier & Fjerdingstad 2001). Predictions in bold are tested in some form in this thesis.

<table>
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<tr>
<th>Costs</th>
<th>Benefits</th>
<th>Predictions</th>
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<tr>
<td>a) Polyandry</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Queens:</td>
<td>Workers:</td>
<td>Sex ratio changes with mating frequency</td>
</tr>
<tr>
<td>– risky mating</td>
<td>– sex allocation manipulation</td>
<td>Genetic diversity contributes to offspring variability (I, II)</td>
</tr>
<tr>
<td>Workers:</td>
<td>Queens and workers:</td>
<td>Genetic diversity contributes to colony fitness</td>
</tr>
<tr>
<td>– indirect fitness loss</td>
<td>– genetic diversity</td>
<td>One male’s sperm is not enough</td>
</tr>
<tr>
<td>– adequate sperm supply</td>
<td></td>
<td></td>
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<tr>
<td>b) Polygyny</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Queens:</td>
<td>Queens:</td>
<td>Adoption of related queens (colony daughters) (II,III,IV)</td>
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<tr>
<td>– direct fitness loss</td>
<td>– avoiding risky dispersal and colony founding</td>
<td>Reproductive skew according to worker interests (IV)</td>
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<tr>
<td>Workers:</td>
<td>Queens and workers:</td>
<td>Rapid queen turnover (III)</td>
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<tr>
<td>– indirect fitness loss</td>
<td>– colony persistence</td>
<td>Local mating (III)</td>
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<td></td>
<td>– colony productivity</td>
<td>Genetic clustering of colonies within populations (III)</td>
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<tr>
<td></td>
<td>– genetic diversity</td>
<td>Isolation by distance between populations</td>
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<tr>
<td></td>
<td></td>
<td>Higher colony survival (III)</td>
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<tr>
<td></td>
<td></td>
<td>Higher colony productivity</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Genetic diversity contributes to colony fitness</td>
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Benefits of polyandry

Some potential benefits of polyandry are laid out in Table 1. One of the strongest arguments for why colonies may benefit from polyandry is that multiple mating enhances genetic variability (Crozier & Fjerdingstad 2001). If genetic variability is connected to colony fitness, this may offset the reduction in relatedness caused by that same variability. Indeed, the benefit of genetic diversity is one of the main hypotheses to explain the evolution of multiple mating in animals in general (Jennions & Petrie 2000), as well as the evolution of polyandry and polygyny in social insects (Sherman et al. 1988; Schmid-Hempel 1998; Schmid-Hempel & Crozier 1998; Crozier & Fjerdingstad 2001). In accordance with the hypothesis, genetically diverse colonies often have better performance or higher growth rate (Page et al. 1995, Wiernasz et al. 2004). There are several mechanisms that could explain this pattern. Many studies show that genetic diversity benefits the colony through increased parasite resistance (e.g. bumblebees: Baer & Schmid-Hempel 2001; honeybees: Tarpy & Seeley 2006; leafcutter ants: Hughes & Boomsma 2004). Genetic diversity may also prevent negative effects of inbreeding (Crozier & Fjerdingstad 2001) and reduce within-colony conflict over sex allocation (Woyciechowski & Lomnicki 1987; Ratnieks & Boomsma 1995).

Lastly, genetic diversity may lead to larger variation in individual traits within the colony. A genetically diverse colony may produce more variable new queen offspring, which may be a benefit in a variable environment (Crozier & Page 1985), or a more diverse worker force and thus better division of labour (Oldroyd et al. 1993). However, this hypothesis depends on to what extent physiological traits are influenced by genetic versus environmental factors, which remains mostly uninvestigated in social insects (but see Fraser et al. 2000; Hughes et al. 2003, Schwander et al. 2005). Chapters I and II test this hypothesis.

Benefits of polygyny

Polygyny may, for its part, provide benefits for all colony members in the presence of strong ecological constraints on independent breeding (table 1). If dispersal risks are high and subsequent colony founding success low, both workers and resident queens favour the adoption of daughter queens into colonies, since these have low chances of reproducing otherwise (Rosengren & Pamilo 1983; Nonacs 1988; Pamilo 1991a; Keller 1995; Cahan et al. 2002). Similarly, when queen life span is short relative to colony life span, resident queens and workers can gain inclusive fitness returns if adopted daughter queens replace deceased queens (Nonacs 1988). In accordance with these predictions, nestmate queens are often related in polygyne ant species (reviewed in Keller 1995), including our study species F. fusa (Hannonen & Sundström 2003a, Hannonen et al. 2004, II, III). Despite a short-term reduction in personal reproduction, adopted queens stand to gain by avoiding dispersal risks and getting a head start in reproduction, as they can forgo the colony growth phase when no reproductive offspring are produced (Oster & Wilson, 1978).

