

INVITED REVIEW

Molecular ecology of social behaviour: analyses of breeding systems and genetic structure

KENNETH G. ROSS

Department of Entomology, University of Georgia, Athens, Georgia 30602–2603, USA

Abstract

Molecular genetic studies of group kin composition and local genetic structure in social organisms are becoming increasingly common. A conceptual and mathematical framework that links attributes of the breeding system to group composition and genetic structure is presented here, and recent empirical studies are reviewed in the context of this framework. Breeding system properties, including the number of breeders in a social group, their genetic relatedness, and skew in their parentage, determine group composition and the distribution of genetic variation within and between social units. This group genetic structure in turn influences the opportunities for conflict and cooperation to evolve within groups and for selection to occur among groups or clusters of groups. Thus, molecular studies of social groups provide the starting point for analyses of the selective forces involved in social evolution, as well as for analyses of other fundamental evolutionary problems related to sex allocation, reproductive skew, life history evolution, and the nature of selection in hierarchically structured populations. The framework presented here provides a standard system for interpreting and integrating genetic and natural history data from social organisms for application to a broad range of evolutionary questions.

Keywords: breeding systems, genetic structure, kin composition, relatedness, social behaviour, social insects

Received 18 May 2000; revision received 20 September 2000; accepted 20 September 2000

Introduction

Complex social behaviour is a monumental achievement of organic evolution that typically entails the integration of genetically nonidentical individuals into cohesive groups that emerge as new units of selection (Queller & Strassmann 1998; Keller & Reeve 1999). Early studies of the molecular ecology of social organisms focused on broadly defining group membership in genetic terms, a focus rooted in kin selection theory and its emphasis on close relatedness as a factor promoting group cohesion and reproductive altruism. More recently, social organisms have become attractive subjects of study to a wider circle of molecular ecologists because they provide striking examples of diverse, fundamental evolutionary phenomena, many of which are not confined to social taxa. Among these are the effects of breeding and dispersal behaviours on the distribution of

genetic variation (Wade 1985; Ross & Keller 1995; Balloux *et al.* 1998), the action of selection in hierarchically structured populations (Wade & Breden 1987; Kelly 1994; Herbers & Stuart 1996; Sugg *et al.* 1996; Pamilo *et al.* 1997; Linhart 1999), the allocation of resources between growth and reproduction and between the sexes (Bourke & Franks 1995; Crozier & Pamilo 1996), and the interplay of conflict and cooperation in social evolution (Queller & Strassmann 1998; Keller & Chapuisat 1999). Increasingly, studies of these problems require detailed knowledge of the kin composition of social groups, as well as the breeding system responsible for this composition and the genetic structure that is a consequence of it (Box 1).

The breeding system comprises important reproductive characteristics of social organisms, including the number of breeders in a social group, the genetic relationships of these breeders, and the extent of variation in parentage among same-sex breeders (Wade 1985; Ross 1993). These attributes determine the kin composition of a social group by prescribing the number of matriline and patriline

Correspondence: Kenneth G. Ross. Fax: 706–542–2279; E-mail: kenross@arches.uga.edu

Box 1

Properties of the breeding system determine group (colony) kin composition which, in turn, specifies group genetic structure. Formal definitions of these terms are as follows.

Breeding system: number of breeders in a social group (colony), their genetic relationships to one another, and the distribution of reproduction among them (see table below).

Group (colony) kin composition: number and representation of classes of individuals with distinct pedigrees in a colony (kin classes), and the genetic relationships between members of the same and different kin classes.

Group (colony) genetic structure: distribution of genetic variation within colonies (e.g. within and between kin classes) and among neighbouring colonies, often summarized as patterns of relatedness.

Components of the breeding system influencing group (colony) kin composition and genetic structure in social animals

NUMBER OF BREEDERS

Number of breeding females*

Number of breeding males†

GENETIC RELATEDNESS OF BREEDERS

Relatedness of Same-Sex Breeders

Relatedness of breeding females in groups with more than one

Relatedness of breeding males in groups with more than one

Relatedness of Different-Sex Breeders

Relatedness of different-sex breeders that are not mates

Relatedness of mates (level of inbreeding)

VARIATION IN PARENTAGE AMONG BREEDERS (REPRODUCTIVE SKEW)

Maternity skew

Paternity skew

*Represented by queens or, in some instances, workers (mated or unmated) in social Hymenoptera; queens or mated supplementary female reproductives in termites; and resident breeding females in other social groups.

†Represented by stored sperm in females of social Hymenoptera and cooperatively breeding vertebrates with extra-group fertilizations; kings or supplementary male reproductives in termites; and resident breeding males in other social groups.

within the group, the nature of pedigree connections between and within these lines, and the relative frequencies of the different types of pedigree connections (see Boxes 2 and 3). The distribution of genetic variation within and among social groups, and thus the potential for selection to occur at various hierarchical levels, is the result of the kin composition of social groups as well as the characteristic mating and dispersal behaviours that are so often closely connected to the social behaviour (Chepko-Sade & Halpin 1987; Ross & Keller 1995; Crozier & Pamilo 1996; Sugg *et al.* 1996). Recent molecular studies of within-group genetic structure have provided intimate glimpses into the internal structure of social life, particularly in eusocial insects. These studies not only have profoundly enriched our understanding of the natural history of these organisms, they have provided essential empirical foundations for testing predictions of kin selection theory and related theories. Thus, studies of within-group genetic structure have contributed to our understanding of parent-offspring conflict, nepotism, the evolution of mating systems, and the evolution of reproductive partitioning (Bourke & Franks 1995; Crozier & Pamilo 1996; Keller & Chapuisat 1999). Moreover, because of the linkage between social and dispersal behaviours,

studies combining data on breeding systems and among-group genetic structure have contributed to life history theory and discussions of selection in structured populations (Bourke & Franks 1995; Heinze & Tsuji 1995; Sundström 1995; Chapuisat *et al.* 1997; DeHeer *et al.* 1999).

The interrelationships of breeding system properties, colony kin composition, and genetic structure are formally portrayed in an explicit conceptual and mathematical framework (Box 3). This framework is used to obtain insights into group composition and genetic structure by quantifying some breeding system properties from genetic and observational data and inferring other properties indirectly from the equations. While this method has been used predominantly to guide studies of social organization in insects, it can serve as a valuable analytical approach for all social taxa in which group membership is relatively stable and some genetic data are available. Although the framework focuses on 'breeding' systems, breeding need not take place in the context of the social group; that is, breeders of one or both sexes may not be group members, as is the case for males in Hymenoptera and in birds with extra-group fertilizations. In fact, the framework can be used to study groups composed exclusively of nonbreeders, such as larval

Box 2

Distinct types of progeny kin composition in social groups are depicted in Fig. 1, along with breeding patterns giving rise to each type. Each breeding male's genetic contribution is represented as coloured dots set on a coloured background representing a breeding female's genetic contribution. Matrilines are demarcated vertically and patriline horizontally, with the relative size of each compartment indicating the proportionate representation of progeny in each matriline/patriline (reproductive skew). The seven discrete categories shown are distinguished on the basis of number of breeders of each sex and, in cases with multiple breeders of both sexes,

on the basis of number of matings with different partners by breeders of each sex. (Number of male matings refers to matings with females in the social group only.) Categories overlap when multiple male or female breeders in a group vary in their tendency to mate multiply. All seven discrete types of group composition are known from or suspected to occur in a single family of eusocial insects, the ants (Formicidae), although the types involving males mating with several nestmate females occur rarely in these insects (Bourke & Franks 1995; Heinze & Tsuji 1995; Heinze 1999). Within each of the six discrete categories with multiple breeders of one or both sexes, continuous variation in kin composition is generated by variation in the relatedness of breeders and in the reproductive skew.

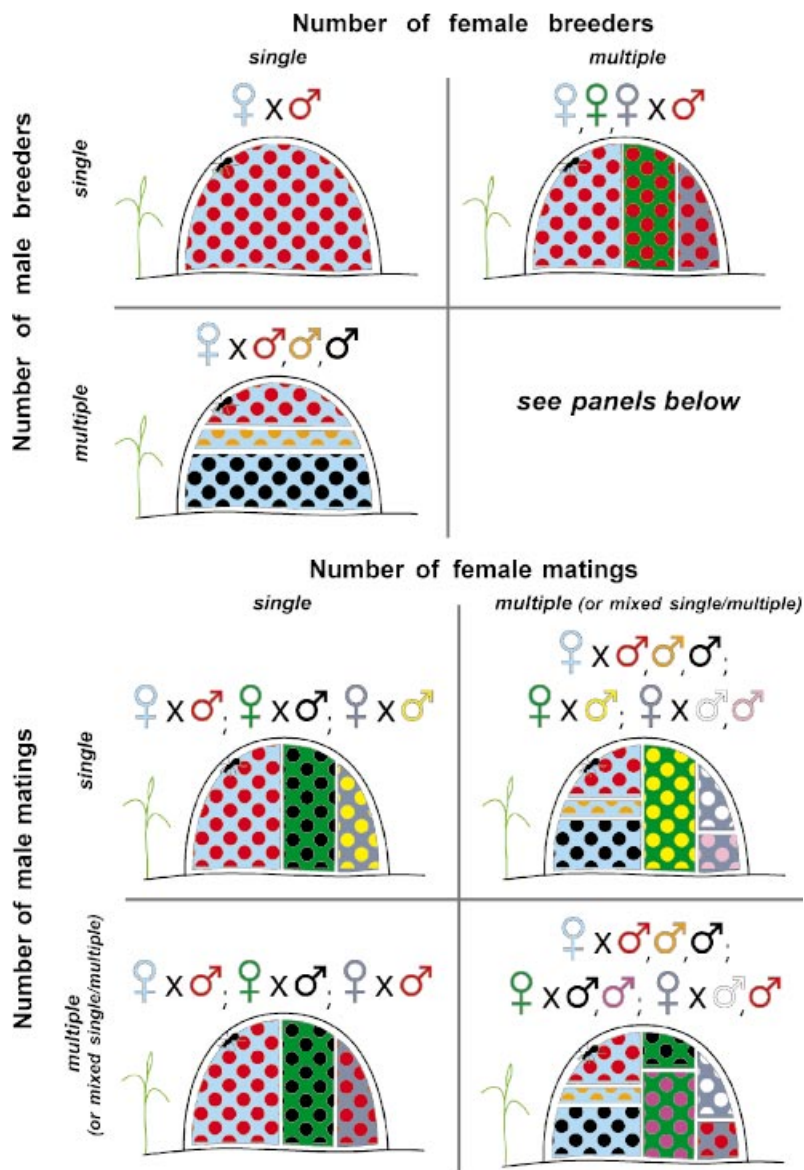


Fig 1

Box 3

The relationships of breeding system components and their effects on kin composition and genetic structure in social groups can be described by the equations presented below (after Wade 1985; Page 1986; Queller 1993; Ross 1993). These equations pertain to relatedness in a single colony for a single generation of diploid progeny with complete sampling of colony members. Modifications of these basic equations for population-level analyses, limited sampling, and haploid male progeny are presented in Pamilo (1993), Queller (1993), Ross (1993), and Boomsma & Ratnieks (1996).

The distribution of genetic variation within and among social groups (group or colony genetic structure) can be summarized as patterns of average genetic relatedness. The average relatedness of diploid progeny in a social group (r_p) is:

$$r_p = r_{sm} \cdot \left(\frac{1}{F}\right) + r_{dm} \cdot \left[\frac{(F-1)}{F}\right], \quad (1)$$

where F is the number of female breeders, r_{sm} is the average relatedness of progeny belonging to the same matriline, and r_{dm} is the average relatedness of progeny belonging to different matriline. This equation shows that the average relatedness in a group is the sum of within- and between-matriline relatednesses, weighted by the relative frequency of occurrence of within- and between-matriline pedigree links. The equation is valid only if the breeding females in a group reproduce equally, that is, there is no skew in maternity. If such skew exists, then F is replaced by the effective number of female breeders (F_e):

$$F_e = \frac{F}{(F^2 \cdot \sigma_F^2 + 1)}, \quad (2)$$

where σ_F^2 is the variance in maternity apportionment in the group. If only one breeding female is present, then $F_e = F = 1$, and from Eqn 1, $r_p = r_{sm}$.

The relatedness of members of different matriline in Eqn 1 can be broken down into the sum of three terms specifying how these individuals are related through their mothers and/or fathers:

$$r_{dm} = \left(\frac{r_f}{4}\right) + \left(\frac{r_{m1}}{2n}\right) + \left(\frac{r_{fm}}{4}\right), \quad (3)$$

where r_f is the average relatedness of the female breeders, r_{m1} is the relatedness of the male breeders that inseminated these females, r_{fm} is the relatedness of different-sex breeders that are not mates, and n is the ploidy level of males (cf. Ross 1993). If one male inseminates all of the female breeders in a group, then $r_{m1} = 1$.

