

## The demise of the standard ant (Hymenoptera: Formicidae)

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### Abstract

The social systems of ants are far more variable than has traditionally been believed. In addition to variation in queen number and queen mating frequency, recent research has documented such bizarre phenomena as the parthenogenetic production of females from unfertilized eggs or genetic caste determination. All these affect the genetic structure of ant societies, and it appears that in a large percentage of species colonies do not consist of a single, singly mated mother and her sterile worker offspring. Though it has long been known that kin selection for reproductive altruism can work well without a relatedness value between workers of 0.75, the recent upsurge of discussions about the role of relatedness in kin selection theory may have confused both myrmecologists and non-specialists. The aim of this review is to give an overview of the large range of ant reproductive systems and to correct some misconceptions about the role of the magic value 0.75 in kin selection theory.

**Key words:** Polygyny, polyandry, worker reproduction, thelytoky, kin selection theory, review.

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### Introduction

*Komm, wir wollen Ameisen zergliedern, Staubfäden zählen; ich werde es doch noch zu irgend einer fürstlichen Liebhaberei bringen.*

*Georg Büchner, Leonce und Lena*

To many biologists not specializing on the biology of ants, the social systems of Formicidae appeared to be rather uniform and uncomplicated until a few decades ago: ant societies, like those of many other social insects, seemed to be simple families, with a singly-mated mother queen (monogyny and monandry) and her sterile worker offspring. Some non-myrmecologists considered ant workers in general to be fullsisters, characterized by the high degree of relatedness of 0.75, which they erroneously thought to be the foundation of kin selection theory.

Not much has remained of this simple version of the ant world. Though already one hundred years ago there was ample evidence that many ant societies contain multiple queens, more recent investigations cast doubt on the view that a suite of monogyny, monandry, and worker sterility represents the predominant social organization of ants. Genetic studies have corroborated observational data about the co-occurrence of multiple fertile nestmate queens, revealed a considerable number of species with effective queen mating frequencies above 1, and proved that workers may or may not be sterile. Furthermore, the spread of professional ant research from the traditionally well-studied temperate zones of the Northern Hemisphere to more exotic places has yielded some unexpected new phenomena (e.g., KELLER 2007): mated workers may replace queens, unmated workers may produce diploid female offspring from unfertilized eggs, long-lived males may engage in lethal fight-

ing, caste determination may be based on genotype, and males may be produced from diploid eggs after expulsion of the maternal nucleus. Nothing is certain in present-day myrmecology, except that nestmate relatedness may vary from nearly zero to one. What does this mean for kin selection theory, and how can all this variation in social and genetic colony structures be explained?

The aim of this review cannot be to develop a life history theory of ants – this would require much more information about the age distribution of ant populations, the survival rate of differently equipped propagules, and other sociometric traits. Instead, I intend to give a broad, though inevitably subjective, overview of the steadily expanding spectrum of ant reproductive systems and some of the current ideas about the causes of this variation and its consequences on the genetic structure of ant societies. Furthermore, I intend to correct common and recurring misconceptions that some ant-practitioners and non-specialists share about the role of the magic value 0.75 in kin selection theory.

### Number and morphology of female reproductives

#### *The queen is dead! Long live the queen!*

Division of reproductive labor is one of the essential components of eusociality. Given that reproduction is often associated with dispersal and colony founding, reproductives and non-reproductives may be highly different in morphology. While they differ little in so-called "primitively" eusocial insects, such as polistine wasps, female reproductives of most ant species are morphologically and physiologically specialized for dispersal and mating flights. In

contrast, non-reproductives are often cheap, disposable all-purpose tools without special adaptations for dispersal (HÖLLDOBLER & WILSON 1990).

Textbook definitions of "queen" often do not distinguish between morphology and function. Unfortunately, nature does. Evolution has provided us with a number of unhandy intermediate phenotypes, and BUSCHINGER & WINTER (1976) therefore suggested using "queen" in a strictly functional sense for all mated egg-layers regardless of morphology. In contrast, PEETERS (1991a) proposed to use "queen" only for those female reproductives that form a discrete category morphologically distinct from the wingless, non-reproductives, and which may or may not bear wings when eclosing (winged vs. ergatoid queens; see also HEINZE 1998). Today, both terminologies are used, but there are phenotypes that do not easily fit either. For example, special "intermorphic workers" may lay large numbers of unfertilized eggs (*Crematogaster smithi*, HEINZE & al. 1995), females smaller than foraging workers may function as reproductives when mated and as nurses when unmated (*Myrmica* sp., MOLET & al. 2007a, b), and reproductives may be externally indistinguishable from non-reproductives but have a higher number of ovarioles (*Eutetramorium mocquerysi*, HEINZE & al. 1999). In contrast to myrmecologists of the early 20th century, I refrain from describing each phenomenon with a distinct name and stick with those that are most uncontroversial and most widely used, e.g., "queens" for females specialized for mating and reproduction in function and morphology, specifying them as "winged" (or, after wing shedding, "dealate") or "intermorphic"; "gamergates" for mated workers (e.g., PEETERS 1991b); and "(female) reproductives", when referring to a general category that contains all types, including other, weirder types of female reproductives.