These considerations allow us to predict that polygyne colonies have longer colony life spans and shorter queen life spans than monogyne
colonies of the same species (Nonacs 1988; Pamilo 1991a). As a result of shorter queen life spans and recruitment of new queens, the rate at which queens are exchanged (queen turnover) should also be higher in polygyne colonies than in monogyne ones (Nonacs 1988). In agreement with this, queen turnover has been demonstrated in polygyne populations (Seppä 1994; Seppä & Walin 1996; Evans 1996; Bourke et al. 1997; Pedersen & Boomsma 1999), whereas colonies in monogyne populations tend to retain the same queen across their entire colony life span (Pamilo 1991b, Sundström 1994, Sundström et al. 2003; but see Heinze & Keller 2000; Sanetra & Crozier 2002). We investigate colony survival and the frequency of queen turnover in chapters III and IV.

**Population-level patterns**

Differences between social forms in dispersal and queen philopatry may be mirrored in the genetic structuring of the population. Monogyne populations are generally outbred with genetically distinct colonies, but with negligible within- and between-population structuring (e.g. Pamilo et al. 1997, Sundström et al. 2005). Conversely, queen philopatry often causes polygyne populations to be characterized by genetically less distinct colonies, but extensive genetic structuring both within populations at a level above individual colonies, and between populations (e.g. Ross 2001, Sundström et al. 2005). Furthermore, if philopatry entails mating within or close to the natal nest, it may lead to increased inbreeding levels in polygyne societies if nestmate (and thus mating partner) relatedness is above zero (Pamilo et al. 1997, Ross 2001).

Studies of genetic and behavioural differences between social forms have generally focused on cases where monogyne and polygyne colonies are confined to different populations, and the level of polygyny is high. Debate reigns, however, over whether similar differences can be expected in populations where the two social forms coexist, and variation in queen number is less extreme (i.e. Chapuisat et al. 2004, DeHeer & Herbers 2004; Sundström et al. 2005; Rosset & Chapuisat, 2006). The studies on populations with a mixture of two social forms suggest that differences typically seen between social forms in allopatry are absent when the two forms occur in sympatry (Chapuisat et al., 2004, Fournier et al., 2004; DeHeer & Herbers, 2004). However, a recent study showed that some life history differences may appear also under panmixis (Rosset & Chapuisat, 2006). We investigate the behaviour and genetic and spatial structuring of social forms in chapter III.

**Individual fitness consequences of polygyny**

In polygyne colonies, the fitness of colony members is also determined by the extent of reproductive skew. Often, reproduction is not shared equally between queens, but instead with a degree of reproductive skew, so that one or a few queens monopolise breeding (Keller 1993b, Bourke & Heinze 1995, Reeve et al. 1998, Hannonen & Sundström 2002, 2003a). The
magnitude and direction of skew will affect all colony members.

Firstly, for individual queens, a strong reproductive skew means that some queens must forsake most of their reproduction. To explain why such reproductive inequality could be evolutionarily stable across animal systems, a modelling framework based on inclusive fitness benefits received by sharing parties has been developed (Keller & Reeve 1994). Models of optimal skew seek to explain division of reproduction by considering factors such as ecological constraints to leaving the group, relatedness of cobreeders and group productivity (reviewed in Reeve & Keller 2001). The plethora of such models that have been developed in recent years (Emlen 1982a,b; Vehrencamp 1983a,b; Reeve & Ratnieks 1993; Keller & Reeve 1994; Reeve & Keller 1995; Reeve et al. 1998; Johnstone & Cant 1999; Johnstone 2000) can be roughly divided into two groups. The transactional models assume that either the dominant (concession models, Reeve & Ratnieks 1993) or the subdominant breeder (restraint models, Johnstone & Cant 1999) controls reproductive sharing, whereas the tug-of-war models (Reeve et al. 1998) view reproductive sharing as an outcome of an ongoing struggle between two parties, both with limited control over sharing.