The equation for the relatedness of members of the same matriline (r_{sm}) when female breeders mate multiply is analogous in form to Eqn 1 for the relatedness of all progeny when there are multiple female breeders:

$$r_{sm} = r_{sp} \cdot \left(\frac{1}{M}\right) + r_{dp} \cdot \left[\frac{(M-1)}{M}\right], \quad (4)$$

where M is the number of mates per female breeder, r_{sp} is the average relatedness of progeny belonging to the same patriline (full siblings), and r_{dp} is the average relatedness of progeny belonging to different patrilines (maternal half siblings)*. In this case, the equation shows that the average relatedness of siblings is the sum of within- and between-patriline relatednesses, weighted by the relative frequency of occurrence of within- and between-patriline pedigree links. Maternal half siblings may be related through their fathers as well as their mother if the males mating with a breeding female are related to one another. Thus, r_{dp} can be broken down into the sum of two terms:

$$r_{dp} = 0.25 + \left(\frac{r_{m2}}{2n}\right), \quad (5)$$

where r_{m2} is the average relatedness of the mates of a single breeding female and n is the ploidy level of males (the value of 0.25 represents the maternal genetic contribution to siblings). Eqn 4 is valid only if the mates of a female sire her offspring in equal proportions, that is, there is no skew in paternity. If such skew exists, then M is replaced by the effective number of male mates (M_e):

$$M_e = \frac{M}{(M^2 \cdot \sigma_M^2 + 1)}, \quad (6)$$

where σ_M^2 is the variance in paternity apportionment for a single female's offspring†. This equation is analogous to Eqn 2 for the effective number of breeding females. If females mate with only a single male, then $M_e = M = 1$, and from Eqn 4, $r_{sm} = r_{sp}$.

Relatedness between mates (inbreeding) tends to inflate group relatedness by affecting values of r_{sp} (the relatedness of full siblings). When inbreeding is detected, the pedigree value of r_{sp} (0.5 under male diploidy and 0.75 under male haploidy) can be adjusted at least approximately to yield \hat{r}_{sp} , the inbreeding-corrected value of r_{sp} :

$$\hat{r}_{sp} = r_{sp} \cdot \left[1 - \frac{2F_{IS}}{(1+F_{IS})}\right] + \frac{2F_{IS}}{(1+F_{IS})}, \quad (7)$$

where F_{IS} is the coefficient of inbreeding (Pamilo 1985; panmictic index of Templeton & Read 1994). The value

of r_{sp} also can be corrected for inbreeding by estimating the relatedness between mates (e.g. Sundström 1993; Husseneder *et al.* 1999; Goodisman *et al.* 2000; Krieger & Keller 2000).

The equations above can be consolidated into the single equation:

$$r_p = \left\{ r_{sp} \cdot \left[1 - \frac{2F_{IS}}{(1+F_{IS})} \right] + \frac{2F_{IS}}{(1+F_{IS})} \right\} \cdot \left[\frac{(M^2 \cdot \sigma_M^2 + 1)}{M} \right] + \left[0.25 + \left(\frac{r_{m2}}{2n} \right) \right] \cdot \left[1 - \frac{(M^2 \cdot \sigma_M^2 + 1)}{M} \right] \cdot \left[\frac{(F^2 \cdot \sigma_F^2 + 1)}{F} \right] + \left[\left(\frac{r_f}{4} \right) + \left(\frac{r_{m1}}{2n} \right) + \left(\frac{r_{fm}}{4} \right) \right] \cdot \left[1 - \frac{(F^2 \cdot \sigma_F^2 + 1)}{F} \right], \quad (8)$$

which shows how the average progeny relatedness in a group (r_p) is influenced by the number of male breeders, number of female breeders, reproductive skew, relatedness of breeders, and relatedness of mating partners (inbreeding) – the components of the breeding system. These components, as well as mating patterns and crucial relatedness parameters, are depicted in Fig. 2 for a social group with complex kin composition. Each breeding male's genetic contribution is represented as coloured dots set on a coloured background representing a breeding female's genetic contribution. Matriline

are demarcated vertically and patriline horizontally, with the relative size of each compartment indicating the proportionate representation of progeny in each matriline/patriline.

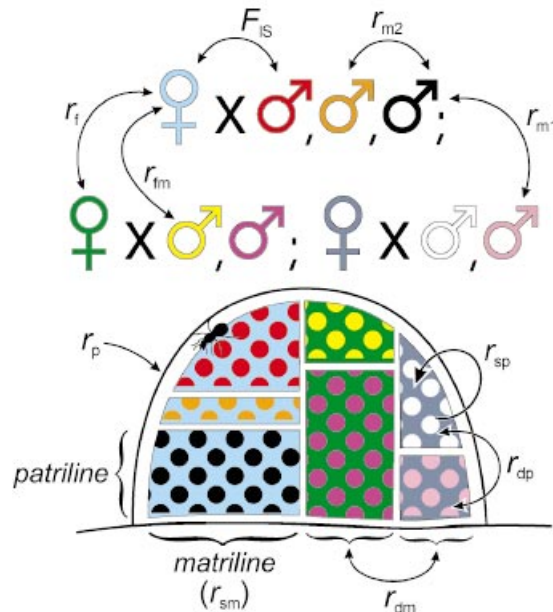


Fig 2

Variables representing relatedness components of the breeding system as shown in Fig. 2.

r_p : relatedness of diploid progeny in a social group

r_{sm} : relatedness of progeny belonging to the same matriline

r_{dm} : relatedness of progeny belonging to different matrilines

r_f : relatedness of female breeders

r_{m1} : relatedness of male breeders that are not mates of a single breeding female

r_{fm} : relatedness of different-sex breeders that are not mates

r_{sp} : relatedness of progeny of a single female belonging to the same patriline

r_{dp} : relatedness of progeny of a single female belonging to different patrilines

r_{m2} : relatedness of male breeders that are mates of a single breeding female

F_{IS} : coefficient of inbreeding (relatedness of mates)

*When a group contains multiple female breeders that mate with differing numbers of males, M in Eqn 4 becomes the harmonic mean number of mates per female (M_h).

†When a group contains multiple female breeders that mate with differing numbers of males, Eqn 6 becomes $M_e = M_h / (M_h \cdot m\sigma_M^2 + 1)$, where M_h is the harmonic mean number of mates per female and $m\sigma_M^2$ is the mean of the number of mates times the paternity variance for each female.

societies of insects (McCauley *et al.* 1988; Costa & Ross 1993; Wade 1994).

The most commonly used metric summarizing the distribution of genetic variation, and hence the kin composition, in social groups is the coefficient of relatedness (r), which

gauges the genetic similarity of focal individuals relative to a reference population (Crozier & Pamilo 1996). The framework described here reveals how the breeding system determines the average relatedness of group members and, thus, the opportunity for selection to occur at the level of

the social group (Wade 1985; Wade & Breden 1987). However, perhaps more importantly, analyses using this framework show how the breeding system sets patterns of relatedness within social groups — that is, how it determines genetic similarity within and between different classes of colony-mates. This information is essential for discerning lines of genetic congruence and conflict of interest and for understanding how cooperation and conflict interact to structure social life (Ratnieks & Reeve 1992; Queller & Strassmann 1998; Keller & Chapuisat 1999; Keller & Reeve 1999).

Many breeding system properties — for example, the number of breeders and the reproductive skew — are expected to be subject to strong ecological selection (Keller & Reeve 1994; Ross & Keller 1995). However, it is important to realize that, through their effects on colony genetic structure, these properties are also subject to strong social (kin) selection (Pamilo *et al.* 1997; Herbers & Benschbach 1999). Moreover, the form of the breeding system can be strongly constrained by features of the reproductive physiology and life history. In most ants, for instance, spermatogenesis and migration of sperm to the ejaculatory ducts is completed long before males mature as adults; thus, ant males typically are limited to a single insemination attempt, and colony composition involving single males siring the offspring of several nestmate females is extremely rare in this group of insects (e.g. Heinze 1999).

I review here recent molecular genetic studies of animal social groups, employing the perspective of the analytical framework described above to organize data derived principally from eusocial insects. Several hundred studies using molecular markers have investigated the kin composition and genetic structure of colonies of ants, termites, social bees and wasps, and other social insects (reviewed in Gadagkar 1991; Ross & Carpenter 1991a; Bourke & Franks 1995; Crozier & Pamilo 1996; Pamilo *et al.* 1997). These studies often are remarkably comprehensive, owing to the fact that, in many social insects, colonies are abundant and can be destructively sampled. This research has revealed enormous variation in the genetic make-up of colonies that reflects parallel variation in kin composition — from simple families composed of a single pair of parents and full-sibling offspring, to highly genetically heterogeneous, genealogically complex, multifamily societies. Estimates of average genetic relatedness for female colony-mates accordingly span an enormous range of values, from zero to over 0.75 (the expected pedigree relatedness value for full sisters with male haploidy). A primary focus of much of this work has been to disentangle the roles of various breeding system components in generating the observed colony genetic structure. Insights into breeding systems and colony structure gained by this approach subsequently have been used to test and extend kin selection and related theories (Bourke & Franks 1995; Crozier & Pamilo 1996; Queller & Strassmann 1998; Keller & Chapuisat 1999).

Number of breeders

The genetically simplest societies comprise families headed by a single breeding female and male — the archetypal simple Hamiltonian families in which indirect fitness benefits of alloparenting are maximal. Genetic evidence for such families comes from simple Mendelian patterns in offspring genotype distributions and/or estimated average progeny relatedness values indistinguishable from those expected for full siblings. Simple-family societies exist in a variety of cooperatively breeding birds and mammals (Emlen 1991; Lehman *et al.* 1992; Jarvis *et al.* 1994; Ligon 1999), wood-dwelling 'subsocial' insects (Choe & Crespi 1997), and eusocial shrimps (Duffy 1996; Duffy & Macdonald 1999), as well as eusocial insects (Ross & Keller 1995; Crozier & Pamilo 1996), although recent molecular studies suggest that they are not as commonplace as earlier believed (Avisé 1994; Ross & Keller 1995; Pamilo *et al.* 1997; Hughes 1998).

In social Hymenoptera, breeding females typically are members of a morphologically or behaviourally distinct queen caste (workers may reproduce more or less regularly in some taxa; Bourke 1988). Males generally are short-lived and play no prominent role in colony life. Sperm are stored for long periods by queens after mating early in life in a special organ (spermatheca), so issues of paternity of colony members arise continuously, even after prospective fathers are long dead. Thus, while the number of breeding females (queens) per colony often can be deduced from observational or dissection data, the number of matings per queen can be inferred reliably only from genetic data (Boomsma & Ratnieks 1996). The predominance of simple-family social groups headed by a once-mated queen (or rarely, a worker) has been confirmed genetically in several taxa of bees (Crozier *et al.* 1987; Packer & Owen 1994; Estoup *et al.* 1995; Peters *et al.* 1999; Schmid-Hempel & Schmid-Hempel 2000), some vespid wasps (Ross & Carpenter 1991a; Arévalo *et al.* 1998; Foster *et al.* 1999, 2000), and several ants (Benschbach & Herbers 1996a; Gadau *et al.* 1996; Sasaki *et al.* 1996; Heinze *et al.* 1997; Ross *et al.* 1997; Satoh *et al.* 1997; Foitzik & Heinze 1998; Herbers & Mouser 1998; Villesen *et al.* 1999; Foitzik & Herbers 2000; Fraser *et al.* 2000) (also Bourke & Franks 1995; Crozier & Pamilo 1996). Simple-family colonies may be characteristic of entire species or larger clades but, at least in ants, they often occur in mixed populations also containing colonies with more complex structure. Also, infrequent events such as occasional multiple mating by queens, superseding of the mother queen, or worker parentage of males can lead to variability in colony composition even in populations or species regarded as quite uniformly comprising simple families. Finally, simple families in some instances constitute transitional stages in a colony life history that features a more complex structure at other times (Herbers & Stuart 1996; Hastings *et al.* 1998). Thus, temporal variation in breeding systems is an important

factor to be considered in analyses of group composition and genetic structure (below).

Colonies of termites contain morphologically distinct egg-laying queens and breeding males (kings) or distinct replacement reproductives of both sexes; breeding males in this order of eusocial insects are long-lived cohabitants with breeding females. Simple-family colonies headed by the founding queen and king are common, although in many instances colony composition becomes more complex later in development, especially in termites that form multiple-nest (polydomous) colonies (Shellman-Reeve 1997). Genetic studies of termites are few, but the common occurrence of simple families has been inferred by use of nuclear or mitochondrial DNA (mtDNA) markers in several species (Atkinson & Adams 1997; Thompson & Hebert 1998; Husseneder *et al.* 1999).

Multiple breeding females

Societies with multiple breeding females are well known in a variety of noninsect social taxa, including several bird species, banded mongooses, various primates, lions, and most social spiders (Emlen 1991; Packer *et al.* 1991; Morin *et al.* 1994; Avilés 1997; Cockburn 1998; Hughes 1998; Cant 2000). In eusocial insects, the common occurrence of multiple breeding queens in single nests is also well established (Keller 1993; Bourke & Franks 1995; Crozier & Pamilo 1996). Multiple-queen social insect nests may occur along with single-queen nests within species or populations (that is, stable polymorphisms in social organization may exist), or the presence of multiple queens may represent a stage in colony ontogeny. Multiple-queen colonies may be effectively nonexistent in some large clades, such as apid bees and some genera of ants and vespine wasps (Ross & Carpenter 1991b); on the other hand, they may be characteristic of other large clades, such as the wasp tribe Epiponini (Jeanne 1991). Questions concerning the evolutionary origin and maintenance of multiple-queen societies have long occupied centre stage among social insect biologists, while interest in the population-genetic consequences of this social organization has only begun to develop more recently (Ross & Keller 1995; Pamilo *et al.* 1997). These two sets of issues are linked to two more fundamental evolutionary problems, the origin of sociality and the nature of selection in hierarchically structured populations.