Across non-parasitic ants, number and morphology of female reproductives are intricately linked (HÖLLDOBLER & WILSON 1990). Young queens of monogynous species are typically specialized for reproduction, dispersal, and solitary founding. In species with small colony sizes, and when the queens forage during the founding phase, queen-worker size dimorphism is often not very pronounced, because queens do not have many more ovarioles than the workers and are not equipped with large nutrient stores for founding. Nevertheless, they are characterized by the full complement of thoracic sclerites for their mating and dispersal flights. In contrast, in species with large colony sizes, in which queens lay dozens of eggs per day, they are often much larger than the workers and have more ovarioles. Such queens may be endowed with large flight muscles and fat bodies that provide enough energy to found new nests claustrally, i.e., without foraging. The relationship between the body sizes of queens and workers appears to be more strongly affected by founding tactics and colony size than phylogenetic constraints: several myrmicine ants, in which founding is semi-claustral, have queens that are not much larger than workers, while ponerines with relatively large colonies may have a marked queen-worker dimorphism (HASKINS & HASKINS 1950, DEJEAN & FÉNERON 1996).

Though winged queens are the rule in monogynous species, there are a few exceptions. It is not surprising that queens of social parasites may be wingless, as in *Harpagoxenus sublaevis* (BUSCHINGER & WINTER 1975), or short-

winged, as in *Leptothorax wilsoni* (HEINZE 1989). However, wingless, short-winged, or at least flightless queens do occur also in several non-parasitic, monogynous taxa, such as army ants, *Cataglyphis cursor*, *Cardiocondyla batesii*, and others. New colonies of army ants are founded by fission, and because the dispersal distance of the colony is limited by the migrating capacity of the wingless workers, queens obviously do not need wings. The other cases of wingless queens in monogynous ants are less easily explained. In *Cataglyphis*, young queens mate in the vicinity of their maternal nests and immediately found their own nests by budding (LENOIR & al. 1988). In a few species of *Cardiocondyla*, monogyny appears to be a derived state (SCHREMPF & HEINZE 2007). Like in the ancestral polygynous species, mating occurs in the nest and queens shed their wings before dispersing on foot to found solitarily (SCHREMPF & al. 2005).

Queens in facultatively polygynous species may found new nests solitarily or by budding. Whenever budding is combined with mating in the maternal nest or on the ground nearby, the structures and resources necessary for dispersal flights and solitary founding are futile. This allows the evolution of relatively small queens with low fat content (KELLER & PASSERA 1989, STILLE 1996) or of wingless, intermorphic or short-winged queens (BUSCHINGER & HEINZE 1992, HEINZE & TSUJI 1995, RÜPPELL & HEINZE 1999, HEINZE & KELLER 2000). Depending on environmental constraints on solitary founding or budding, flightless queens may either co-exist with or completely replace winged queens. In cases of queen polymorphism, larger, winged queens are thought to disperse and to colonize new habitat patches, while small or wingless queens return into their multiply-queened maternal nests and found through budding, which allows the local exploitation of the maternal habitat patch. However, most evidence from field data is as yet correlative: colonies either contain one large, dealate queen or several small, often wingless or intermorphic queens (e.g., HEINZE 1993a, FERSCH & al. 2000), but the dispersal behavior of the different morphs has usually not been observed in the field. At least in *Myrmica* (e.g., BRIAN & BRIAN 1955) and *Temnothorax rugatulus* (RÜPPELL & al. 2001) the capture rate of different queen morphs suggests a higher dispersal activity of large queens. In contrast, the small queen morph is thought to disperse in *Ectatomma ruidum* (LACHAUD & al. 1999), and both long-winged and short-winged queens of *Cardiocondyla batesii* similarly disperse on foot and found solitarily (SCHREMPF & HEINZE 2007).

Independent founding by solitary queens has apparently been completely lost in a number of obligatorily polygynous species, such as *Linepithema humile*, *Monomorium pharaonis*, and other invasive species. Successful founding requires that queens are accompanied by a minimum number of workers (e.g., HEE & al. 2000). Budding may lead to dense networks of interlinked nests amongst which brood and adults are freely exchanged. Genetic bottlenecks during the accidental transfer into new biogeographic areas appear to contribute to the resulting unicoloniality, which again is seen as one cause of the ecological dominance of successful invasive ant species (TSUTSUI & al. 2000, 2003).

It is obvious that dispersing queens are selected against when dispersal is costly, either due to environmental con-

straints (such as cold, draught, predation pressure) or habitat saturation (HERBERS 1986). Solid data on the geographical distribution of polygyny are still lacking but many species found in northernmost Eurasia and America are facultatively polygynous (HEINZE 1993b). Unfortunately, most belong to a few species-rich genera, such as *Formica* or *Myrmica*, and thus cannot be considered as independent data points. Information about the few ant species occurring at high latitudes in the Southern Hemisphere would thus be helpful to investigate the importance of climate for queen number.

Another factor affecting the occurrence of multiple queening is habitat stability. Polygynous colonies usually produce sexuals earlier than monogynous colonies and may thus out-compete monogynous species during the colonization of empty habitat patches (e.g., TSUJI & TSUJI 1996). They therefore abound in unstable habitats and are among the first colonizers of such patches (HÖLLDOBLER & WILSON 1977, HÖLLDOBLER & WILSON 1990, YAMAUCHI & OGATA 1995). When long-range dispersal is needed to reach these patches, species with a dispersal polyphenism obviously are at an advantage. However, the success of invasive tramp species indicates that propagation exclusively by budding, assisted by a highly mobile vector, such as human commerce, is a very successful way of spreading at least throughout man-made and otherwise anthropogenically disturbed habitats. Other natural vectors may probably also contribute to the long-range dispersal of those relatively immobile ant colonies that lack dispersing queens. The widespread occurrence of *Platythyrea punctata*, a thelytokous ant with apparently flightless queens and founding by budding, throughout the Caribbean Islands might indicate that colonies are occasionally dispersed across large distances with driftwood.