The predictions of optimal skew models have been tested on a variety of species (vertebrates: Jamieson 1997; Clutton-Brock et al. 2001; Engh et al. 2002; Haydock & Koenig 2002; social insects: reviewed in Reeve & Keller 2001; Fournier & Keller 2001; Hannonen & Sundström 2003a; Paxton et al. 2002; Seppä et al. 2002; Sumner et al. 2002; Langer et al. 2004, 2006), but no clear trend has emerged in favour of a particular model (Reeve & Keller 2001). In this thesis, the predictions of optimal skew models were tested using two factors: relatedness of cobreeding queens and colony productivity (II). Previous research of our study species F. fusca found that relatedness covaried negatively with reproductive skew, which is in line with restraint or tug-of-war models (Hannonen & Sundström 2003a).

Most models of optimal skew look at skew at one point in time only. However, it is possible that reproductive skew fluctuates over time, so that dominant breeders are replaced. This may alleviate the situation for subdominants, because they may gain a chance to reproduce in the future. In many species of polygynous ants, replacement of breeders (queen turnover) is, indeed, frequent (Evans et al. 1996; Pedersen & Boomsma 1999). Accordingly, future fitness benefits are increasingly being incorporated into models of optimal skew (Kokko and Johnstone 1999; Ragsdale 1999).

For workers, reproductive skew may raise inclusive fitness benefits, since a high skew means colony relatedness remains high. However, this is true only if the dominant queen is a close relative of the workers. It has been suggested that workers may act as a “collective dominant” to ensure that their relatives gain reproductive benefits (Reeve & Keller 2001; Reeve & Jeanne 2003). Evidence for such nepotistic actions is rare in social insects, but intriguingly, Hannonen & Sundström (2003b)
found that in F. fusca, workers influence reproductive skew by recognising and favouring their relatives during offspring development.

**Skew in sexual versus worker offspring**

A final issue concerns the division of reproduction into sexual and worker offspring. In social insects, males are produced from haploid eggs and females (queens and workers) from diploid eggs. Caste determination between workers and sexual females is considered to be due to environmental factors, such as the quantity or quality of the food provided to larvae by workers (but see Cahan & Keller 2003; Fournier et al. 2005 for some exceptions). However, from an evolutionary perspective, sterile workers are a dead end. Therefore, competition between queens may be stronger over the production of sexuals than over that of workers, leading to differences in reproductive skew between offspring castes. Such a difference has been found in Pheidole, Myrmica and Solenopsis ants (Fournier et al. 2004; Ross 1988; Ross 1993; Pamilo & Seppä 1994; but see Heinze et al. 2001). This may create a situation where the queens that specialize on sexual production effectively parasitize on those that invest in colony maintenance and produce new workers. Indeed, socially parasitic species (inquilines) are thought to have arisen this way (Bourke & Franks 1991; Heinze & Keller 2000).

A difference in skew between worker and sexual reproduction may also have adverse effects on the inclusive fitness of workers. In Pheidole ants, there is a trade-off between a queen’s production of worker and sexual offspring, so that the queens producing more workers produce less sexuals (Fournier et al. 2004). Thus, reproductive skew may actually decrease, instead of increase, the inclusive fitness benefits for workers. The correlation between sexual and worker skew, and its impact on worker indirect fitness, was tested in chapter IV.

2. Social semantics: Altruism and spite

Recently, several reviews have argued that the language used to discuss social interactions is sometimes confusing, up to the point that it hinders the development of the field (Lehmann & Keller 2006; West et al. 2006a). According to the authors, the semantic confusion partly stems from different fields using different words for the same concepts, and partly from wide-spread terms being ill-suited to begin with (West et al. 2006a). An example of the latter is the term reciprocal altruism acts, which do not really represent altruism since the eventual payback from reciprocity means the act does not bear a cost to the actor on the long term (West et al. 2006a). In the last chapter of this thesis, we join this effort to clarify concepts by investigating two key concepts of social evolution, namely altruism and spite.

According to Hamilton’s original definitions, altruism is defined as an act that helps the receiver while decreasing the fitness of the actor. Spite, i.e. behaviours that harm both the actor and the receiver of the behaviour, has been seen as a phenomenon quite distinct from altruism (Vickery et al. 2003; West et al. 2006a). For a long time, spite was thought unlikely to occur in animals (Keller et al. 1994), but several recent studies have put forward examples of
spiteful interactions (Foster et al. 2000, 2001; Gardner & West 2004a; Gardner et al. 2004), as well as modelled the dynamics of these (Vickery et al. 2003; Gardner & West 2004b, Engelstädter & Charlot 2006).