Genetic variation among offspring is expected to increase, and relatedness to decrease, when a second female breeder is added to a social group ($F > 1$), because a new class of relationships between progeny not sharing a mother appears (see Boxes 2 and 3). As the number of female breeders increases, within-matriline pedigree links decrease in frequency relative to between-matriline links, with higher-value r_{sm} links substituted by lower-value r_{dm} links. This dilution of relatedness with additional female breeders

has been demonstrated in comparative genetic studies of conspecific ant populations composed of single-queen or multiple-queen colonies (Ward 1983; Stille *et al.* 1991; Sundström 1993; Seppä 1994; Heinze *et al.* 1995a; Banschbach & Herbers 1996a; Herbers & Stuart 1996; Ross *et al.* 1997). It has been shown further in ants that relatedness is negatively associated with the population-wide average colony queen number (Seppä & Walin 1996), and at least two studies have demonstrated that relatedness in single nests decreases with increased queen number (Ross 1993; Heinze *et al.* 1995b). The presence of multiple female breeders is important not only because it decreases average progeny relatedness, but also because it generates potential genetic conflict between members of different matriline, which may be expressed, for example, as nepotism or as 'policing' by workers during brood rearing in social Hymenoptera (Bourke & Franks 1995; Keller & Chapuisat 1999). The magnitude of such potential conflict is determined by the disparity in relatedness within and between matriline, which is affected by other breeding system properties (number of matings by, and relatedness of, cohabiting female breeders).

Average relatedness for workers in colonies of social Hymenoptera with multiple queens has been found to vary from zero to almost 0.75 (Heinze 1995; Herbers & Stuart 1996; Seppä & Walin 1996; Seppä 1996; Ross *et al.* 1997; Satoh *et al.* 1997; Hastings *et al.* 1998; Chapuisat & Keller 1999a; Pedersen & Boomsma 1999a; Krieger & Keller 2000; see also Crozier & Pamilo 1996). Reasons for this large range of values include not only variation in the number of queens, but also variation in two other breeding system properties, relatedness of the queens and extent of maternity skew (queen mating frequency generally is a less important factor; Boomsma & Ratnieks 1996; Goodnight *et al.* 1996). Thus, genetic studies of multiple-queen societies often evaluate all three properties concurrently; additional reasons for wishing to understand their effects on genetic structure stem from theoretical considerations of the evolution of multiple-queen societies, outlined briefly as follows.

The reduction in progeny relatedness (r_p) associated with adding queens to established colonies implies a parallel reduction in indirect fitness benefits to workers rearing the brood; that is, there are apparent selective costs to workers in tolerating multiple nestmate queens. Thus, much effort has been devoted to learning what fitness benefits may accrue to colony members to offset these costs (see Keller 1993; Bourke & Franks 1995; Crozier & Pamilo 1996). Current explanations typically invoke ecological factors. In epiponine wasps and termites, multiple queens may be needed to support high egg-laying rates necessary to sustain large, successful colonies (Jeanne 1991; Thorne *et al.* 1999). In ants, ecological constraints on nest-founding by solitary queens, including high levels of predation and nest site limitation, often are invoked as the primary evolutionary

factors favouring the recruitment and retention of multiple queens per colony (Bourke & Franks 1995; Ross & Keller 1995; Seppä *et al.* 1995; Herbers & Benschbach 1999; Pedersen & Boomsma 1999a). These constraints can be viewed as analogous to the selection pressures originally favouring group living over solitary breeding, so that theoretical concerns about the evolution of multiple-queen societies in many respects parallel those raised by the origin of social life (Bourke & Franks 1995; Keller 1995).

Kin selection theory predicts that selection favouring acceptance of supernumerary queens will depend on details of the breeding system and genetic structure, such as the relatedness between different classes of nestmates and the extent of inbreeding (Crozier & Pamilo 1996). In all cases, acceptance is most likely when potential new queens are relatives of existing colony members, as they would be, for instance, if they were daughter queens reared in the colony. This single theoretical conclusion leads to two important predictions. First, queens in multiple-queen societies should be philopatric. This implies a shift in dispersal and mating behaviours from the long-distance dispersal and mating on the wing characteristic of many single-queen social insects (Keller 1995; DeHeer *et al.* 1999) and the emergence of local genetic structure possibly relevant to the action of natural selection (Kelly 1994; Bourke & Franks 1995; Benschbach & Herbers 1996b). Second, queens in multiple-queen societies should be significantly related to one another (and, by extension, to the workers that reared them), with consequences for resulting within-colony relatedness patterns. These predictions have been tested in a large number of genetic studies (below). These same studies also have contributed to a general understanding of colony composition and genetic structure, which in turn has stimulated further development of theory to explain details of colony organization and social behaviour in multiple-queen societies (e.g. reproductive skew and sex allocation theories).

Multiple breeding males

Multiple breeding males, represented by group residents or by the sperm of nonresident males stored by resident females, are common in diverse vertebrate societies (Emlen 1991; Balloux *et al.* 1998; Cockburn 1998; Hughes 1998; Ligon 1999; Cant 2000; Worthington Wilmer *et al.* 2000), social spiders (Avilés 1997), termites with supplementary reproductives (Shellman-Reeve 1997), and eusocial thrips (Kranz *et al.* 1999). In most of these cases, multiple male breeders co-occur with multiple female breeders, but even in such a situation each female may mate with and use the sperm of only a single male (monandry) (see Box 2; also Emlen 1991; Cockburn 1998).

In eusocial Hymenoptera, multiple male parentage ($M > 1$) can occur in association with monandry when

multiple queens inhabit single nests [e.g. fire ants (Ross & Keller 1995) and epiponine wasps (Goodnight *et al.* 1996)]. However, far more attention has been paid to the occurrence of multiple male breeders that results from multiple matings by queens (polyandry). Polyandry is widespread in social Hymenoptera (Boomsma & Ratnieks 1996; Crozier & Pamilo 1996), although, as is also true for multiple maternity, it is rare in some clades [e.g. stingless bees (Peters *et al.* 1999) and fire ants (Ross *et al.* 1988)] and there may be variation within populations in its occurrence (Boomsma & Ratnieks 1996; Seppä & Walin 1996; Chapuisat 1998; Fjerdingstad *et al.* 1998; Bekkevold *et al.* 1999; Paxton 2000). In one major respect, polyandry is of interest for much the same reason as multiple female breeders: its occurrence changes the distribution of genetic variation and decreases average relatedness (r_p) within social groups. Polyandry introduces a new class of progeny related as half-siblings rather than full-siblings and, as the level of polyandry increases, the frequency of within-patriline pedigree links decreases relative to between-patriline links, with higher-value r_{sp} links substituted by lower-value r_{dp} links (see Boxes 2 and 3). Thus, as is the case with multiple queens, polyandry influences the potential for colony-level selection and for within-group conflict, with the latter possibly manifested as nepotism, worker policing of reproduction, or biased patterns of sex allocation (in Hymenoptera). On the other hand, explanations for the evolution of polyandry tend to differ from those for multiple-queen colonies in that they often emphasize the potential selective benefits of increased genetic diversity within colonies (Boomsma & Ratnieks 1996; Crozier & Pamilo 1996).

The occurrence of polyandry and its effects in decreasing offspring relatedness have been shown in genetic studies of single-queen hymenopteran colonies in the field and laboratory. In a few cases, the number of queen matings has been explored by genotyping sperm in the queen's spermatheca (Peters *et al.* 1995; Gadau *et al.* 1996; Goodnight *et al.* 1996; Arévalo *et al.* 1998; Chapuisat 1998; Haberl & Tautz 1998; Hastings *et al.* 1998; Krieger & Keller 2000), a technical feat made possible by the sensitivity of the polymerase chain reaction (PCR) for amplifying small amounts of DNA and the fact that individual males' spermatozoa are genetically identical (because of male haploidy). Levels of polyandry vary widely in social Hymenoptera and can differ strongly even among populations of single species (Boomsma & Van der Have 1998). Some facultatively polyandrous ant queens seldom mate with more than two males (Chapuisat 1998; Pedersen & Boomsma 1999b; also Boomsma & Ratnieks 1996), whereas queens in several honey bee species (genus *Apis*) routinely mate with over 10 males (Lobo & Kerr 1993; Estoup *et al.* 1994; Haberl & Moritz 1994; Moritz *et al.* 1995; Oldroyd *et al.* 1995, 1997, 1998; Haberl & Tautz 1998). Intermediate numbers of matings by queens are found in some leaf-cutter ants (Reichardt & Wheeler 1996; Fjerdingstad

et al. 1998; Boomsma *et al.* 1999) and yellowjacket wasps (Ross 1986; Goodisman *et al.* 2000). Polyandry in social Hymenoptera results in average relatedness values for sisters that range from close to 0.75 when few males contribute very unequally to paternity (Boomsma & Ratnieks 1996; Seppä & Walin 1996; Foster *et al.* 1999) to near the theoretical minimum of 0.25 in highly polyandrous honey bee species (Estoup *et al.* 1994; Oldroyd *et al.* 1997, 1998).

The occurrence of polyandry modifies the potential for within-colony conflict by affecting relatedness patterns. In social Hymenoptera, a clear example of the outcome of this conflict is the manipulation of sex ratios in single-queen colonies with sterile workers. Workers' average relatedness to female brood decreases with a switch from single to multiple paternity, while their relatedness to male brood is unchanged (because of male haploidy). Workers are, therefore, expected to produce more male-biased sexual broods when queens mate multiply than when they mate singly (Crozier & Pamilo 1996; Chapuisat & Keller 1999b), a prediction demonstrated in diverse taxa (Queller & Strassmann 1998). Conflict between the queen and collective worker force is reduced under polyandry because workers' preferred sex allocation approaches the equal allocation favoured by the queen (who is equally related to her sons and daughters). On the other hand, polyandry increases the potential for conflict between workers of different patrilineages regarding the rearing and treatment of new female sexuals, because workers potentially can favour more closely related full-sisters over less closely related half-sisters. Despite extensive study, however, there is little empirical evidence to indicate that such potential conflict is translated into actual nepotism of this form in social insects (Keller 1997).

In addition to the usual reasons cited for why female animals may mate multiply, polyandry may evolve in social taxa for reasons directly related to their social behaviour (Boomsma & Ratnieks 1996; Crozier & Pamilo 1996). For instance, queens of social Hymenoptera may mate repeatedly in order to acquire enough sperm to fertilize the large number of eggs needed to sustain populous colonies over long periods (Cole 1983). This hypothesis is unlikely to be general because many large-colony species are monandrous, and individual males in some polyandrous species produce enough sperm to fully inseminate queens (cf. Fjerdingstad & Boomsma 1998). A speculative hypothesis is that polyandry is favoured in Hymenoptera because, as described above, it can reduce potential conflict between queens and workers over patterns of sex allocation and the maternity of males (Ratnieks & Boomsma 1995; Chapuisat & Keller 1999b). One increasingly popular set of hypotheses for polyandry relies on suggested benefits of increased genetic diversity (Crozier & Page 1985; Bourke & Franks 1995), in terms of enhancing division of labour or parasite resistance, or in minimizing the detrimental effects of sterile-

male production‡. The first of these requires a genetic basis to worker task performance thresholds, a supposition for which there is mounting evidence (Pamilo *et al.* 1997). Support for the importance of polyandry and genetic diversity for colony fitness recently has been offered for single-queen bumble bees and harvester ants, in which colony growth rates, productivity, or survival are positively associated with number of queen matings and diversity of the worker force (Baer & Schmid-Hempel 1999; Cole & Wiernasz 1999). A final explanation for polyandry is that it is merely an unselected consequence of changes in mating location that reduce the cost of re-mating (Pedersen & Boomsma 1999b). Future genetic studies of appropriate focal taxa will help shed light on how colony kin structure in different lineages has been altered historically by changes in queen mating frequency (Oldroyd *et al.* 1998; Foster *et al.* 1999; Villesen *et al.* 1999), with such results informing broader evolutionary discussions such as those pertaining to the evolution of sex (Kraus & Page 1998).

Turnover of breeders

Group composition in many social organisms is not static. Older breeders senesce and die, or may be challenged by subordinates, and new breeders replace or augment previous breeders. In social vertebrates, such new breeders may be helpers long resident in the social group or they be recent immigrants from other social groups (Emlen 1991; Ligon 1999). In social spiders, termites, and social thrips, breeder turnover typically involves supplementary breeders of both sexes produced in the colony (Atkinson & Adams 1997; Avilés 1997; Shellman-Reeve 1997; Kranz *et al.* 1999; Thorne *et al.* 1999), whereas in social Hymenoptera it generally involves mated queens that may or may not have been reared in the colony. Breeder turnover is important because it adds another, temporal variable affecting colony genetic structure, which may considerably complicate theoretical and empirical analyses of breeding system properties such as reproductive skew (e.g. Ross 1993; Field *et al.* 1998; see also Costa 1998).