Similar arguments as above might also be useful to explain variation in the number of mated workers. An early stage in the evolution of ant sociality presumably consisted of societies with mated and unmated, dealate and wingless reproductives, in which dominance status decided about reproductive rights, such as in *Pachycondyla tridentata* (SOMMER & HÖLLDOBLER 1992). During the course of evolution, wingless individuals in several subfamilies apparently lost the capability of mating – one might speculate that a seasonally restricted availability of mating chances in temperate environments may have contributed to the loss of totipotency. In a number of genera of the poneromorph subfamilies, but also in the myrmecine *Myrmecia pyriformis* (DIETEMANN & al. 2004) and one species of the myrmicine genus *Metapone* (HÖLLDOBLER & al. 2002), workers have retained the capability of mating. In some of these taxa, gamergates may serve as additional or replacement reproductives, similar to neotenics in termites or the "intercastes" in *Technomyrmex albipes* (YAMAUCHI & al. 1991), which are produced after queen death and serve to increase colony size and reproductive output (e.g., *Rhytidoponera metallica*, WARD 1986; *Harpegnathos saltator* PEETERS & al. 2000, LIEBIG & POETHKE 2004; *Gnamptogenys menadensis*, GOBIN & al. 1998). Like facultatively polygynous species with multiple queens, such species are thus characterized by fast local propagation through budding and long-range dispersal through winged queens. Though several of these species might therefore make good tramp ants, the behavioral and dietary restric-

tions of poneromorphs (e.g., the almost general lack of trail recruitment, trophallaxis, and trophobiotic symbioses, e.g., WILSON & HÖLLDOBLER 2005) probably impair their fast spread across biogeographic barriers. The most widespread among those ponerine ants that are regularly transferred by human commerce, *Hypoponera punctatissima* and a few related, cryptic species (MCGLYNN 1999, DELABIE & BLARD 2002) do not have gamergates, but winged and wingless queens (SEIFERT 2003).

Other taxa, such as *Diacamma* (e.g., PEETERS & HIGASHI 1989, PEETERS & al. 1992), *Dinoponera* (MONNIN & PEETERS 1998), and *Streblognathus* (ROBERTSON 2002), have completely lost winged queens and replaced them by a single gamergate per colony. Aggressive interactions, including the mutilation and immobilization of nestmates or ritualized domination, result in a division of reproduction between a top-ranking gamergate and non-reproductives of lower rank (e.g., PEETERS & HIGASHI 1989, ITO & HIGASHI 1991, PEETERS & al. 1992, MONNIN & PEETERS 1999). In contrast to monogynous ants, which are usually doomed once the reproductive dies, high-ranking or freshly eclosing workers can replace the gamergate after its death, mate, and lay fertilized eggs (e.g., ANDRÉ & al. 2001, SCHLÜNS & al. 2006).

Genetic studies on fire ants, *Solenopsis invicta*, have added a fascinating perspective to dispersal polymorphisms and queen number variation. The acceptance of young, inseminated queens appears to be mediated by their genotype at the polymorphic locus Gp-9 (e.g., KELLER & ROSS 1999). Young, heterozygote queens with genotype Bb are tolerated by workers when starting to reproduce in an established nest, leading to polygyny. Larvae with genotype bb rarely develop into adult queens, and BB queens are attacked and killed and thus will be forced to found solitarily in the field, leading to monogyny. Most aggression against BB queens is initiated by Bb workers, and KELLER & ROSS (1998) concluded that allele b constitutes a "green beard allele", which selfishly spreads through cooperation among individuals bearing a copy of this allele and aggression against individuals without. Recent research suggests that Gp-9 is an odorant-binding protein (KRIEGER & ROSS 2002), and that the presence of the b-allele also affects colony structure in other, though not all species of *Solenopsis* (ROSS & al. 2003, KRIEGER & ROSS 2005).

**Relation to relatedness:** Obviously, the presence of multiple reproductives, be it queens or gamergates, affects the genetic structure of ant societies. Nestmate relatedness in highly polygynous species, such as *Solenopsis invicta* or *Formica aquilonia*, may be much below 0.75 and eventually drop to values close to zero (e.g., CROZIER & PAMILO 1996).

### Mating frequency

Monogamists are going against some of the deepest-seated evolutionary inclinations with which biology has endowed most creatures.

David Barash & Judith Eve Lipton, *Myth of Monogamy: Fidelity and Infidelity in Animals and People*

Males of most animals can increase their reproductive success by mating with multiple females, while mating with a single male usually provides a female with sufficient

sperm for fertilizing all its eggs. Mating is costly because it prolongs the time span during which a female is exposed to predators and cannot feed, and also because it increases the risk of acquiring venereal diseases. On a superficial glance, females are therefore expected to mate singly, but in many species they do not behave accordingly. Multiple mating by females (polyandry) is thus of considerable interest to evolutionary biologists. Hypotheses forwarded to explain polyandry in general have been examined also in the context of multiple mating in ants. In principle, females mate multiply a) to avoid being further harassed by the males (e.g., SCHREMPF & al. 2005, TRONTTI & al. 2007), and b) because it is advantageous, for example by decreasing the risks of sperm depletion or of producing diploid males, or by increasing the efficiency or disease resistance of the work force (e.g., KELLER & REEVE 1994, BOURKE & FRANKS 1995, BOOMSMA & RATNIEKS 1996, CROZIER & PAMILO 1996, BROWN & SCHMID-HEMPEL 2003).