However, the distinction between spite and altruism is not straightforward. This can be illustrated by an example. A well-known form of nepotism in brood rearing in social insects concerns sex allocation. Due to the haplodiploid sex determination system of social Hymenoptera, workers are more related to female than male offspring and would hence benefit from biasing the sex ratio produced by the colony towards females. Such sex ratio biasing has been observed in several species (Sundström 1994; reviewed in Ratnieks et al. 2006) and is based on workers killing male offspring to gain resources to raise more females (Sundström et al. 1996). Because of its dual nature favouring more related females and harming less related males, this behaviour has been seen as an example of both altruism (Sundström et al. 1996) and spite (Foster et al. 2000, 2001).

Additionally, confusion reigns in that some models of spite incorporate two components when investigating a supposedly spiteful behaviour: one harming less related individuals and another helping more related individuals (Gardner & West 2004). This issue relates to Foster et al.’s (2000, 2001) definition of two kinds of spite: Hamiltonian spite, where the harming is directed towards negatively related individuals, and Wilsonian spite, where harming helps the more related individuals by reducing competition. In chapter V, we attempted to clarify these issues by modelling the fitness effects of altruism and spite, as well as helping and harming behaviours.

3. Material and methods

Study species (I-IV)
Two study species were used in this thesis: the wood ant Formica truncorum (I) and the black ant Formica fusca (II, III, IV). Both these species exhibit variation in social form, both in the extent of multiple mating and multiple queening, and are therefore suited for studies investigating traits in different social systems. Additionally, due to its small colony size and below ground nesting strategy, F. fusca is easily kept under laboratory conditions during experimental work (see also Hannonen 2002; Helanterä 2004).

Field studies (I, III-IV)
To study heritability of size in a natural setting (I), we sampled colonies in two years from a population of F. truncorum in Tvärminne, SW Finland that has been studied over many years (e.g. Sundström 1994; Sundström 1995a,b, Sundström et al. 1996, 2003). To study the causes and consequences of social polymorphism in F. fusca (III, IV), data on the same colonies were obtained over several years from a population located on an island in Siuntio, SW Finland.

Experiments (II)
In chapter II, experiments were conducted to assess the importance of colony productivity on offspring traits as well as on reproductive skew, using laboratory two-queen colonies of F. fusca. The use of laboratory colonies enabled us to manipulate colony productivity as well as reliably assign offspring to either of the queens. Field manipulations are not possible.
in *F. fusca* since colonies are built underground, and easily move if disturbed. Moreover, direct parentage assignment is impossible in field colonies, due to the difficulty of sampling colony queens during the reproductive season when they dwell deep underground. However, queens can be gathered for experimental use before the onset of egglaying in early spring, when the colony aggregates close to the surface to warm up.

**Genetic analyses (I-IV)**

Microsatellites developed for *Formica* ants (Chapuisat 1996; Gyllenstrand et al. 2002) were used for detecting genetic differentiation (III) and kin structure (II, III, IV) as well as determining paternity (I) and maternity (II) of offspring. Microsatellites are powerful tools for analysing such patterns (Queller et al. 1993; Goldstein & Schlötterer 1999).

**Modeling (V)**

In chapter V, the connection between spite and altruism was clarified using an indirect fitness modeling framework. In this method, the inclusive fitness function of a mutant allele is given as a sum of the effects of a focal individual bearing the mutant trait on the fitness of all individuals in the population, weighted by their relatedness to the focal individual. The method is completely congruent with direct fitness modelling (Taylor & Frank 1996; Rousset & Billiard 2000, Taylor et al. 2007). We analytically examined the fitness effects of harming and helping traits. In an example, we investigated the selective pressures for the spread of a harming trait in a subdivided population.

4. Main results and discussion

**Genetic diversity and within-colony variability in *F. truncorum* and *F. fusca* (I, II)**

To look at the effect of genetic diversity on individual traits, we tested whether multiple mating affected the size distribution of workers and queens, and whether size is heritable in *F. truncorum* (I). This was done by comparing monogamous and polyandrous colonies, as well as half-sibs within polygyne colonies. We also looked at how worker size is affected by an extrinsic factor, i.e. the number of workers taking care of larvae in *F. fusca* (II).

In *F. truncorum*, we found a significant and strong heritable component for queen size ($h^2=0.51$) in one year, but not in the other. Similarly, genetic variability increased queen size variation in the year exhibiting size heritability, but not in the other year. The heritability of worker size was low ($h^2=0.09$) and non-significant, and genetic variability did not increase worker size variation.