In primitively eusocial Hymenoptera, in which queen/worker caste dimorphism is weak and behavioural dominance hierarchies govern reproductive roles, superseding queens (sometimes by mated workers) can be common throughout colony development (Kukuk *et al.* 1987; Packer & Owen 1994; Strassmann *et al.* 1994; Richards *et al.* 1995; Field *et al.* 1998). In the epiponine wasps and some ants with multiple-queen colonies, bouts of recruitment of new queens are tied to cyclical or seasonal reductions in the number of old queens (Keller *et al.* 1989; Hastings *et al.*

‡This latter hypothesis is restricted to social Hymenoptera with complementary sex determination, in which diploid zygotes homozygous at the sex-determining loci develop into sterile males.

1998). Queen turnover in ants and wasps has been inferred from unexpectedly high colony genetic variation (relative to the number of resident queens found), the presence of colony members with genotypes incompatible with maternity by the resident queens, or comparison of genotype distributions within and between offspring age cohorts (Seppä 1994, 1996; Banschbach & Herbers 1996a; Evans 1996; Seppä & Walin 1996; Bourke *et al.* 1997; Field *et al.* 1998; Pedersen & Boomsma 1999a).

Turnover of male breeders in social Hymenoptera, where queens store sperm for long periods, can occur via sequential or fluctuating use of the sperm of different mates by polyandrous queens. If the timescale of such sperm turnover is sufficiently long, relatedness between workers and the brood they rear can be considerably increased relative to random use of all sperm in the spermatheca (Crozier & Brückner 1981; Boomsma & Ratnieks 1996). However, genetic studies of sequential offspring cohorts from single queens of ants, bees, and wasps have revealed that patriline proportions generally remain quite stable over time (Ross 1986; Estoup *et al.* 1994; Keller *et al.* 1997; Haberk & Tautz 1998; Bekkevold *et al.* 1999), suggesting that uneven sperm use typically does not strongly affect colony composition and genetic structure in these insects.

Genetic relatedness of breeders

Relatedness of same-sex breeders

Relatedness of same-sex breeders in social groups with multiple breeders is important because it determines relatedness between matriline and patriline within the group, thus affecting overall relatedness as well as the disparity in relatedness within and between different classes of colony-mates. In social Hymenoptera, it is primarily breeding females (queens) rather than males that tend to be related, whereas in social vertebrates, social spiders, termites, and social thrips, multiple breeders of either or both sexes may be related (Hoelzer *et al.* 1994; Jarvis *et al.* 1994; Crozier & Pamilo 1996; Avilés 1997; Shellman-Reeve 1997; Balloux *et al.* 1998; Chapman & Crespi 1998; Hughes 1998; Ligon 1999; SurrIDGE *et al.* 1999). In social vertebrates, related breeders often are members of the philopatric (non-dispersing) sex, although coalitions of dispersing same-sex relatives are formed in some species (Emlen 1991; Packer *et al.* 1991; Koenig *et al.* 1992; Morin *et al.* 1994; Cockburn 1998). In societies of a few birds and mammals, same-sex breeders may be unrelated (Packer *et al.* 1991; Brooke & Hartley 1995; Cockburn 1998; Mitani *et al.* 2000).

Relatedness of breeding females. The relatedness of breeding females influences group genetic structure through its effects on both average progeny relatedness and the relative differences in relatedness within and between matriline

(see Box 3). Increased relatedness of breeding females (r_f) raises the relatedness between individuals of different matriline (r_{dm}), thereby increasing average progeny relatedness (r_p) and reducing the disparity between the relatedness within and between matriline (r_{sm} vs. r_{dm}). Both general effects are relevant to social evolution: the first influences the opportunity for colony-level selection and the second the opportunity for within-colony conflict. In social Hymenoptera, queen relatedness is of further importance because it reflects the mating and social biology prevalent in a population; thus, its measurement can yield valuable insights into these natural history features and, in so doing, help test models for the evolution of multiple-queen social organization (Bourke & Franks 1995; Keller 1995; Ross & Keller 1995).

Values of queen relatedness in established nests of Hymenoptera estimated from genetic markers cover the range of possible values (Keller 1995; Ross & Keller 1995; Crozier & Pamilo 1996; Reeve *et al.* 2000), with queens in epiponine wasps and some ants related as closely as full sisters (0.75) (Banschbach & Herbers 1996a; Satoh *et al.* 1997; Hastings *et al.* 1998) and queens in a few ants effectively unrelated (Seppä 1996; Goodisman & Ross 1998; Pedersen & Boomsma 1999a). The significantly positive queen relatedness values typically reported mean that, even in colonies with considerable numbers of queens, offspring relatedness still can be relatively high (Queller *et al.* 1993; Herbers & Stuart 1996; Ross *et al.* 1996, 1997; Satoh *et al.* 1997). Moreover, such positive estimates imply that queens primarily are recruited into their natal nests as new breeders and, in ants, that mating must occur in or around the nest (ant queens are thought to lack the capacity to orient and return to their natal nest after a long-distance mating flight). Additional evidence for natal nest recruitment comes from similarities in queen and worker relatedness values, which also have been reported commonly in ants (Pamilo *et al.* 1997; Chapuisat & Keller 1999a). Natural history data for termites suggest that supplementary egg-layers of both sexes usually are recruited by their natal colonies, and nuclear gene and mtDNA data from two species support this view (Atkinson & Adams 1997; Thorne *et al.* 1999). Thus, a chief prediction of kin selection models for the evolution of multiple-queen societies, that nestmate queens are the philopatric kin of the workers that reared them, is upheld in most social insects (Keller 1995). Nonetheless, mtDNA and microsatellite studies of several ants have revealed that unrelated foreign queens (or reproductive workers) can be accepted as new egg-layers, sometimes at substantial rates (Stille & Stille 1992; Evans 1996; Carew *et al.* 1997; Tay *et al.* 1997; Goodisman & Ross 1998). In these cases, individual-level selection (mediated by parasitism or mutualism), selection acting at levels other than the individual (e.g. selfish genetic elements, demes), or stochastic population perturbations may drive the evolution of multiple-queen social organization (Bourke & Franks 1995; Crozier

& Pamilo 1996; Evans 1996; Queller *et al.* 2000; Tsutsui *et al.* 2000; M. C. Mescher & K. G. Ross, unpublished). Much empirical and theoretical work remains to be done to solve the riddle of how colonies of unrelated queens can persist in some taxa.

An apparent strong imprint of kin selection on the evolution of multiple-queen social organization can be seen in the mechanism by which high queen relatedness is maintained in epiponine wasps. Cyclical variation in colony queen number is well documented in this group (Jeanne 1991), and extensive genetic studies show that workers respond to changing patterns of relatedness associated with these cycles by rearing new queens only when these queens will be most closely related to the workers — that is, when only one or very few mother queens are present (see Queller *et al.* 1993; Hastings *et al.* 1998). Thus, daughter queens are mostly full sisters, which mate and take up reproduction on the natal colony or swarm as a group to found a new colony, restoring multiple-queen organization with closely related nestmate queens. Linkage between periodic reduction in queen number and elective queen rearing by workers may also explain the maintenance of high queen relatedness in other multiple-queen wasps and ants (Heinze *et al.* 1995b; Seppä 1996; Evans 1998; Tay & Crozier 2000; Tsuchida *et al.* 2000). These examples illustrate the important point that breeding system properties can be both the products of selection of diverse origin (ecology, life history) as well as agents of subsequent social selection by virtue of their effects on group genetic structure (Pamilo *et al.* 1997; Herbers & Bensch 1999).

Queen relatedness affects the disparity in relatedness within and between progeny matriline in a colony. The maximal disparity, and thus greatest potential for conflict, exists when nestmate queens are unrelated and singly mated, a situation observed in multiple-queen colonies of introduced fire ants and Argentine ants (Ross & Keller 1995; Krieger & Keller 2000). Here, members of the same matriline are full-sisters related by 0.75 and members of different matrilines are unrelated, so there is extensive overlap of genetic interest between sisters and none between nonsisters, a situation maximally conducive to the development of within-colony nepotism. Even in this most favourable circumstance, however, there is no evidence in fire ants that nepotism is displayed by workers toward newly produced queens (DeHeer & Ross 1997; see also Keller 1997). Nonetheless, it is important to continue searching for such predicted behavioural manifestations of within-group conflict in appropriate social taxa, a task that requires detailed understanding of colony kin composition and genetic structure.

Relatedness of breeding males. Relatedness between nestmate male breeders (represented by sperm in queens' spermathecae in Hymenoptera) affects group genetic structure in a

manner analogous to relatedness between female breeders (see Boxes 2 and 3). Relatedness between mates of a single breeding female (r_{m2}) raises the relatedness between offspring in different patriline nested within the same matriline (r_{dp}), causing an increase in average progeny relatedness (r_p) and reducing the difference in the within- and between-patriline relatedness values (r_{sp} vs. r_{dp}). Relatedness between mates of different females (r_{m1}) raises the relatedness between offspring in different matrilines (r_{dm}), also causing an increase in average progeny relatedness while reducing the difference in within- and between-matriline relatedness values (r_{sm} vs. r_{dm}). Genetic estimates of male breeder relatedness are uncommon for Hymenoptera, even though they are relatively straightforward to obtain by genotyping the progeny of single queens or the sperm stored in a queen's spermatheca. These estimates invariably have proved to be low, although they occasionally are statistically greater than zero (Sundström 1993; Peters *et al.* 1995; Seppä & Walin 1996; Pedersen & Boomsma 1998; Chapuisat & Keller 1999a; Paxton 2000). In termites, progeny males recruited into their natal nest as replacement breeders characteristically are closely related (Atkinson & Adams 1997; Thorne *et al.* 1999).

Relatedness of different-sex breeders

Relatedness of different-sex breeders that are not mates. This component (r_{fm}) has seldom received explicit study (see Hughes 1998; Hohmann *et al.* 1999) but can influence overall progeny relatedness and the difference in relatedness within and between matrilines (r_{sm} vs. r_{dm}).

Relatedness of mates (level of inbreeding). Inbreeding generally increases average relatedness in groups while decreasing relatedness differences between different kin classes, although its specific effects on group genetic structure depend on the details of the mating system (Pamilo 1985; Michod 1993). Because of its role in boosting group relatedness, inbreeding has been suggested to play a role in promoting social evolution in some systems (Wade & Breden 1987; Bourke & Franks 1995; Crozier & Pamilo 1996; Shellman-Reeve 1997). Inbreeding is a common feature of termite and thrips societies with multiple supplementary (replacement) breeders (Crozier & Pamilo 1996; Atkinson & Adams 1997; Chapman & Crespi 1998; Thompson & Hebert 1998; Husseneder *et al.* 1999; Kranz *et al.* 1999; Thorne *et al.* 1999; Chapman *et al.* 2000), and apparently also is characteristic of most social spiders (Smith & Hagen 1996; Avilés 1997). Molecular markers have suggested that inbreeding occurs in the eusocial naked mole rats (Jarvis *et al.* 1994; cf. Braude 2000; Ciszek 2000) and in a social shrew (Ballou *et al.* 1998), but mating between first-degree relatives evidently is rare in most cooperatively breeding birds (Cockburn 1998). In all cases where it occurs, inbreeding

should be accounted for if relatedness values for group members are to be interpreted in terms of recent pedigree links (Box 3) (Pamilo 1985, 1993).

Most genetic studies of social Hymenoptera have failed to detect pronounced local inbreeding as indicated by significant F_{IS} values (Ross & Keller 1995; Crozier & Pamilo 1996; Herbers & Stuart 1996; Seppä 1996; Bourke *et al.* 1997; Pedersen & Boomsma 1998; Goodisman *et al.* 2000; Krieger & Keller 2000; Tsuchida *et al.* 2000; cf. Evans 1996). On the other hand, inbreeding is likely to occur in some ants that are social parasites, have lek mating systems, or display atypical colony reproductive modes (Tsuji & Yamauchi 1994; Cole & Wiernasz 1997; see also Bourke & Franks 1995; Pedersen & Boomsma 1999a). Cole & Wiernasz (1997) make the point that many genetic studies lack the statistical power required to detect even substantial amounts of inbreeding; however, this criticism is less applicable to the increasing number of studies using many highly variable markers and large sample sizes. In multiple-queen ants and epiponine wasps in which daughter queens are recruited into their natal nests, inbreeding apparently is minimized by extensive male dispersal, active discrimination against kin during mate choice, or the presence of many nestmate breeders (Ross & Keller 1995; Pedersen & Boomsma 1998; Chapuisat & Keller 1999a).

Variation in parentage (reproductive skew)

Reproductive skew is the unequal sharing of parentage among same-sex breeders in a social group (Keller & Reeve 1994; Bourke & Franks 1995). Deviations from equal parentage increase the proportion of offspring that are members of the same matriline and/or patriline, and because nestmate relatedness is the weighted average of relatednesses within and between such lines, skew typically increases average group relatedness. Said differently, maternity skew ($\sigma_F^2 > 0$) results in lower-value between-matriline pedigree links (r_{dm}) being exchanged for higher-value within-matriline links (r_{sm}), while paternity skew ($\sigma_M^2 > 0$) results in lower-value between-patriline links (r_{dp}) being exchanged for higher-value within-patriline (r_{sp}) links (Box 3). These effects of skew are embodied in the concept of *genetically effective parentage*, an idealized parameter corresponding to the number of parents that would produce the observed average colony-mate relatedness were they to reproduce equally (Queller 1993; Ross 1993; Boomsma & Ratnieks 1996; Crozier & Pamilo 1996). The effective number of parents will be lower than the actual number with any degree of skew, and the disparity between the two measures grows with increasing inequity in parentage. In the Fig. 2, three nestmate ant queens vary considerably in the number of daughters each produces, so the genetically effective maternity is lower than three (the exact difference depends on other breeding system properties that affect the

disparity between r_{sm} and r_{dm}). The two mates of the green queen differ greatly in their apportionment of paternity of her daughters, so the effective paternity in this matriline is closer to one than two (again, the exact difference depends on other breeding system properties, in this case those that affect the disparity between r_{sp} and r_{dp}).