In most species, in which queen mating frequencies have been determined with genetic markers, nestmate workers are all or almost all offspring of a single father (STRASSMANN 2001). Only in army ants, leaf-cutter ants, and harvester ants, have queens been reported to regularly mate with several, occasionally more than a dozen males (e.g., VILLESSEN & al. 1999, KRONAUER & al. 2004, 2006, RHEINDT & al. 2004). All these taxa have very large colonies. Multiple mating might protect queens from running out of sperm, even though they are known to be extraordinarily frugal in the usage of the sperm they received early in their reproductive lives (TSCHINKEL & PORTER 1988). An additional explanation of polyandry is that genetic diversity of the workers positively affects colony-level efficiency and / or pathogen resistance. The latter might be of particular importance for species with large colonies, because parasites can generally better persist and thrive in large host populations but are quickly lost from small populations (e.g., SCHMID-HEMPEL 1998).

Currently, the most convincing data on the potential benefits of multiple mating come from research with honeybee colonies with naturally or instrumentally inseminated queens. Several studies document that genetically diverse colonies are better capable of maintaining homeostasis during environmental perturbations (e.g., OLDROYD & FEWELL 2007): they grow faster after swarming (MATTILA & SEELEY 2007), maintain a more stable brood nest temperature (JONES & al. 2004) and fare better when infected with fungal pathogens (TARPY 2003). Similar experiments with ants are difficult due to the lack of methods for instrumental insemination and of controlled mating in the laboratory, but indirect evidence suggests that genetic diversity through multiple mating may serve a similar purpose as in honeybees. For example, worker polymorphism has a genetic basis in several polyandrous ants (HUGHES & al. 2003, RHEINDT & al. 2005, JAFFÉ & al. 2007), and genetically heterogeneous groups of *Acromyrmex* ants were more resistant to a fungal parasite (HUGHES & BOOMSMA 2004). Furthermore, *Pogonomyrmex occidentalis* colonies headed by queens with high mating frequency grew faster than colonies with queens with low mating frequency (COLE & WIERNASZ 1999, WIERNASZ & al. 2004).

If colony-level genetic diversity were the decisive parameter, multiple-queening would have more or less the same

effect as multiple mating and having both would be superfluous (KELLER & REEVE 1994). Though a cross-species analysis did not find support for a negative correlation between queen number and mating frequency (SCHMID-HEMPEL & CROZIER 1999), species of army ants appear to be either monogynous and highly polyandrous or polygynous with low queen mating frequency (KRONAUER & BOOMSMA 2007).

Female reproductives of social Hymenoptera do generally not have the option of re-mating later in life and are thus forced to rely on the sperm they received from one or a few mating partners early in their reproductive life – a condition that probably contributed to the evolutionary origin and the maintenance of eusociality in these taxa (e.g., BOOMSMA & al. 2005, BOOMSMA 2007). They might therefore be expected to be quite particular about the quality of their mates. Nevertheless, evidence for female choice is as yet surprisingly scarce in ants and other social insects. Several male traits have been found to differ between mating and non-mating *Pogonomyrmex* males, but this might reflect scramble competition among males rather than female choice (e.g., WIERNASZ & al. 2001), and in some species female sexuals even seem to mate indiscriminately with the first encountered partner (e.g., WOYCIECHOWSKI 1990).

Multiple mating is not often an option for ant males. In a number of species, mating is suicidal, because the genitalia of the male are injured during copulation or remain attached to the female abdomen until the male is killed and cut up by workers (e.g., *Diacamma*: FUKUMOTO & al. 1989; *Dinoponera*: MONNIN & PEETERS 1998; army ants: GOTWALD 1995). Furthermore, the sperm mass of adult ant males usually suffices only for one or a few copulations, because their testes degenerate when the male reaches sexual maturity and the supplies cannot be replenished. Almost nothing is known about the distribution of mating frequencies, but it is obvious that due to this limitation the reproductive skew among ant males must be much smaller than in other animals. For example, under semi-natural conditions in flight cages, about one third of all sexually active males of *Leptothorax gredleri* did not succeed in copulating. Of the successful males, most mated once and the highest observed number of copulations was four (OBERSTADT & HEINZE 2003). Because of their limited likelihood to mate multiply, ant males are expected to be similarly choosy as female sexuals. Data again are scarce. Size-assortative mating in *Pogonomyrmex* was interpreted as evidence for both male and female choice: both sexes prefer large mating partners, which leads to small female sexuals ending up with small males (DAVIDSON 1982), but the extreme commonness of hybrids in some ant taxa (e.g., SEIFERT 1999) speaks against careful mate choice in either sex. The often extreme temporal and spatial limitations of the mating period and the associated high competitiveness for mating changes might strongly impair inter- and intrasexual selection.