In *F. fusca*, worker size was strongly influenced by resource levels, so that large colonies produced, on average, 5% larger workers. Queen condition or size had no effect on worker offspring size. This result corresponds to a study in cooperatively breeding meerkats, where maternal characteristics have little influence on pups after weaning, and offspring size is instead determined by colony traits, such as the number of carers available (Russell et al. 2002). These results demonstrate the power of the social environment in determining offspring traits, enabling colonies to adjust the number and size of workers raised according to resource levels.
Overall, our results suggest that in the species we studied, worker size is highly plastic, with environmental factors overshadowing possible heritable effects (see also Hughes et al. 2003; Schwander et al. 2005). This implies genetic diversity is not needed to maintain efficient division of labour. Obviously, our results do not rule out other benefits of genetic diversity, such as parasite resistance or inbreeding avoidance.

Although the genetic component for queen size is potentially strong and enables polyandrous colonies to produce more variable offspring queens, the extent of fluctuation in the estimated heritability between sampling times indicates that often, environmental factors may override genetic ones. Thus, it is unlikely that genetic variation in offspring queen size confers large fitness benefits to polyandrous colonies. In addition, the inconsistency of the estimates highlights the problems of studying heritability in the field, where environmental conditions are not static (Hoffmann & Merilä 1999, Wilson et al. 2006).

*Population-level patterns of social polymorphism and life history traits in F. fusca (III)*

To study the patterns of social polymorphism, we used long-term field data from a field population of *F. fusca* (III, IV). Workers, worker pupae and sexual pupae were sampled from the same nests during two years (1997 and 1999). From genotypes of workers from the first sampling occasion, nests were assigned as monogyne or polygyne. Population genetic methods were used to investigate whether the social form of colonies corresponded with genetic or spatial differentiation. Queen turnover was measured over four generations of workers in both monogyne and polygyne colonies.

Our study revealed no strong pattern of spatial or genetic patterning in the population, or between social forms. However, the young age of our study population prompts us to consider the possibility that the observed pattern may not represent a stable state. One form may come to dominate due to selective pressures, or differences in behaviour may cause partial or total genetic isolation between the two forms (Bourke & Heinze 1994; Ross & Keller 1995; Gyllenstrand et al. 2005; Sundström et al. 2005). On the other hand, the transient and dynamic character of populations of pioneer species such as *F. fusca*, which expand rapidly but persist only for a short time (Savolainen & Vepsäläinen 1988), may prevent the build-up of genetic differentiation between social forms, or prevent the eventual domination of one form altogether. In accordance with this, the populations of *F. fusca* studied to date all encompass a mixture of monogyne and polygyne colonies (Hannonen et al., 2004; Helanterä 2004).

Despite the lack of genetic or spatial differentiation, colony-level behaviours partly conformed to our expectations. Although we did not find a difference in colony survival between social forms, which could be due to the limited sample size, queen turnover differed dramatically between social forms. In the monogyne colonies, queen turnover was absent and the same queen was retained over the whole study period. In the polygyne colonies, we found that queen replacement was frequent between years. In addition, no colonies switched social structure.
in the four years examined. Our results, in conjunction with previous studies (Chapuisat et al., 2004; Fournier et al., 2004; DeHeer & Herbers, 2004, Rosset & Chapuisat, 2006), imply that differences between social forms may appear independently from one another, even when the forms occur in sympathy.

A proximate reason for the differences between social forms in the amount of queen turnover may be that queens in polygynous colonies are in worse condition than queens in monogynous colonies (Ross & Shoemaker 1997; Rüppell et al. 2001a,b). In accordance with this, in F. fusca, queen condition decreases with increasing queen number (II). It may be that this is due to polygynous colonies investing fewer resources into new queens, since many daughter queens can avoid the energetically costly dispersal and colony founding stage and instead remain in the natal colony (Keller 1995; Heinze & Keller 2000). Another possibility is that the lower condition reflects a trade-off for the queens between reproduction and somatic maintenance. In polygynous colonies, competition between queens over reproduction may force queens to invest more into reproduction than they would if breeding alone. If this is the case, queen turnover may be the result of fluctuations in fecundity over time, rather than queen mortality. These possibilities are discussed further in the section on reproductive skew.

**Reproductive skew in F. fusca (II, IV)**

Reproductive skew was the focus of two chapters (II, IV). In chapter II, we tested assumptions of reproductive skew theory in two-queen colonies of the black ant, Formica fusca. We investigated the effect of colony productivity and queen relatedness on reproductive skew by carefully manipulating and measuring productivity. As found in previous studies, reproductive skew varied from equal sharing to complete domination by one queen. Despite large differences in productivity between experimental treatments, we did not find a connection between the extent of offspring sharing between queens and productivity. Reproductive skew was on the same level in both treatments, and did not correlate with colony productivity within treatments. This goes against predictions of transactional models of reproductive skew.