Reproductive skew is a fundamental property of animal societies that is predicted to respond over evolutionary time to, among other factors, the relatedness of breeders, another element of the breeding system (Keller & Reeve 1994; Johnstone *et al.* 1999). Thus, there is interest in measuring skew in animal societies in order both to understand how this breeding system component affects genetic structure, and to test skew theory as an explanatory model for social evolution. Such measurements made with genetic data are becoming increasingly common for social vertebrates (Packer *et al.* 1991; Avise 1994; Keane *et al.* 1994; Cockburn 1998; Hughes 1998) as well as social insects. These genetic data are of great value in revealing details of social organization that often cannot be inferred reliably from behavioural or other data (Trunzer *et al.* 1999; Cant 2000; Worthington Wilmer *et al.* 2000).

Maternity skew

Skew in reproduction among multiple nestmate queens of social insects has been assessed both indirectly or directly using genetic markers. The indirect approach, which requires information on other breeding system components, assesses skew by comparing observed colony genetic diversity with that expected given the numbers of queens found (that is, by comparing actual and effective queen numbers). Most of the literature investigating maternity skew in social Hymenoptera has followed this approach (see Ross & Keller 1995; Herbers & Stuart 1996; Bourke *et al.* 1997). These studies reveal that skew in the maternity of offspring females often can be minimal (e.g. epiponine wasps and some ants), but in other cases is extreme (including effectively single maternity in multiple-queen leptothoracine ants; Heinze 1995). One potential limitation of the indirect approach is that it usually makes use of population data, and so generates an overall image of average skew patterns rather than an accurate depiction for any single colony. A potentially more serious limitation stems from the fact that multiple-queen societies seldom are 'closed'; workers and queens may leave or join, queens may die and be replaced, and single nests may be part of larger composite colonies (polydomy). All of these factors tend to inflate offspring diversity (decrease relatedness), with the result that considerable skew (which has the opposite effect) could be masked.

Maternity skew in Hymenoptera has been assessed directly by assigning parentage to sampled offspring using highly polymorphic markers in natural colonies, or by using artificially constructed laboratory colonies with genetically recognizable matriline. The former approach has been

used to document increasing skew during colony development in paper wasp foundress associations (Peters *et al.* 1995; Field *et al.* 1998; Reeve *et al.* 2000), in accord with predictions of skew theory, and congruence of behavioural and reproductive dominance among workers in queenless colonies of a ponerine ant (Trunzer *et al.* 1999). As is the case with the indirect method, breeder turnover can complicate such skew analyses based on maternity assignment (Field *et al.* 1998). Artificially constructed laboratory colonies were used to directly demonstrate variable but generally extensive maternity skew in fire ants (Ross 1988). This latter study further showed that skew was greater for sexual (queen) offspring than worker offspring, an important consideration in social insects with an effectively sterile worker caste. Indeed, comparison of maternity skew for offspring of the two castes potentially opens up many new avenues of research into individual reproductive tactics in such social insects (see also Pamilo & Seppä 1994; Bourke & Franks 1995).

Paternity skew

In social mammals, paternity skew is likely to reflect primarily behavioural interactions among rival males rather than contest competition among sperm of different ejaculates, because sperm generally have a short life-span and females are unable to store sperm for extended periods (Gomendio *et al.* 1998). At the other extreme, sperm of social Hymenoptera are held in the queen's spermathecae for long periods, so interactions of different ejaculates with each other and with the female reproductive tract are prolonged and potentially significant with respect to fertilization success. Most genetic data concerning paternity contributions by the mates of polyandrous Hymenoptera queens come from several species of honey bees (*Apis*), which typically are highly polyandrous. In these bees, paternity often differs substantially among the mates of single queens (Estoup *et al.* 1994; Haberl & Moritz 1994; Oldroyd *et al.* 1995, 1996, 1997; 1998; Haberl & Tautz 1998), with the result that the effective number of queen matings can be considerably lower than the actual number and worker relatedness can be moderately higher than would be the case with equal paternity. Recent genetic studies of other taxa of social Hymenoptera have also shown that paternity skew can be considerable in some progenies (Pamilo 1993; Seppä & Walin 1996; Keller *et al.* 1997; Boomsma & Van der Have 1998; Fjerdingstad *et al.* 1998; Bekkevold *et al.* 1999; Goodisman *et al.* 2000; Paxton 2000), with such skew contributing to low values for effective numbers of queen matings in most ants (Boomsma & Ratnieks 1996). The stability of paternity patterns over time reported in several hymenopteran species (above) suggests that the observed skew reflects the amount of sperm of each male stored in a queen's spermatheca, with considerable mixing of the different ejaculates following sperm acquisition and minimal sperm precedence (also

Boomsma & Ratnieks 1996). No genetic data are available on the effect of mating order on paternity skew in social Hymenoptera, most likely because of the difficulties of observing natural matings and staging matings in the laboratory.

Local population genetic structure

It is important to consider genetic structure above the level of the social group when assessing breeding systems and within-group genetic structure for several reasons. First, because the mating and dispersal behaviours that shape local structure are intimately associated with social organization, knowledge of these causes of higher-level structure can enrich understanding of the determinants of colony-level structure (Wade 1994; Ross & Keller 1995; Sugg *et al.* 1996; Pamilo *et al.* 1997; Balloux *et al.* 1998). A second, related reason is that correct evaluation of some components of the breeding system requires knowledge of local genetic structure (Ross & Carpenter 1991a; Queller *et al.* 1992; Crozier & Pamilo 1996; Chapuisat *et al.* 1997). For instance, attempts to infer pedigree connections from average relatedness values or the magnitude of skew from comparison of actual and effective breeder numbers are improved by correcting for local structure (see Box 4). Finally, local structure signals another hierarchical level at which selection may occur, in some cases potentially rivalling in strength selection at the level of the social group (Kelly 1994; Banschbach & Herbers 1996b; Chapuisat *et al.* 1997; Linhart 1999).

Local genetic structure is expected to be important in many social organisms because philopatry by one or both sexes typically is associated with social behaviour (Chepko-Sade & Halpin 1987; Koenig *et al.* 1992; Crozier & Pamilo 1996; Sugg *et al.* 1996; Balloux *et al.* 1998; Cockburn 1998; Hughes 1998; DeHeer *et al.* 1999; Piertney *et al.* 1999; SurrIDGE *et al.* 1999). This is especially true in social insects with multiple-queen societies, where queen dispersal often is limited, colonies may inhabit several nests, and colonies generally multiply by budding (Ross & Keller 1995; Pamilo *et al.* 1997; Shellman-Reeve 1997). Indeed, significant local structure has been detected in many such social insects (Ross & Keller 1995; Chapuisat *et al.* 1997; Ross *et al.* 1997, 1999; Herbers & Mouser 1998; Husseneder *et al.* 1998; Pedersen & Boomsma 1999a; Thorne *et al.* 1999). As expected given that queens, but not necessarily males, may exhibit reduced dispersal in multiple-queen Hymenoptera, local differentiation in several ants appears especially strong at mtDNA markers relative to nuclear DNA markers (Stille & Stille 1993; Ross *et al.* 1997, 1999; Ross & Shoemaker 1997; Tay *et al.* 1997; Foitzik & Herbers 2000). Of particular interest here are studies of ants that have revealed local nuclear and/or mtDNA structure in multiple-queen but not in single-queen populations of the same or a closely related species (Sundström 1993; Seppä & Pamilo 1995; Banschbach & Herbers 1996a; Ross *et al.* 1997, 1999). These comparisons illustrate

Box 4

Local genetic structure elevates relatedness measured within social groups above that due to immediate pedigree links when relatedness is calculated without correcting for this structure. The added component of relatedness stems from members of neighbouring social groups being related to one another through distant pedigree connections, the result of limited dispersal in previous generations. Within-group relatedness values reflecting recent pedigree links (r_{ps}) can be obtained using the formula:

$$r_{ps} = \frac{(r_{pt} - r_{st})}{(1 - r_{st})}$$

where r_{pt} is the within-group relatedness measured with respect to the entire population and r_{st} is the relatedness between members of neighbouring groups (Pamilo 1984). This equation shows that relatedness due to recent pedigree links is the standardized difference between the total uncorrected within-group relatedness and the relatedness between neighbouring groups, as depicted conceptually below (Fig. 3) using a genetic topography in which elevation corresponds to average level of genetic similarity or relatedness (see also Costa 1998). The small hills represent social groups and the plateaus represent neighbourhoods of elevated among-group relatedness (local genetic structure).

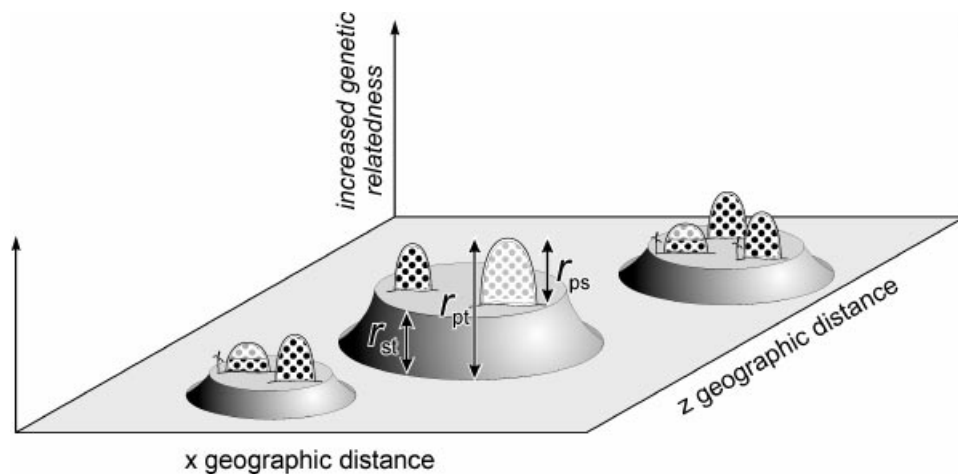


Fig 3

dramatically how changes in the breeding system (and the social organization to which it is coupled) can influence the distribution of genetic variation not only within but among social groups.

In vertebrates, significant local genetic structure commonly is associated with social behaviour (Lehman *et al.* 1992; Jarvis *et al.* 1994; Balloux *et al.* 1998; Kays *et al.* 2000; Kerth *et al.* 2000) and, as has been found in ants, such structure may differ between the mtDNA and nuclear genomes in accordance with sex-specific dispersal tendencies (Avise 1994; Hoelzer *et al.* 1994; Morin *et al.* 1994; Hoelzel *et al.* 1998; Escorza-Treviño & Dizon 2000).

Conclusions

Molecular ecologists are accumulating genetic data on group structure in social animals at a rapid pace. These studies usually have the common goals of understanding the evolu-

tionary causes of social behaviour as well as its population genetic consequences. The analytical framework described here is well suited to these purposes, because it provides a standard approach and terminology for organizing and interpreting such data by explicitly linking properties of the breeding system to group kin composition and genetic structure. Analyses using this framework reveal how changes in the number of breeders in a group, the relatedness of breeders, or skew in their parentage affect group structure and influence the opportunities for cooperation and conflict to evolve within groups, as well as how such breeding system changes alter the distribution of variation and potential for selection at hierarchical levels above the social group. Detailed assessment of group kin structure using the framework outlined here often can benefit from formal parentage analyses (e.g. Neff *et al.* 2000), and many of the parameters to be estimated for these analyses also are employed in the 'breeding group' models of Chesser, Sugg,

and colleagues (Sugg *et al.* 1996), which emphasize larger-scale population genetic properties such as metapopulation diversity and structure. Thus, researchers have available conceptually linked systems for analysing genetic data along a continuum of scales relevant to the evolutionary biology of social organisms.

The framework described here has been used to provide fairly comprehensive accounts of all components of the breeding system and resulting group genetic structure for a handful of social insects (e.g. Ross 1993; Sundström 1993; Estoup *et al.* 1994; Seppä 1994; Banschbach & Herbers 1996a; Hastings *et al.* 1998; Chapuisat & Keller 1999a; Pedersen & Boomsma 1999a,b; Peters *et al.* 1999), and the insights provided by such accounts increasingly are being used to infer the nature of hierarchically structured selection acting in these populations (Banschbach & Herbers 1996b; Chapuisat *et al.* 1997). Perhaps most importantly, such studies have stimulated the development and extension of kin selection theory to predict the potential for conflict in genetically structured groups, and have encouraged the search for evidence of the outcome of such conflict. Thus, much effort has been devoted to understanding biased sex allocation, reproductive skew, 'policing' of reproduction by subordinates, and nepotism in terms of genetic conflicts of interest in heterogeneous social groups (Bourke & Franks 1995; Pamilo *et al.* 1997; Field *et al.* 1998; Queller & Strassmann 1998; Chapuisat & Keller 1999b; Keller & Chapuisat 1999; Peters *et al.* 1999). While some of these phenomena are unique to social Hymenoptera because of their particular genetic or social systems, others are expected to be general features of social organisms. Adoption of a standard framework for analysing group genetic structure will facilitate exploration of the complex selective dynamics favouring the evolution of these and other important features of social life.