However, as in almost every other aspect of ant biology, recent studies have revealed a number of striking exceptions from this rule. For example, wingless males of some *Cardiocondyla* species engage in lethal fighting and attempt to monopolize mating with a harem of female sexuals (KINOMURA & YAMAUCHI 1987, STUART & al. 1987), which they can all inseminate because of their unique life-long spermatogenesis (HEINZE & HÖLLDOBLER 1993), and

wingless males of several *Hypoponera* for hours cling to the cocoons of female sexuals, insert their genitalia into it and secure their reproductive success by mating with the still encased female sexual (YAMAUCHI & al. 2001, FOITZIK & al. 2002).

**Relation to relatedness:** Like polygyny, polyandry has a strong impact on nestmate relatedness, which in monogynous colonies with increasing effective queen mating frequencies approximates 0.25 (e.g., CROZIER & PAMILO 1996).

### Worker reproduction

Z, what are you doing? Don't you understand? This is for the good of the colony.

General Mandible, ANTZ

With the above-mentioned exceptions, ant workers have lost a functional spermatheca and do not mate. However, in most species they have retained more or less well-developed ovaries and can lay viable, unfertilized eggs. Because of the different degrees of relatedness, workers could increase their fitness better by producing sons from their own haploid eggs and, in a monogynous, monandrous society, by rearing nephews, than by rearing their brothers. In contrast, in a polyandrous society or when a colony contains multiple, related queens, workers should object the production of males by workers other than themselves, leading to the phenomenon known as "worker policing": by egg eating or aggression against workers with developed ovaries, workers prevent other workers from enforcing their own selfish interests (RATNIEKS 1988). In addition, worker reproduction may affect the relation between costs and benefits of helping in HAMILTON's inequality (HAMILTON 1964). For example, it might disrupt the division of labor in the society or lead to costly conflicts among workers about who lays eggs and who continues to forage, nurse the brood, and defend the nest (COLE 1986, RATNIEKS 1988, GOBIN & al. 2003, HARTMANN & al. 2003).

The relative importance of relatedness in worker reproduction is still debated. While HAMMOND & KELLER (2004) found no evidence for a predominant role, in a study by WENSELEERS & RATNIEKS (2006) monogyny and monandry were associated with worker reproduction, and polyandry and polygyny with worker policing. However, of the six species explicitly listed as monogynous and monandrous species with egg-laying workers, four have a very special biology and are by no means "standard ants". Two are slave-makers (*Polyergus rufescens*, *Protomognathus americanus*), in which workers might more strongly pursue their own selfish reproductive interests than in non-parasitic species because they do not engage in brood care and therefore are presumably incapable of manipulating sex allocation (e.g., TRIVERS & HARE 1976). Another species in the list is the queenless *Dinoponera quadricaps*, in which all workers are totipotent and hierarchy rank decides about mating and reproduction (MONNIN & PEETERS 1998, 1999). The fourth species, *Crematogaster smithi*, has a peculiar third female caste, which is morphologically and functionally specialized for producing viable, haploid eggs, most of which serve as food for the brood and adult nestmates, while some may eventually survive and develop into males (HEINZE & al. 1995). The remaining two species, *Myrmica punctiventris* and *M. tahoensis*, have ordinary life histories, but worker reproduction appears to be

common throughout this genus, regardless of queen number (ELMES 1980, SMEETON 1981). Thus, the dominant role of variation in relatedness is less obvious in ants than predicted from theory (HELANTERÄ & SUNDSTRÖM 2007), and it appears that worker reproduction is usually prevented by queen policing, e.g., aggression and egg eating in small societies, and / or self-policing and mutual worker policing in larger societies, regardless of their genetic structure.

Eventually, this might lead to the complete loss of ovaries in workers (RATNIEKS 1988): when it is virtually impossible for an individual worker to reproduce, because colonies are very large and / or contain many queens and therefore are rarely queenless, it does not pay to invest energy in ovaries. A comprehensive list of species in which workers lack ovaries still needs to be compiled, but a short glance at a few exemplary taxa indicates that the identification of a common ultimate cause of ovary loss will not be easy. Workers do not have ovaries in so diverse ant taxa as *Cardiocondyla*, *Eciton*, *Hypoponera*, *Monomorium*, *Solenopsis* and *Tetramorium* (including its parasite *Strongylognathus*, J. Heinze, unpubl.) (BOURKE & FRANKS 1995). Colonies are virtually never queenless in some of these taxa, such as *Eciton* or *Monomorium pharaonis*, but queenless colonies are commonly found in others, such as *Cardiocondyla obscurior* (e.g., HEINZE & DELABIE 2005). Why have workers of these species lost their ovaries?

A comparison of *Cardiocondyla* and the closely related *Leptothorax*, in which workers have ovaries, might help solving this puzzle. Both species have similar average queen numbers and similarly small colony sizes, and one might conclude that the probabilities of workers being able to start reproducing because their colonies have become queenless are identical. However, within a few weeks after being orphaned, colonies of *Cardiocondyla* rear replacement queens, which readily mate in the nest, whereas female sexuals of *Leptothorax* require at least several months of hibernation to develop and mate outside the nest. Thus, the capability of quickly starting new colonies from orphaned groups of workers and brood might be associated with the evolutionary loss of worker reproduction. The same capability was suggested to contribute to the success of invasive ant species (ARON 2001), which might explain why most of them have sterile workers (PASSERA 1994). It remains to be determined whether this explanation is more broadly applicable also to strictly monogynous taxa with completely sterile workers, such as *Tetramorium* spp.