Most surprisingly, queen relatedness, which was previously found by Hannonen & Sundström (2003a) to correlate negatively with reproductive skew, did not have an effect on skew in our study. The main difference between the two studies was that laboratory colonies were collected from slightly different places. This may imply that patterns of reproductive skew vary between populations, making it more difficult to draw general conclusions.

The failure to find support for the models of reproductive skew, as well as the conflicting results compared to earlier studies, lead us to question the applicability of optimal skew theory to our study system. Observed differences in skew patterns between studies of the same species have caused some authors to suggest that optimal skew may function on a larger scale than individual colonies. For instance, in a certain population, most colonies will experience the same ecological conditions, and it may make more sense to correlate the extent of skew with traits of populations or species.
rather than individual colonies (Hannonen et al. 2004; Liebert & Starks 2006).

Alternatively, it may be that models of reproductive skew are not well suited to describe reproductive sharing in highly derived social systems such as polygyne ants. Many of the assumptions of the optimal skew models (i.e. that individuals possess an option to leave the group, as well as accurate information on the reproduction of others, and of surrounding ecological conditions) may not be fulfilled in multiple-queen colonies (Kokko 2003; Liebert & Starks 2006; Nonacs et al. 2006). Thus, we may have to abandon the hope that models of optimal skew will serve as a “unifying framework” (Reeve & Ratnieks 1993; Keller & Reeve 1994) for understanding cooperation across animal systems (Kokko 2003; Leibert & Starks 2006; Nonacs et al. 2006).

On a proximate level, previous studies suggest that initial queen fertility is the key factor influencing who gains reproductive majority (Hannonen et al. 2002; Hannonen & Sundström 2002). Fecundity may fluctuate over time, for instance if it is associated with age (Brian, 1988, Bourke, 1991; Hannonen et al., 2002). Such fluctuations would give rise to a pattern of high queen turnover in colonies, like the one observed in chapter III. This would imply that at any point in time, a colony will consist of queens at their reproductive peak and queens who are either past their reproductive peak or are yet to reach it. The implication of this is that any measure of skew taken at one point in time may not reflect the lifetime reproductive success of individuals. This highlights the importance of incorporating future fitness benefits into reproductive skew (Kokko & Johnstone 1999; Ragsdale 1999).

Finally, the question of skew in different offspring castes was investigated in chapter (IV). Reproductive skew was found to be higher in sexual offspring than in worker offspring (IV). This implies that there may indeed be large fitness differences between queens, with some queens dominating the production of sexuals. However, shifts in breeders across seasons, as observed in chapter III, may alleviate the potential fitness differences between individual queens. Nevertheless, fewer queens produced sexual offspring than worker offspring, which suggests that only a subset of all queens ever come to produce gynes.

Proximately, differences in reproductive apportionment to the two castes could be due to the timing of egglaying. In F. fusca, sexuals are produced from the first eggs laid (pers. obs.). If a subset of queens start egglaying early, these will produce most of the gynes, leaving worker production to the later egglayers. Accordingly, laboratory studies show that reproduction is often highly skewed at the onset of egglaying (R.Ovaska and K. Bargum, in prep.)

Interestingly, the difference in reproductive skew favoured worker interests. Adult workers were significantly more related to the reproductive brood than to the worker brood. As a result, tending workers gained enhanced inclusive fitness returns. The non-random pattern of queen contribution to workers and sexuals raises the critical relatedness between workers and sexuals, thereby promoting colony cohesion.

Two mechanisms could be creating higher relatedness between adult workers and sexuals. Switches could be connected to the age of the queen, so that queens who have already reproduced once (and therefore are mothers of
the current workers) are in a head start position at commencement of egg laying, leading to the observed pattern of higher worker relatedness to gynes. On the other hand, the result is consistent with workers intervening to ensure that the sexuals raised are their close relatives. Such nepotism could be accomplished either by helping queens which are their closest relatives gain a head start, or by raising closely related larvae into gynes rather than into workers.

In conclusion, regardless of whether or not direct nepotism occurs, the system serves the inclusive fitness benefit of workers, in turn alleviating the dilution of relatedness caused by polygyny. An analogous example of this pattern can be found in cooperatively breeding groups of white-winged choughs, where individuals with a consort of relatives more often obtain dominance status than single individuals (Heinsohn et al. 2000). Thus, by serving kin interests, breeding systems including multiple breeders may nevertheless enhance social cohesion.