Future studies of the molecular ecology of social behaviour can be expected to significantly advance the field by emphasizing the following objectives touched upon in this review.

- 1 Comparative and experimental studies should attempt to pinpoint ecological selection pressures that shape breeding system attributes (e.g. Herbers & Banschbach 1999; Pedersen & Boomsma 1999a), with the goal of distinguishing such 'extrinsic' forces from 'intrinsic' social forces related to within-group competition and cooperation.
- 2 Renewed emphasis should be placed on acquiring natural history data (behavioural, ecological, life history) to complement and inform genetic data on breeding systems.
- 3 Phylogenetic analyses should be employed to illuminate the routes and pace of evolution of breeding system components affecting group genetic structure (Ross *et al.* 1988; Ross & Carpenter 1991a,b; Oldroyd *et al.* 1998; Foster *et al.* 1999; Villesen *et al.* 1999; Chapman *et al.* 2000).
- 4 Behavioural studies focusing on individuals within colonies should be coupled with genetic analyses to continue the search for predicted as well as unanticipated manifestations of within-group conflict.
- 5 The empirical approaches of developmental and physiological genetics should be adopted to study the genetic bases of variation in individual reproductive success and group breeding behaviour in social animals (Page & Robinson 1994; Moritz *et al.* 1996; Robinson *et al.* 1997; Ross & Keller 1998; Osborne & Oldroyd 1999; Young *et al.* 1999). The resulting data should be used to learn how specific genotypes confer higher fitness under social selection and to generate detailed mechanistic and evolutionary hypotheses of how social evolution drives changes in colony and population genetic structure (e.g. Ross *et al.* 1999).

One final, empirical issue to consider in studies of breeding systems and colony genetic structure is whether it is preferable to characterize relatively few social groups in detail by reconstructing pedigrees and directly determining reproductive success, or instead to use surrogate measures of average kinship and reproduction (e.g. relatedness patterns) to generalize across populations of social groups. The former approach prevails in studies of social vertebrates and primitively eusocial Hymenoptera in which groups may be small and uncommon, and in which direct observational data on parentage can be obtained. The latter approach is typical of studies of highly eusocial insects in which colonies are populous and often abundant, and in which important details of reproduction and brood care may be hidden from the investigator. The choice depends not only on the characteristics of the social organism under study but also on the questions motivating the work — in particular, the extent to which variation among social groups in a given breeding characteristic is relevant to the action of selection. Thus, for instance, tests of predicted split sex ratios in social Hymenoptera require data from individual colonies, whereas inferences of the strength of colony-level selection may best rely on population-wide average colony relatedness values. To a growing extent, the availability of highly polymorphic, easy-to-use molecular markers narrows the gap between the two approaches by making possible near-complete descriptions of the composition and genetic structure of large numbers of social groups. The framework reviewed here readily accommodates data from both types of approaches in interpreting group kin composition and genetic structure.

Acknowledgements

I thank Laurent Keller, Michael Wade, and an anonymous reviewer for helpful comments on an earlier draft of this paper. Support for this work was provided by grants to the author from the National Geographic Society and the U.S. National Science Foundation.

References

- Arévalo E, Strassmann JE, Queller DC (1998) Conflicts of interest in social insects: male production in two species of *Polistes*. *Evolution*, **52**, 797–805.
- Atkinson L, Adams ES (1997) The origins and relatedness of multiple reproductives in colonies of the termite *Nasutitermes corniger*. *Proceedings of the Royal Society of London B*, **264**, 1131–1136.
- Avilés L (1997) Causes and consequences of cooperation and permanent-sociality in spiders. In: *The Evolution of Social Behavior in Insects and Arachnids*, (eds Choe JC, Crespi BJ), pp. 476–498. Cambridge University Press, Cambridge.
- Avise JC (1994) *Molecular Markers, Natural History and Evolution*. Chapman & Hall, New York.
- Baer B, Schmid-Hempel P (1999) Experimental variation in polyandry affects parasite loads and fitness in a bumble-bee. *Nature*, **397**, 151–154.
- Balloux F, Goudet J, Perrin N (1998) Breeding system and genetic variance in the monogamous, semi-social shrew, *Crocodyrus russula*. *Evolution*, **52**, 1230–1235.
- Banschbach VS, Herbers JM (1996a) Complex colony structure in social insects: I. Ecological determinants and genetic consequences. *Evolution*, **50**, 285–297.
- Banschbach VS, Herbers JM (1996b) Complex colony structure in social insects: II. Reproduction, queen-worker conflict, and levels of selection. *Evolution*, **50**, 298–307.
- Bekkevold D, Frydenberg J, Boomsma JJ (1999) Multiple mating and facultative polygyny in the Panamanian leafcutter ant *Acromyrmex echinator*. *Behavioral Ecology and Sociobiology*, **46**, 103–109.
- Boomsma JJ, Fjerdingstad EJ, Frydenberg J (1999) Multiple paternity, relatedness and genetic diversity in *Acromyrmex* leaf-cutter ants. *Proceedings of the Royal Society of London B*, **266**, 249–254.
- Boomsma JJ, Ratnieks FLW (1996) Paternity in eusocial Hymenoptera. *Philosophical Transactions of the Royal Society of London B*, **351**, 947–975.
- Boomsma JJ, Van der Have TM (1998) Queen mating and paternity variation in the ant *Lasius niger*. *Molecular Ecology*, **7**, 1709–1718.
- Bourke AFG (1988) Worker reproduction in the higher eusocial Hymenoptera. *Quarterly Review of Biology*, **63**, 291–311.
- Bourke AFG, Franks NR (1995) *Social Evolution in Ants*. Princeton University Press, Princeton.
- Bourke AFG, Green HAA, Bruford MW (1997) Parentage, reproductive skew and queen turnover in a multiple-queen ant analysed with microsatellites. *Proceedings of the Royal Society of London B*, **264**, 277–283.
- Braude S (2000) Dispersal and new colony formation in wild naked mole-rats: evidence against inbreeding as the system of mating. *Behavioral Ecology*, **11**, 7–12.
- Brooke MD, Hartley I (1995) Nesting Herderson reed-warblers (*Acrocephalus vaughani tati*) studied by DNA fingerprinting: unrelated coalitions in a stable habitat. *Auk*, **112**, 77–86.
- Cant MA (2000) Social control of reproduction in banded mongooses. *Animal Behaviour*, **59**, 147–158.
- Carew ME, Tek Tay W, Crozier RH (1997) Polygyny via unrelated queens indicated by mitochondrial DNA variation in the Australian meat ant *Iridomyrmex purpureus*. *Insectes Sociaux*, **44**, 7–14.
- Chapman TW, Crespi BJ (1998) High relatedness and inbreeding in two species of haplodiploid eusocial thrips (Insecta: Thysanoptera) revealed by microsatellites. *Behavioral Ecology and Sociobiology*, **43**, 301–306.
- Chapman TW, Crespi BJ, Kranz BD, Schwarz MP (2000) High relatedness and inbreeding at the origin of eusociality in gall-inducing thrips. *Proceedings of the National Academy of Sciences of the USA*, **97**, 1648–1650.
- Chapuisat M (1998) Mating frequency of ant queens with alternative dispersal strategies, as revealed by microsatellite analysis of sperm. *Molecular Ecology*, **7**, 1097–1105.
- Chapuisat M, Goudet J, Keller L (1997) Microsatellites reveal high population viscosity and limited dispersal in the ant *Formica paralugubris*. *Evolution*, **51**, 475–482.
- Chapuisat M, Keller L (1999a) Extended family structure in the ant *Formica paralugubris*: the role of the breeding system. *Behavioral Ecology and Sociobiology*, **46**, 405–412.
- Chapuisat M, Keller L (1999b) Testing kin selection with sex allocation data in eusocial Hymenoptera. *Heredity*, **82**, 473–478.
- Chepko-Sade BD, Halpin ZT, eds (1987) *Mammalian Dispersal Patterns: the Effects of Social Structure on Population Genetics*. University of Chicago Press, Chicago.
- Choe JC, Crespi BJ, eds (1997) *The Evolution of Social Behavior in Insects and Arachnids*. Cambridge University Press, Cambridge.
- Ciszek D (2000) New colony formation in the 'highly inbred' eusocial naked mole-rat: outbreeding is preferred. *Behavioral Ecology*, **11**, 1–6.
- Cockburn A (1998) Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics*, **29**, 141–177.
- Cole BJ (1983) Multiple mating and the evolution of social behavior in the Hymenoptera. *Behavioral Ecology and Sociobiology*, **12**, 191–201.
- Cole BJ, Wiernasz DC (1997) Inbreeding in a lek-mating ant species, *Pogonomyrmex occidentalis*. *Behavioral Ecology and Sociobiology*, **40**, 79–86.
- Cole BJ, Wiernasz DC (1999) The selective advantage of low relatedness. *Science*, **285**, 891–893.
- Costa JT (1998) Social behavior and its effects on colony- and microgeographic genetic structure in phytophagous insect populations. In: *Genetic Structure and Local Adaptation in Natural Insect Populations: Effects of Ecology, Life History, and Behavior* (eds Mopper S, Strauss SY), pp. 205–238. Kluwer, Boston.
- Costa JT, Ross KG (1993) Seasonal decline in intracolony relatedness in eastern tent caterpillars: implications for social evolution. *Behavioral Ecology and Sociobiology*, **32**, 47–54.
- Crozier RH, Brückner D (1981) Sperm clumping and the population genetics of Hymenoptera. *American Naturalist*, **117**, 561–563.
- Crozier RH, Page RE (1985) On being the right size: male contributions and multiple mating in social Hymenoptera. *Behavioral Ecology and Sociobiology*, **18**, 105–115.
- Crozier RH, Pamilo P (1996) *Evolution of Social Insect Colonies; Sex Allocation and Kin Selection*. Oxford University Press, Oxford.
- Crozier RH, Smith BH, Crozier YC (1987) Relatedness and population structure of the primitively eusocial bee *Lasiglossum zephyrum* (Hymenoptera: Halictidae) in Kansas. *Evolution*, **41**, 902–910.
- DeHeer CJ, Goodisman MAD, Ross KG (1999) Queen dispersal strategies in the multiple-queen form of the fire ant *Solenopsis invicta*. *American Naturalist*, **153**, 660–675.
- DeHeer CJ, Ross KG (1997) Lack of detectable nepotism in multiple-queen colonies of the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology*, **40**, 27–33.
- Duffy JE (1996) Eusociality in a coral-reef shrimp. *Nature*, **381**, 512–514.
- Duffy JE, Macdonald KS (1999) Colony structure of the social snapping shrimp *Synalpheus fildigitus* in Belize. *Journal of Crustacean Biology*, **19**, 283–292.
- Emlen ST (1991) Evolution of cooperative breeding in birds and mammals. In: *Behavioural Ecology, An Evolutionary Approach*