**Relation to relatedness:** Worker reproduction per se does not affect nestmate relatedness, but as has been shown above, relatedness is expected to critically affect the reproductive decisions of workers.

### Weird genetics: diploid offspring without paternal contributions

Evolution: revenge of the clones!

Edward M. Sykes & Stuart A. West (2005)

In a small number of species, workers and / or queens have evolved the surprising capability of producing female offspring from unfertilized eggs (thelytoky). Many earlier claims about this phenomenon have meanwhile been refuted and attributed to the long survival rate of queen-derived brood in orphaned colonies. For example, thely-



toky has not been confirmed in any of the ant species listed by SLOBODCHIKOFF & DALY (1971), including such well-studied species as *Lasius niger* and *Formica polyctena*. As yet, careful experiments have documented thelytokous parthenogenesis by workers in a few species scattered throughout the Formicidae (Formicinae: *Cataglyphis cursor*, CAGNIANT 1983, LENOIR & CAGNIANT 1986; Anoploleptidae: *Anoplolepis gracilipes*, DRESCHER & al. 2007; Myrmicinae: *Pristomyrmex punctatus*, ITOW & al. 1984, TSUJI 1988, HASEGAWA & al. 2001; *Messor capitatus*, GRASSO & al. 1998, 2000; Cerapachyinae: *Cerapachys biroi*, RAVARY & JAISSON 2004, TSUJI & YAMAUCHI 1995; Ponerinae: *Platythyrea punctata* HEINZE & HÖLLDOBLER 1995) and suggestive evidence exists for a number of other taxa (e.g., the myrmicine *Mycocepurus smithii*, FERNÁNDEZ-MARÍN & al. 2006). Queens are capable of thelytokous reproduction in *Cataglyphis cursor* (PEARCY & al. 2004, 2006), *Wasmannia auropunctata* (FOURNIER & al. 2005), and probably also *Vollenhovia emeryi* (OHKAWARA & al. 2006). In these species, unfertilized, queen-laid eggs develop into female sexuals, whereas fertilized eggs develop into workers. In addition, males of *Wasmannia auropunctata* appear to develop from fertilized eggs after exclusion of the maternal nucleus (FOURNIER & al. 2005), resulting in the unique and bizarre situation of male and female sexuals forming completely separate genetic lineages.

In many plants and animals, parthenogenesis arises through hybridization and involves polyploidy or aneuploidy, but there is little evidence for these phenomena in ants. Thelytokous *Platythyrea punctata* has a chromosome number of  $2n = 84$  (K. Schilder, unpubl.), which is much higher than in *Platythyrea quadridenta* ( $2n = 18$ , IMAI & al. 1983), with reproduction by mated workers and queens (ITO 1990), but similar to that in *Platythyrea tricuspidata*, another species with "normal" reproduction ( $2n = 92-94$ , IMAI & al. 1983, 1990). This enormous intrageneric diversity in karyotype might simply reflect the surprising instability of chromosome numbers also known from other genera (e.g., IMAI & al. 1990) rather than explain the origin of thelytokous parthenogenesis.

Thelytoky in ants also appears to be independent of infestation with endosymbiotic bacteria, which commonly causes the production of diploid offspring by virgin females in solitary Hymenoptera (*Wolbachia* and microsporidians, STOUTHAMER & al. 1990, STOUTHAMER & WERREN 1993, WERREN & al. 1995, ZCHORI-FEIN & al. 2001). Though infections with *Wolbachia* are widespread among ants (WENSELEERS & al. 1998, REUTER & KELLER 2003, VAN BORM & al. 2003), treatment with antibiotics did not "cure" any case of thelytoky (K. Schilder, unpubl. in SCHILDER & al. 1999) and *Wolbachia*-specific primers did not reveal the presence of these bacteria in thelytokous ants (GRASSO & al. 2000, WENSELEERS & BILLEN 2000). In the Cape honeybee, *Apis mellifera capensis*, thelytokous parthenogenesis appears to be genetically determined by a single locus, which also influences other traits, such as egg production and the synthesis of queen pheromones by fertile workers (LATTORFF & al. 2005, 2007), but similarly thorough genetic analyses have as yet not been done with thelytokous ants.

Proximally, thelytoky can involve several cytogenetic mechanisms, which differently affect progeny genotype. Automixis, the mechanism most commonly reported in

Hymenoptera, involves the fusion of two haploid cells after meiosis, and, like inbreeding, usually results in increased homozygosity (SUOMALAINEN & al. 1987, VAN WILGENBURG & al. 2006). In the Cape honey bee, it is due to the fusion of the two central polar nuclei of the second meiotic division (central fusion, VERMA & RUTTNER 1983). Nevertheless, offspring are often genetically identical to their mother, because of a reduced rate of recombination (MORITZ & HABERL 1994, BAUDRY & al. 2004). In contrast, automixis in *Cataglyphis cursor* is associated with a considerable reduction of heterozygosity, which, however, is counteracted by the occasional production of female sexuals from fertilized eggs and predominantly also from unfertilized, worker-produced eggs (PEARCY & al. 2004, 2006). From the clonality of colonies of *Platythyrea punctata* and the high heterozygosity at five microsatellite loci, SCHILDER & al. (1999) concluded that thelytoky here is due to ameiotic parthenogenesis (apomixis).