**Altruism and spite (V)**

In the final chapter, we investigated the dynamics of altruism and spite. From our analysis, it is clear that any trait that reduces the fitness of less related individuals necessarily increases that of related ones. Therefore, from a fitness perspective any behaviour qualifying as spiteful also classifies as altruistic. Additionally, the difference between Hamiltonian and Wilsonian spite disappears: the reduction of fitness for negatively related individuals automatically leads to an increase of fitness for positively related ones. Thus, there is no need for a separate helping component for the behaviour to qualify as Wilsonian, as is sometimes assumed (Gardner & West 2004).

However, this is not to say that both helping and harming cannot occur at the same time. In fact, either is likely to evolve more easily with the help of the other. To return to our original example of sex ratio biasing, harming the male larvae may be favoured already by alleviating resource competition for the female larvae. That workers then help the females by feeding them the males may further strengthen the selection for sex ratio biasing.

Since altruism and spite are two sides of the same coin, chapter V suggests it would be clearer to classify behaviours according to their effect on the direct recipient (i.e. harming or helping). The study further investigated when harming can be selected for. The results suggest that in large populations, helping relatives is favoured over harming non-relatives. This is because helping specifically increases the productivity of kin, while the benefit of reduced competition due to harming is diluted in a large population (Gardner & West 2004b). In contrast, harming is favoured over helping in small populations. In this situation, the reduction of competition caused by harming creates two benefits for the actor (i.e. the individual performing the harming action). Firstly, the actor’s own offspring are more likely to survive (resulting in a direct benefit) and second, relatives of the actor have a higher chance of survival (providing a kin-selected benefit). The combination of both benefits makes harming a more efficient strategy than helping in small populations. Accordingly, the examples of harming traits found in nature are often connected with small effective population sizes (i.e. few gene lineages), such as sex ratio biasing in ants (Sundström 1994; Sundström et al. 1996), or bacteriocine production by bacteria (Gardner et al. 2004).
5. Implications and future directions

Methodological implications

The results of this thesis have some implications for the methodology used in social insect research. The rapid replacements of breeders shown in polygyne colonies of *F. fusca* (III, IV) indicates that measuring the individual fitness of queens may not be a straightforward enterprise. Since all queens may not reproduce at one single point in time, quantifying lifetime reproductive success would require many, rather than one, sampling occasion. Therefore, it may prove interesting to follow a queen throughout her reproductive lifespan. The feasibility of this is further discussed in the section on queen fecundity below.

An additional methodological issue is raised by the finding that the genetic composition of worker offspring differs from that of sexual offspring (IV). This indicates that measures of effective queen numbers, effective population size and reproductive skew gained by using worker offspring does not reflect the pattern of gene flow through the generations, which happens mainly through sexuals. Hence, regardless if we are interested in evolutionary questions of who reproduces, or conservation aspects of how genetic variation is maintained and spread, we should sample sexual offspring instead of workers. However, this raises both practical and ethical issues. Firstly, sexual offspring may not be easily available. In most species of ants, sexual offspring are only present for a short time in the colony. Sometimes, the developmental time of sexual brood stretches over several seasons, and some ant species, like *Formica fusca*, do not regularly produce sexual brood in the laboratory. Secondly, from a research ethical perspective, sampling sexual offspring may have a larger effect on the population than sampling workers. Collecting sterile workers in the field is akin to non-lethal sampling, whereas collecting sexual offspring deprives the population of potential future reproductives.

Unresolved issues

As is the case with all scientific endeavours, the work presented in this thesis raises as many questions as it answers. Below, I discuss a few of these questions, and ponder ways to resolve them through future work.

What determines queen fecundity?

This thesis together with previous work on *F. fusca* suggests that queens vary in their fecundity, and that fecundity is a proximate reason for reproductive domination (Hannonen 2002, II). Natural colonies show frequent queen replacement, and this may also be due to temporal shifts in fecundity (III). This raises the so far unresolved issue of what determines queen fecundity.

Fecundity may be a heritable trait, and subsequently could be studied through a quantitative genetic framework. Although we found a heritable component to queen size in the species *F. truncorum* (I), there was no evidence that queen size or queen condition influenced fecundity in *F. fusca* (Hannonen & Sundström 2002, II). There may, however, be other individual, heritable characteristics that influence fecundity. Overall, introducing a quantitative genetic framework may prove fruitful in social insects, due to comparatively easy sampling, large sample sizes and clear generations (Tsuji 1995; Wiernazs & Cole 2003, I).