- (eds Krebs JR, Davies NB), pp. 301–335. Blackwell Scientific, Oxford.
- Escorza-Treviño S, Dizon AE (2000) Phylogeography, intraspecific structure and sex-biased dispersal of Dall's porpoise, *Phocoenoides dalli*, revealed by mitochondrial and microsatellite DNA analyses. *Molecular Ecology*, **9**, 1049–1060.
- Estoup A, Scholl A, Pouvreau A, Solignac M (1995) Monoandry and polyandry in bumble bees (Hymenoptera; Bombinae) as evidenced by highly variable microsatellites. *Molecular Ecology*, **4**, 89–93.
- Estoup A, Solignac M, Cornuet J-M (1994) Precise assessment of the number of patrines and of genetic relatedness in honeybee colonies. *Proceedings of the Royal Society of London B*, **258**, 1–7.
- Evans JD (1996) Queen longevity, queen adoption, and posthumous indirect fitness in the facultatively polygynous ant *Myrmica tahoensis*. *Behavioral Ecology and Sociobiology*, **39**, 275–284.
- Evans JD (1998) Parentage and sex allocation in the facultatively polygynous ant *Myrmica tahoensis*. *Behavioral Ecology and Sociobiology*, **44**, 35–42.
- Field J, Solís CR, Queller DC, Strassmann JE (1998) Social and genetic structure of paper wasp cofoundress associations: tests of reproductive skew models. *American Naturalist*, **151**, 545–563.
- Fjerdingstad EJ, Boomsma JJ (1998) Multiple mating increases the sperm stores of *Atta colombica* leafcutter ant queens. *Behavioral Ecology and Sociobiology*, **42**, 257–261.
- Fjerdingstad EJ, Boomsma JJ, Thoren P (1998) Multiple paternity in the leafcutter ant *Atta colombica*—a microsatellite DNA study. *Heredity*, **80**, 118–126.
- Foitzik S, Heinze J (1998) Nest site limitation and colony takeover in the ant *Leptothorax nylanderi*. *Behavioral Ecology*, **9**, 367–375.
- Foitzik S, Herbers JM (2000) Colony structure of a slavemaking ant: I. Intra-colony relatedness, worker reproduction and polydomy. *Evolution*, in press.
- Foster KR, Ratnieks FLW, Raybould AF (2000) Do hornets have zombie workers? *Molecular Ecology*, **9**, 735–742.
- Foster KR, Seppä P, Ratnieks FLW, Thoren PA (1999) Low paternity in the hornet *Vespa crabro* indicates that multiple mating by queens is derived in vespine wasps. *Behavioral Ecology and Sociobiology*, **46**, 252–257.
- Fraser VS, Kaufmann B, Oldroyd BP, Crozier RH (2000) Genetic influence on caste in the ant *Camponotus consobrinus*. *Behavioral Ecology and Sociobiology*, **47**, 188–194.
- Gadagkar R (1991) On testing the role of genetic asymmetries created by haplodiploidy in the evolution of eusociality in the Hymenoptera. *Journal of Genetics*, **70**, 1–31.
- Gadau J, Heinze J, Hölldobler B, Schmid M (1996) Population and colony structure of the carpenter ant *Camponotus floridanus*. *Molecular Ecology*, **5**, 785–792.
- Gomendio M, Harcourt AH, Roldán ERS (1998) Sperm competition in mammals. In: *Sperm Competition and Sexual Selection* (eds Birkhead TR, Møller AP), pp. 667–753. Academic Press, New York.
- Goodisman MAD, Matthews RW, Crozier RH (2001) Multiple mating and worker reproduction in the European wasp, *Vespula germanica*. *Behavioral Ecology and Sociobiology*, in press.
- Goodisman MAD, Ross KG (1998) A test of queen recruitment models using nuclear and mitochondrial markers in the fire ant *Solenopsis invicta*. *Evolution*, **52**, 1416–1422.
- Goodnight KF, Strassmann JE, Klingler CJ, Queller DC (1996) Single mating and its implications for kinship structure in a multiple-queen wasp, *Parachartergus colobopterus*. *Ecology and Evolution*, **8**, 191–198.
- Haberl M, Moritz RFA (1994) Estimation of intracolony worker relationship in a honey bee colony (*Apis mellifera* L.) using DNA fingerprinting. *Insectes Sociaux*, **41**, 263–272.
- Haberl M, Tautz D (1998) Sperm usage in honey bees. *Behavioral Ecology and Sociobiology*, **42**, 247–255.
- Hastings MD, Queller DC, Eischen F, Strassmann JE (1998) Kin selection, relatedness, and worker control of reproduction in a large-colony epiponine wasp, *Brachygastra mellifica*. *Behavioral Ecology*, **9**, 573–581.
- Heinze J (1995) Reproductive skew and genetic relatedness in *Leptothorax* ants. *Proceedings of the Royal Society of London B*, **261**, 375–379.
- Heinze J (1999) Male polymorphism in the ant species *Cardiocondyla minutior* (Hymenoptera: Formicidae). *Entomologia Generalis*, **23**, 251–258.
- Heinze J, Lipski N, Hölldobler B, Bourke AFG (1995a) Geographical variation in the social and genetic structure of the ant, *Leptothorax acervorum*. *Zoology*, **98**, 127–135.
- Heinze J, Lipski N, Schlehmeier K, Hölldobler B (1995b) Colony structure and reproduction in the ant, *Leptothorax acervorum*. *Behavioral Ecology*, **6**, 359–367.
- Heinze J, Puchinger W, Hölldobler B (1997) Worker reproduction and social hierarchies in *Leptothorax* ants. *Animal Behaviour*, **54**, 849–864.
- Heinze J, Tsuji K (1995) Ant reproductive strategies. *Researches on Population Ecology*, **37**, 135–149.
- Herbers JM, Banschbach VS (1999) Plasticity of social organization in a forest ant species. *Behavioral Ecology and Sociobiology*, **45**, 451–465.
- Herbers JM, Mouser RL (1998) Microsatellite DNA markers reveal details of social structure in forest ants. *Molecular Ecology*, **7**, 299–306.
- Herbers JM, Stuart RJ (1996) Multiple queens in ant nests: Impact on genetic structure and inclusive fitness. *American Naturalist*, **147**, 161–187.
- Hoelzer AR, Dahlheim M, Stern SJ (1998) Low genetic variation among killer whales (*Orcinus orca*) in the eastern North Pacific and genetic differentiation between foraging specialists. *Journal of Heredity*, **89**, 121–128.
- Hoelzer GA, Dittus WPJ, Ashley MV, Melnick DJ (1994) The local distribution of highly divergent mitochondrial DNA haplotypes in toque macaques *Macaca sinica* at Polonnaruwa Sri Lanka. *Molecular Ecology*, **3**, 451–458.
- Hohmann G, Gerloff U, Tautz D, Fruth B (1999) Social bonds and genetic ties: kinship, association and affiliation in a community of bonobos (*Pan paniscus*). *Behaviour*, **136**, 1219–1235.
- Hughes C (1998) Integrating molecular techniques with field methods in studies of social behavior: a revolution results. *Ecology*, **79**, 383–399.
- Husseneder C, Brandl R, Epplen C, Epplen JT, Kaib M (1998) Variation between and within colonies in the termite: morphology, genomic DNA, and behaviour. *Molecular Ecology*, **7**, 983–990.
- Husseneder C, Brandl R, Epplen C, Epplen JT, Kaib M (1999) Within-colony relatedness in a termite species: genetic roads to eusociality? *Behaviour*, **136**, 1045–1063.
- Jarvis JUM, O'Riain JO, Bennett NC, Sherman PW (1994) Mammalian eusociality: a family affair. *Trends in Ecology and Evolution*, **9**, 47–51.
- Jeanne RL (1991) The swarm-founding Polistinae. In: *The Social Biology of Wasps* (eds Ross KG, Matthews RW), pp. 191–231. Cornell University Press, Ithaca, New York.
- Johnstone RA, Woodroffe R, Cant MA, Wright J (1999) Reproductive skew in multimember groups. *American Naturalist*, **153**, 315–331.

- Kays RW, Gittleman JL, Wayne RK (2000) Microsatellite analysis of kinkajou social organization. *Molecular Ecology*, **9**, 743–751.
- Keane B, Waser PM, Creel SR *et al.* (1994) Subordinate reproduction in dwarf mongooses. *Animal Behaviour*, **47**, 65–75.
- Keller L (1995) Social life: the paradox of multiple-queen colonies. *Trends in Ecology and Evolution*, **10**, 355–360.
- Keller L (1997) Indiscriminate altruism: unduly nice parents and siblings. *Trends in Ecology and Evolution*, **12**, 99–103.
- Keller L, ed. (1993) *Queen Number and Sociality in Insects*. Oxford University Press, New York.
- Keller L, Chapuisat M (1999) Cooperation among selfish individuals in insect societies. *Bioscience*, **49**, 899–909.
- Keller L, Passera L, Suzzoni JP (1989) Queen execution in the Argentine ant *Iridomyrmex humilis* (Mayr). *Physiological Entomology*, **14**, 157–163.
- Keller L, Reeve HK (1994) Partitioning of reproduction in animal societies. *Trends in Ecology and Evolution*, **9**, 98–102.
- Keller L, Reeve HK (1999) Dynamics of conflicts within insect societies. In: *Levels of Selection in Evolution* (ed. Keller L), pp. 153–175. Princeton University Press, Princeton, New Jersey.
- Keller L, Sundström L, Chapuisat M (1997) Male reproductive success: paternity contribution to queens and workers in *Formica* ants. *Behavioral Ecology and Sociobiology*, **41**, 11–15.
- Kelly JK (1994) The effect of scale dependent processes on kin selection: mating and density regulation. *Theoretical Population Biology*, **46**, 32–57.
- Kerth G, Mayer F, König B (2000) Mitochondrial DNA (mtDNA) reveals that female Bechstein's bats live in closed societies. *Molecular Ecology*, **9**, 793–800.
- Koenig WD, Pitelka FA, Carmen WJ, Mumme RL, Stanback MT (1992) The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology*, **67**, 111–150.
- Kranz BD, Schwarz MP, Mound LA, Crespi BJ (1999) Social biology and sex ratios of the eusocial gall-inducing thrips *Kladothrips hamiltoni*. *Ecological Entomology*, **24**, 432–442.
- Kraus B, Page RE (1998) Parasites, pathogens, and polyandry in social insects. *American Naturalist*, **151**, 383–391.
- Krieger MJB, Keller L (2000) Mating frequency and genetic structure of the Argentine ant *Linepithema humile*. *Molecular Ecology*, **9**, 119–126.
- Kukuk PF, Eickwort GC, May B (1987) Multiple maternity and multiple paternity in the first generation brood from single foundress colonies of the sweat bee *Dialictus zephyrus* (Hymenoptera: Halictidae). *Insectes Sociaux*, **34**, 131–135.
- Lehman N, Clarkson P, Mech LD, Meier TJ, Wayne RK (1992) A study of the genetic relationships within and among wolf packs using DNA fingerprinting and mitochondrial DNA. *Behavioral Ecology and Sociobiology*, **30**, 83–94.
- Ligon JD (1999) *The Evolution of Avian Breeding Systems*. Oxford University Press, Oxford.
- Linhart YB (1999) Mosaic landscapes, family structure and evolution. *Trends in Ecology and Evolution*, **14**, 376–377.
- Lobo JA, Kerr WE (1993) Estimation of the number of matings in *Apis mellifera* — extensions of the model and comparison of different estimates. *Ecology and Evolution*, **5**, 337–345.
- McCauley DE, Wade MJ, Breden FJ, Wohlman M (1988) Spatial and temporal variation in group relatedness: evidence from the imported willow leaf beetle. *Evolution*, **42**, 184–192.
- Michod RE (1993) Inbreeding and the evolution of social behavior. In: *The Natural History of Inbreeding and Outbreeding; Theoretical and Empirical Perspectives* (ed. Thornhill NW), pp. 74–96. University of Chicago Press, Chicago.
- Mitani JC, Merriwether DA, Zhang CB (2000) Male affiliation, cooperation and kinship in wild chimpanzees. *Animal Behaviour*, **59**, 885–893.
- Morin PA, Moore JJ, Chakraborty R *et al.* (1994) Kin selection, social structure, gene flow, and the evolution of chimpanzees. *Science*, **265**, 1193–1201.
- Moritz RFA, Kryger P, Allsopp MH (1996) Competition for royalty in bees. *Nature*, **384**, 31.
- Moritz RFA, Kryger P, Koeniger G *et al.* (1995) High degree of polyandry in *Apis dorsata* queens detected by DNA microsatellite variability. *Behavioral Ecology and Sociobiology*, **37**, 357–363.
- Neff BD, Repka J, Gross MR (2000) Parentage analysis with incomplete sampling of candidate parents and offspring. *Molecular Ecology*, **9**, 515–528.
- Oldroyd BP, Clifton MJ, Parker K *et al.* (1998) Evolution of mating behavior in the genus *Apis* and an estimate of mating frequency in *Apis cerana* (Hymenoptera: Apidae). *Annals of the Entomological Society of America*, **91**, 700–709.
- Oldroyd BP, Clifton MJ, Wongsiri S *et al.* (1997) Polyandry in the genus *Apis*, particularly *Apis andreniformis*. *Behavioral Ecology and Sociobiology*, **40**, 17–26.
- Oldroyd BP, Smolenski AJ, Cornuet J-M *et al.* (1995) Levels of polyandry and intracolony genetic relationships in *Apis florea*. *Behavioral Ecology and Sociobiology*, **37**, 329–335.
- Oldroyd BP, Smolenski AJ, Cornuet J-M *et al.* (1996) Levels of polyandry and intracolony genetic relationships in *Apis dorsata* (Hymenoptera: Apidae). *Annals of the Entomological Society of America*, **89**, 276–283.
- Osborne KE, Oldroyd BP (1999) Possible causes of reproductive dominance during emergency queen rearing by honeybees. *Animal Behaviour*, **58**, 267–272.
- Packer C, Gilbert DA, Pusey AE, O'Brien SJ (1991) A molecular genetic analysis of kinship and cooperation in African lions. *Nature*, **351**, 562–565.
- Packer L, Owen RE (1994) Relatedness and sex ratio in a primitively eusocial halictine bee. *Behavioral Ecology and Sociobiology*, **34**, 1–10.
- Page RE (1986) Sperm utilization in social insects. *Annual Review of Entomology*, **31**, 297–320.
- Page RE, Robinson GE (1994) Reproductive competition in queenless honey bee colonies (*Apis mellifera* L.). *Behavioral Ecology and Sociobiology*, **35**, 99–107.
- Pamilo P (1984) Genotypic correlation and regression in social groups: multiple alleles, multiple loci and subdivided populations. *Genetics*, **107**, 307–320.
- Pamilo P (1985) Effect of inbreeding on genetic relatedness. *Hereditas*, **103**, 195–200.
- Pamilo P (1993) Polyandry and allele frequency differences between the sexes in the ant *Formica aquilonia*. *Heredity*, **70**, 472–480.
- Pamilo P, Gertsch P, Thorén P, Seppä P (1997) Molecular population genetics of social insects. *Annual Review of Ecology and Systematics*, **28**, 1–25.
- Pamilo P, Seppä P (1994) Reproductive competition and conflicts in colonies of the ant *Formica sanguinea*. *Animal Behaviour*, **48**, 1201–1206.
- Paxton RJ (2000) Genetic structure of colonies and a male aggregation in the stingless bee *Scaptotrigona postica*, as revealed by microsatellite analysis. *Insectes Sociaux*, **47**, 63–69.
- Pedersen JS, Boomsma JJ (1998) Direct genetic evidence for local mate competition in ants. *Naturwissenschaften*, **85**, 593–595.
- Pedersen JS, Boomsma JJ (1999a) Effect of habitat saturation on the number and turnover of queens in the polygynous ant, *Myrmica sulcinodis*. *Journal of Evolutionary Biology*, **12**, 903–917.