The ultimate causes of thelytoky in ants are even less well understood. At present, the ease with which colonies of *Cerapachys biroi*, *Pristomyrmex punctatus*, or *Platythyrea punctata* undergo budding makes them adept colonizers of man-made, disturbed habitats. But because clones cannot easily adapt to environmental changes, obligate thelytoky might be a short-lived phenomenon that sooner or later vanishes. Evolutionary perspectives are different when thelytoky is combined with mating and recombination. For example, in *Platythyrea punctata*, males, gamergates, and mated or virgin queens sporadically occur in the Caribbean populations, and a single colony studied from mainland Central America had three gamergates and workers that were incapable of thelytoky (HARTMANN & al. 2005). Similarly, thelytoky and sexual reproduction co-occur in *Cataglyphis cursor* and *Wasmannia auropunctata*, in which workers generally develop from fertilized eggs while queens develop through thelytoky from queen-laid or, in *C. cursor*, also worker-laid eggs. This pattern leads to a high genetic diversity of workers, which helps colonies to better cope with environmental stress. At the same time, mother queens efficiently transmit all their genes to their female sexual offspring, which, because they found by budding, are usually protected against environmental changes by the workers.

A related pattern of non-environmental caste differentiation has been documented from several genetically different lineages of *Pogonomyrmex* harvester ants and *Solenopsis* fire ants, where diploid eggs resulting from cross-lineage mating develop into workers, whereas diploid eggs resulting from within-lineage mating develop into queens (for a review see NONACS 2006 and references therein). Colonies with multiply-mated *Pogonomyrmex* queens or multiple, single mated *Solenopsis* queens therefore exhibit genetic division of labor between heterozygous workers and homozygous female sexuals. Sperm of those males, which ended up mating with a female sexual from the "wrong" lineage or species, is only used to produce non-reproductive workers. Males are therefore selected to evolve counter-measures. The strange pattern of reproduction in *Wasmannia auropunctata* mentioned above, with the exclusion of the maternal nuclei from fertilized eggs to produce males (FOURNIER & al. 2005), might be the males' strategy to regain fitness after genetic caste determination had evolved (UMPHREY 2006).

It is quite likely that the increasing availability of sensitive genetic markers will lead to the detection of additional cases of unexpected genetic systems in ants and other social Hymenoptera. In addition to thelytoky and genetic caste determination new mechanisms of sex determination may be discovered. For example, diploid males have repeatedly been found to be functionally reproductive and to produce viable offspring in both solitary and social Hymenoptera (COWAN & STAHLHUT 2004, LIEBERT & al. 2004), while the absence of such diploid males even after 10 generations of prolonged brother-sister mating in *Cardiocondyla obscurior* (SCHREMPF & al. 2006) suggests a sex determination mechanism other than the usual single-locus complementary sex determination.

**Relation to relatedness:** The occurrence of thelytokous parthenogenesis, genetic caste determination, and hybridization may scramble nestmate relatedness and inclusive fitness considerations. For example, the life-for-life relatedness between workers of *Cataglyphis cursor* and clonally produced female sexuals is considerably less than 0.75 (PEARCY & ARON 2006), and hybrid workers offspring of *Solenopsis xyloni* queens that mated with *S. geminata* males do not have any sexual sisters (HELMS CAHAN & VINSON 2003).

### The erosion of relatedness = the fall of kin selection theory?

En outre, les théories d'inspiration darwinienne expliquant l'apparition de l'altruisme dans les populations animales par un avantage sélectif qui en résulterait pour l'ensemble du groupe ont fait l'objet de calculs imprécis, multiples, contradictoires, avant de finalement sombrer dans la confusion et l'oubli.

Michel Houellebecq, La possibilité d'une île

Though insect societies are generally more or less complex families composed of relatives, genetic data document that nestmate relatedness is often much lower than the magical value of 0.75. Does the frequent occurrence of polygyny, polyandry, and other, more unusual deviations from the traditionally assumed genetic and social structure of insect societies make Hamilton's inclusive fitness theory obsolete? Not at all.

Several authors have argued that because many insect societies are composed of only distantly related individuals, kin selection and inclusive fitness must be less important for the evolution and maintenance of eusociality than traditionally assumed (e.g., WILSON 2005). Of the numerous alternative explanations for the origin and maintenance of sociality, most have meanwhile turned out to be inapplicable, re-formulations of inclusive fitness theory, or simply wrong. But once opened, this Pandora box of alternative models has been difficult to close, and "kin selection bashing" has not only led to agitated discussions in scientific journals but also found its way into fine arts, as exemplified by the above-cited quotation.

Almost 30 years ago DAWKINS (1979) attempted to correct common misunderstandings of kin selection theory, but many of them still abound. I do not intend to repeat all the arguments that have been brought forward in defense of kin selection theory. They are nicely summarized in a number of recent papers (e.g., FOSTER & al. 2006a, b,

LEHMANN & KELLER 2006, HELANTERÄ & BARGUM 2007, WEST & al. 2007). Instead, I will shortly focus on just three important issues.