Another factor affecting queen fecundity may be queen age. Several studies of cobreeding
vertebrates have shown that age may correlate with fecundity, but tracking the age of insects presents challenges. To study the effect of queen age in *F. fusca* would ideally involve following colonies with queens of known ages over time. However, pilot experiments have revealed the difficulty in introducing new queens into colonies with a species with strong nestmate recognition. A more promising road may lie in utilizing indirect cues to queen age, such as physiological changes in queens, and correlating these to fecundity.

**What is the role of the workers in determining offspring identity?**

Kin selection theory predicts that individuals favour their kin over unrelated individuals. In multiple queen colonies we may therefore expect that workers would favour queens and offspring according to their degree of relatedness to these. Currently, evidence for such nepotism is sparse, but studies on *F. fusca* have indicated that nepotism may, in fact, play a role in offspring production (Hannonen & Sundström 2003b; IV). However, further studies are needed to elucidate whether this is indeed the case, and what the mechanisms of such a choice are. This also raises the question of why the phenomenon has not been demonstrated in other species (reviewed in Keller 1997; Tarpy et al. 2004; Ratnicks et al. 2006).

Firstly, it is worthwhile to note the low impact of nepotism on offspring production in *F. fusca*. Changes are small and relative, i.e. shifts in the identity of eggs versus pupae, or, potentially, between workers and sexual offspring, and therefore possible to distinguish only by comparison. This is in accordance with kin selection theory, which predicts that the benefit of nepotistic acts will be balanced against costs on the colony level, such as decreased colony productivity. Hence, nepotism bearing a large cost (reducing productivity or overt aggression) will be evolutionarily unstable, whereas low-cost changes are more probable (Keller 1997). Thus, studies in other species could benefit from concentrating on looking for small shifts, rather than major effects.

Furthermore, it is important to consider species-specific differences when predicting in which study system we may find nepotism. Nepotism requires recognising differences in relatedness between individuals. However, different social systems may affect the feasibility of such recognition, leading to informational constraints. For instance, chemical analyses show that in *F. truncorum*, half-sibs with different fathers are probably not different enough to enable workers to distinguish between patrilines (Boomsma et al. 2004). Recognition may therefore require that individuals differ in both their paternal and maternal genome as well as through maternal effects, as is the case with offspring of different queens in multiple-queen colonies (Dani et al. 2004). Consequently, nepotism may be more likely in polygynous, rather than polyandric species, such as the honeybee (Tarpy et al. 2004). On the other hand, extreme polygyny may lead to an overload of recognition cues, again making it impossible to distinguish between individuals. Accordingly, in many strongly polygynous species even nestmate recognition is lost, and colonies will raise eggs laid by non-nestmate queens. In these circumstances, lack of nepotism comes as no surprise (DeHeer & Ross 1997; Holzer et al. 2006). Hence, it would seem that to resolve the question of the importance of nepotism in multiple-queen colonies, further studies should concentrate on detecting small nepotistic acts in species with weak polygyny and good recognition systems.
Concluding remarks

In conclusion, this thesis shows that social polymorphism has the potential to affect individual behaviour and traits. However, the thesis also demonstrates that spatial and temporal variation between both populations and environments may affect individual and colony traits, to the degree that results obtained in one place or at one time may not be applicable in other situations. It may thus prove fruitful to investigate the factors which can explain these differences. The accumulating amount of both data and theory opens up opportunities for large-scale spatial and temporal comparisons, as well as meta-analyses and review work (i.e. on reproductive skew: Reeve & Keller 2001; Nonacs et al. 2006). Additionally, we may benefit from focusing on life-history traits and trade-offs to explain variation between individuals. Here, the social insect research could learn from the study of social vertebrates, where such traits have long been studied.

This also raises the issue of pluralism versus synthesis. To what extent can we expect social systems to conform to the same rules? In the effort to bring together many fields, it is important to keep in mind differences in the systems analysed. Sometimes, as in the case of reproductive skew, we may analyse the same phenomenon using many different models, without one model necessarily being superior to others. On the other hand, the case of altruism and spite demonstrates how different terms may be applied to what is essentially the same thing. Hence, the study of social interactions stands before the challenge of simultaneously striving for pluralism and maintaining a unitary framework (Cahan et al. 2002; Lehmann & Keller 2006, West et al. 2006a).

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7. Literature cited


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