- Pedersen JS, Boomsma JJ (1999b) Positive association of queen number and queen-mating frequency in *Myrmica* ants: a challenge to the genetic-variability hypotheses. *Behavioral Ecology and Sociobiology*, **45**, 185–193.
- Peters JM, Queller DC, Imperatriz-Fonseca VL, Roubik DW, Strassmann JE (1999) Mate number, kin selection and social conflicts in stingless bees and honeybees. *Proceedings of the Royal Society of London B*, **266**, 379–384.
- Peters JM, Queller DC, Strassmann JE, Solís CR (1995) Maternity assignment and queen replacement in a social wasp. *Proceedings of the Royal Society of London B*, **260**, 7–12.
- Piertney SB, MacColl ADC, Lambin X, Moss R, Dallas JF (1999) Spatial distribution of genetic relatedness in a moorland population of red grouse (*Lagopus lagopus scoticus*). *Biological Journal of the Linnean Society*, **68**, 317–331.
- Queller DC (1993) Genetic relatedness and its components in polygynous colonies of social insects. In: *Queen Number and Sociality in Insects* (ed. Keller L), pp. 132–152. Oxford University Press, Oxford.
- Queller DC, Strassmann JE (1998) Kin selection and social insects. *Bioscience*, **48**, 165–175.
- Queller DC, Strassmann JE, Hughes CR (1992) Genetic relatedness and population structure in primitively eusocial wasps in the genus *Mischocyttarus* (Hymenoptera: Vespidae). *Journal of Hymenopteran Research*, **1**, 81–89.
- Queller DC, Strassmann JE, Solís CR, Hughes CR, Deloach DM (1993) A selfish strategy of social insect workers that promotes social cohesion. *Nature*, **365**, 639–641.
- Queller DC, Zacchi F, Cervo R *et al.* (2000) Unrelated helpers in a social insect. *Nature*, **405**, 784–787.
- Ratnieks FLW, Boomsma JJ (1995) Facultative sex allocation by workers and the evolution of polyandry by queens in social Hymenoptera. *American Naturalist*, **145**, 969–993.
- Ratnieks FLW, Reeve HK (1992) Conflict in single-queen hymenopteran societies: the structure of conflict and processes that reduce conflict in advanced eusocial species. *Journal of Theoretical Biology*, **158**, 33–65.
- Reeve HK, Starks PT, Peters JM, Nonacs P (2000) Genetic support for the evolutionary theory of reproductive transactions in social wasps. *Proceedings of the Royal Society of London B*, **267**, 75–79.
- Reichardt AK, Wheeler DE (1996) Multiple mating in the ant *Acromyrmex versicolor*: a case of female control. *Behavioral Ecology and Sociobiology*, **38**, 219–225.
- Richards MH, Packer L, Seger J (1995) Unexpected patterns of parentage and relatedness in a primitively eusocial bee. *Nature*, **373**, 239–241.
- Robinson GE, Fahrback SE, Winston ML (1997) Insect societies and the molecular biology of social behavior. *Bioessays*, **19**, 1099–1108.
- Ross KG (1986) Kin selection and the problem of sperm utilization in social insects. *Nature*, **323**, 798–802.
- Ross KG (1988) Differential reproduction in multiple-queen colonies of the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology*, **23**, 341–355.
- Ross KG (1993) The breeding system of the fire ant *Solenopsis invicta*: effects on colony genetic structure. *American Naturalist*, **141**, 554–576.
- Ross KG, Carpenter JM (1991a) Population genetic structure, relatedness, and breeding systems. In: *The Social Biology of Wasps* (eds Ross KG, Matthews RW), pp. 451–479. Cornell University Press, Ithaca, New York.
- Ross KG, Carpenter JM (1991b) Phylogenetic analysis and the evolution of queen number in eusocial Hymenoptera. *Journal of Evolutionary Biology*, **4**, 117–130.
- Ross KG, Keller L (1995) Ecology and evolution of social organization: insights from fire ants and other highly eusocial insects. *Annual Review of Ecology and Systematics*, **26**, 631–656.
- Ross KG, Keller L (1998) Genetic control of social organization in an ant. *Proceedings of the National Academy of Sciences of the USA*, **95**, 14232–14237.
- Ross KG, Krieger MJB, Shoemaker DD, Vargo EL, Keller L (1997) Hierarchical analysis of genetic structure in native fire ant populations: results from three classes of molecular markers. *Genetics*, **147**, 643–655.
- Ross KG, Shoemaker DD (1997) Nuclear and mitochondrial genetic structure in two social forms of the fire ant *Solenopsis invicta*: insights into transitions to an alternate social organization. *Heredity*, **78**, 590–602.
- Ross KG, Shoemaker DD, Krieger MJB, DeHeer CJ, Keller L (1999) Assessing genetic structure with multiple classes of molecular markers: a case study involving the introduced fire ant *Solenopsis invicta*. *Molecular Biology and Evolution*, **16**, 525–543.
- Ross KG, Vargo EL, Fletcher DJC (1988) Colony genetic structure and queen mating frequency in fire ants of the subgenus *Solenopsis* (Hymenoptera: Formicidae). *Biological Journal of the Linnean Society*, **34**, 105–117.
- Ross KG, Vargo EL, Keller L (1996) Social evolution in a new environment: the case of introduced fire ants. *Proceedings of the National Academy of Sciences, USA*, **93**, 3021–3025.
- Sasaki K, Satoh T, Obara Y (1996) Cooperative foundation of colonies by unrelated foundresses in the ant *Polyrhachis moesta*. *Insectes Sociaux*, **43**, 217–226.
- Satoh T, Masuko K, Matsumoto T (1997) Colony genetic structure in the mono- and polygynous sibling species of the ants *Camponotus nawai* and *Camponotus yamaokai*: DNA fingerprint analysis. *Ecological Research*, **12**, 71–76.
- Schmid-Hempel R, Schmid-Hempel P (2000) Female mating frequencies in *Bombus* spp. from central Europe. *Insectes Sociaux*, **47**, 36–41.
- Seppä P (1994) Sociogenetic organization of the ants *Myrmica ruginodis* and *Myrmica lobicornis*: number, relatedness and longevity of reproducing individuals. *Journal of Evolutionary Biology*, **7**, 71–95.
- Seppä P (1996) Genetic relatedness and colony structure in polygynous *Myrmica* ants. *Ethology Ecology and Evolution*, **8**, 279–290.
- Seppä P, Pamilo P (1995) Gene flow and population viscosity in *Myrmica* ants. *Heredity*, **74**, 200–209.
- Seppä P, Sundström L, Punttila P (1995) Facultative polygyny and habitat succession in boreal ants. *Biological Journal of the Linnean Society*, **56**, 533–551.
- Seppä P, Walin L (1996) Sociogenetic organization of the red ant *Myrmica rubra*. *Behavioral Ecology and Sociobiology*, **38**, 207–217.
- Shellman-Reeve JS (1997) The spectrum of eusociality in termites. In: *The Evolution of Social Behavior in Insects and Arachnids* (eds Choe JC, Crespi BJ), pp. 52–93. Cambridge University Press, Cambridge.
- Smith DR, Hagen RH (1996) Population structure and interdemec selection in the cooperative spider *Anelosimus eximius*. *Journal of Evolutionary Biology*, **9**, 589–608.
- Stille M, Stille B (1992) Intra- and inter-nest variation in mitochondrial DNA in the polygynous ant *Leptothorax acervorum* (Hymenoptera; Formicidae). *Insectes Sociaux*, **39**, 335–340.

- Stille M, Stille B (1993) Intrapopulation nest clusters of maternal mtDNA lineages in the polygynous ant *Leptothorax acervorum* (Hymenoptera: Formicidae). *Insect Molecular Biology*, **1**, 117–121.
- Stille M, Stille B, Douwes P (1991) Polygyny, relatedness and nest founding in the polygynous myrmicine ant *Leptothorax acervorum* (Hymenoptera; Formicidae). *Behavioral Ecology and Sociobiology*, **28**, 91–96.
- Strassmann JE, Hughes CR, Turillazzi S, Solís CR, Queller DC (1994) Genetic relatedness and incipient eusociality in stenogastrine wasps. *Animal Behaviour*, **48**, 813–821.
- Sugg DW, Chesser RK, Dobson FS, Hoogland JL (1996) Population genetics meets behavioral ecology. *Trends in Ecology and Evolution*, **11**, 338–342.
- Sundström L (1993) Genetic population structure and sociogenetic organisation in *Formica truncorum* (Hymenoptera; Formicidae). *Behavioral Ecology and Sociobiology*, **33**, 345–354.
- Sundström L (1995) Dispersal polymorphism and physiological condition of males and females in the ant, *Formica truncorum*. *Behavioral Ecology*, **6**, 132–139.
- SurrIDGE AK, Ibrahim KM, Bell DJ *et al.* (1999) Fine-scale genetic structuring in a natural population of European wild rabbits (*Oryctolagus cuniculus*). *Molecular Ecology*, **8**, 299–307.
- Tay WT, Cook JM, Rowe DJ, Crozier RH (1997) Migration between nests in the Australian arid-zone ant *Rhytidoponera* sp. 12 revealed by DGGE analyses of mitochondrial DNA. *Molecular Ecology*, **6**, 403–411.
- Tay WT, Crozier RH (2000) Microsatellite analysis of gamergate relatedness of the queenless ponerine ant *Rhytidoponera* sp. 12. *Insectes Sociaux*, **47**, 188–192.
- Templeton AR, Read B (1994) Inbreeding: one word, several meanings, much confusion. In: *Conservation Genetics* (eds Loeschcke V, Tomiuk J, Jain SK), pp. 91–105. Birkhäuser, Basel.
- Thompson GJ, Hebert PDN (1998) Population genetic structure of the neotropical termite *Nasutitermes nigriceps* (Isoptera: Termitidae). *Heredity*, **80**, 48–55.
- Thorne BL, Traniello JFA, Adams ES, Bulmer M (1999) Reproductive dynamics and colony structure of subterranean termites of the genus *Reticulitermes* (Isoptera Rhinotermitidae): a review of the evidence from behavioral, ecological, and genetic studies. *Ethology Ecology and Evolution*, **11**, 149–169.
- Trunzer B, Heinze J, Hölldobler B (1999) Social status and reproductive success in queenless ant colonies. *Behaviour*, **136**, 1093–1105.
- Tsuchida K, Itô Y, Katada S, Kojima J (2000) Genetical and morphological colony structure of the Australian swarm-founding polistine wasp, *Ropalidia romandi* (Hymenoptera, Vespidae). *Insectes Sociaux*, **47**, 113–116.
- Tsuji K, Yamauchi K (1994) Colony level sex allocation in a polygynous and polydomous ant. *Behavioral Ecology and Sociobiology*, **34**, 157–167.
- Tsutsui ND, Suarez AV, Holway DA, Case TJ (2000) Reduced genetic variation and the success of an invasive species. *Proceedings of the National Academy of Sciences of the USA*, **97**, 5948–5953.
- Villesen P, Gertsch PJ, Frydenberg J, Mueller UG, Boomsma JJ (1999) Evolutionary transition from single to multiple mating in fungus-growing ants. *Molecular Ecology*, **8**, 1819–1825.
- Wade MJ (1985) The influence of multiple inseminations and multiple foundresses on social evolution. *Journal of Theoretical Biology*, **112**, 109–121.
- Wade MJ (1994) The biology of the imported willow leaf beetle, *Plagioderia versicolora* (Laicharting). In: *Novel Aspects of the Biology of Chrysomelidae* (eds Jolivet PH, Cox ML, Petitpierre E), pp. 541–547. Kluwer, Boston.
- Wade MJ, Breden FJ (1987) Kin selection in complex groups: mating structure, migration structure, and the evolution of social behaviors. In: *Mammalian Dispersal Patterns: the Effects of Social Structure on Population Genetics* (eds Chepko-Sade BD, Halpin ZT), pp. 273–283. University of Chicago Press, Chicago.
- Ward PS (1983) Genetic relatedness and colony organization in a species complex of ponerine ants. I. Phenotypic and genotypic composition of colonies. *Behavioral Ecology and Sociobiology*, **12**, 285–299.
- Worthington Wilmer J, Overall AJ, Pomeroy PP, Twiss SD, Amos W (2000) Patterns of paternal relatedness in British grey seal colonies. *Molecular Ecology*, **9**, 283–292.
- Young LJ, Nilsen R, Waymire KG, MacGregor GR, Insel TR (1999) Increased affiliative response to vasopressin in mice expressing the V_{1a} receptor from a monogamous vole. *Nature*, **400**, 766–768.

The author's research focuses on the evolutionary genetics of social Hymenoptera, with much of his work concerning native and introduced fire ant populations. Current projects on these ants include studies of the molecular systematics, large-scale population genetic structure, and the genetic basis of social organization.