First, though it is almost unanimously agreed that kinship is important in the evolution of sociality, the role of exceptionally high relatedness, such as among fullsisters in Hymenoptera, has occasionally been over-emphasized after the publication of Hamilton's twin papers and the advance of molecular methods for quantifying kinship into insect sociobiology (e.g., WEST & al. 2007). A number of researchers erroneously adopted the idea that haplodiploidy with its 0.75 relatedness among fullsisters is the explanation of eusociality. Ingenious calculations were made to explain eusociality in termites through inbreeding cycles or chromosome structure (BARTZ 1979, LACY 1980) but were quickly shown to be incorrect (e.g., CROZIER & LUYKX 1985). It has long been known that the asymmetric genetic relationships resulting from haplodiploidy alone do not explain the evolution of eusociality (e.g., BOURKE & FRANKS 1995, CROZIER & PAMILO 1996). HAMILTON's inequality ( $C < rB$ ) consists of three components, and relatedness is just one of them. Helping can be stable even at low levels of relatedness  $r$ , if it is associated with an appropriate ratio of benefits  $B$  and costs  $C$ , which depends, for example, on the ecology of a given species (e.g., HAMILTON 1964, KORB & HEINZE 2004, in press, FOSTER & XAVIER 2007). Furthermore, in particular the highly social insects appear to have reached a level of mutual interdependence at which within-group selection is overridden by between-group selection. Variation in kinship among nestmates has therefore probably less influence on an individual's inclusive fitness than overall group performance, which minimizes individual selfishness.

Second, relatedness is not a simple, absolute quantity. Though population genetic studies appear to be straight forward and made simple through handy software packages, the exact meaning of relatedness and the appropriate level of analysis of inclusive fitness may occasionally remain vague to non-specialists (e.g., DAWKINS 1979, QUELLER 1996). Relatedness is a measure of similarity among individuals relative to the average similarity in a reference population, which is defined as zero. It is vitally important that the correct reference population is chosen to understand the fitness interests of individuals. For example, *Cardiocondyla* males are often extremely close relatives due to inbreeding and intranidal mating. It may therefore seem counter-intuitive that they nevertheless engage in lethal fighting for access to female sexuals (e.g., KINOMURA & YAMAUCHI 1987). However, because male competition is local, the appropriate level of analysis is the nest, and the level of kinship becomes unimportant, as explicitly shown for the case of lethal fighting among fig wasp males (WEST & al. 2001).

Third, inclusive fitness theory and new group selection models are not mutually exclusive ways of explaining cooperation and altruism but have long been shown to be mathematically congruent (e.g., QUELLER 1985, LEHMANN & KELLER 2006, WEST & al. 2007). Either approach may have its particular advantages over the other in a certain context, but they make essentially the same predictions about which conditions favor the evolution and maintenance of cooperation.

## Conclusion

It's only when you look at an ant through a magnifying glass on a sunny day that you realize how often they burst into flames.

Harry Hill

Careful investigations of ant societies, be it with behavioral, sociometric or molecular methods, again and again prove that ants are a magic well, to use a well-known quotation by Karl von Frisch about his favorite social insects, the honey bees. Honey bee researchers have a choice of just a dozen species, but myrmecologists can select among approximately 13,000 species. This certainly has many advantages – ants provide suitable model systems for studying almost every zoological problem, be it about orientation, self-organization, chemical or tactile communication, invasiveness, symbiosis, or parasitism. But this fascinating diversity is also associated with disadvantages – for each problem there is a different suitable model system. While researchers studying the ecology, physiology, and genetics of honey bees all had to adjust their methodology to the specific requirements of *Apis*, visual orientation in ants is studied in *Cataglyphis*, male reproductive tactics in *Cardiocondyla*, and territoriality in *Myrmecocystus* and *Pogonomyrmex*. While honeybee researchers quickly agreed about which genome to sequence, there are so many fascinating ants that we will have to wait a while longer before the first complete ant sequence will be published.

Furthermore, though substantial progress has been made after Tschinkel's request for more comprehensive data collection (TSCHINKEL 1991), we are still far from understanding the evolution of ant life histories, and enormous gaps still exist in our knowledge of fundamental characteristics even of well-studied species. We are still lacking a general theory of the variation of colony cycles in social insects (STARR 2006) and methods for determining the age distribution of insect societies, and unknown numbers of species with bizarre colony structures are waiting to be discovered. Myrmecology has a promising future.

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## Zusammenfassung

Ameisenstaaten sind sehr viel unterschiedlicher strukturiert als oft angenommen wurde. Die Variabilität der Anzahl und Paarungshäufigkeit von Königinnen ist Myrmekologen seit langem vertraut. Daneben konnten jüngste Untersuchungen aber auch Phänomene, wie etwa die Produktion von Weibchen aus unbefruchteten Eiern oder eine genetische Kastendetermination aufdecken, die ebenfalls die genetische und soziale Struktur von Ameisenstaaten beeinflussen. Offensichtlich bestehen Kolonien eines großen Teils der Ameisenarten nicht aus einer einzigen, einfach begatteten Königin und ihren sterilen Nachkommen, den Arbeiterinnen. Zwar ist schon lange bekannt, dass Verwandtenselektion auch ohne eine Verwandtschaft von 0,75 zu reproduktivem Altruismus führen kann, aber die neu entfachte Diskussion über die Rolle der Verwandtschaft in der Verwandtenselektionstheorie mag sowohl bei Myrmekologen als auch bei Laien zu Verwirrung geführt haben.

Ziel dieser Abhandlung ist es, einen Überblick über das Spektrum der Strukturen von Ameisenstaaten zu geben und einige falsche Vorstellungen über die Rolle des Werts 0,75 in der Theorie der Verwandtenselektion zu korrigieren.

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