Ant Reproductive Strategies

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Abstract. In contrast to what is generally believed, the reproductive strategies of ants are remarkably diverse and include such different phenomena, as wingless female and male sexuals, reproduction by mated workers, thelytokous parthenogenesis, and complete workerlessness. We review the various reproductive life histories and investigate them in the light of recent models on the evolution of dispersal strategies and multiple-queening. It appears that most deviations from "normal" colony propagation can be explained by a decreased success of dispersal and solitary founding by solitary queens in certain types of habitats. Consequently, alternative reproductive strategies are found especially in those species, in which environmental conditions or a highly specialized way of life are thought to make solitary founding costly. Among the key factors, which determine the success of reproductive strategies, appear to be spatial and temporal distribution of habitats and the availability of nest sites.

Key words: dispersal, life history, queen number, wing polymorphism, ants.

Introduction

To most people, and not so long ago even to many specialists devoted to the study of social insects, ant reproduction is unexcitingly simple and uniform. It is generally believed that in the vast majority of species, males and virigin queens mate during a swarming and dispersal flight, after which the males die and the queens shed their wings, seal themselves off in a small cavity and begin to lay eggs. Mature colonies are thought to contain typically a single queen ("monogyny"), and because she is singly-mated ("monandry"), the high genetic relatedness between workers and female sexual offspring results which, as many people assume, lies at the heart of Hamilton's kin selection theory (Hamilton 1964).

Exceptions from this fundamental reproductive life history have been known for a long time (Wheeler 1910; Wilson 1971; Hölldobler and Bartz 1985; Hölldobler and Wilson 1977, 1990), but only over the past few years it has become evident that these exceptions are by far more common than previously assumed. Rather than being adaptations of a small number of ant species specialized to

peculiar life histories, exceptional reproductive strategies appear in fact to be more widespread than swarming flight, monogyny and monandry, and ants, in which nestmate workers are sterile fullsisters, are perhaps only a minority.

Several papers have focussed on the evolutionary significance of variation in queen number and mating frequency (Buschinger 1974; Keller 1993; Bourke and Heinze 1994; Keller and Reeve 1994a). However, the presence of several queens per colony ("polygyny") and mating with multiple males ("polyandry") appear to be just the tip of an iceberg of alternative reproductive strategies, which include phenomena, such as polymorphic queens and males, queenless workers, workerless parasitic queens, and long-lived males, which monopolize harems of queens.

In this review we want to document the diversity of ant reproductive strategies and to connect the various types of reproduction to models which have been designed to explain multiple-queening in ants (Hölldobler and Wilson 1977; Rosengren and Pamilo 1983; Rosengren et al. 1993; Bourke and Heinze 1994; Tsuji and Tsuji in press) and dispersal polymorphism in non-social insects (Harrison 1980; Roff 1986; Wagner and Liebherr 1992; Denno 1994). We will do so by, firstly, outlining current models for the evolution of multiple-queening in ants, which relate queen-number to the costs of dispersal and non-

dispersal. Secondly, we summarize data which show that variation of queen morphology may in a similar way be correlated to dispersal strategies. Thirdly, we extend the dispersal model to those species in which queens and workers both may reproduce sexually, or in which morphological queens have been lost, and, fourth, we examine the origin of social parasitism in ants in the light of dispersal strategies. In a last paragraph we summarize observations on the occurrence and significance of polymorphic males in ants.

Queen number and dispersal strategies in ants

In a number of studies it has been shown that inter- and intraspecific variation in queen number is part of a more fundamental dichotomy between two different colony founding strategies (e.g., Hölldobler and Wilson 1977, 1990; Keller 1991; Keller 1993). Monogyny is typically associated with mating on the wing, dispersal, and independent colony founding, whereas in polygynous species queens mate within the nest or in its immediate neighborhood and new colonies are founded by the fragmentation of large colonies, i.e., "budding". Colony subunits may grow into completely separated, mutually hostile colonies or, as in some *Formica* wood ants, may retain firm ties to the maternal colony with the exchange of workers, brood, and reproductives. In the latter case, colonies thus may become "polydomous", i.e. inhabit several nest sites. In some "unicolonial" species, colony boundaries have been lost completely and the whole species can be considered to form a single huge polydomous colony.

Among the hypotheses which have been proposed to explain variation in queen number, several explicitly or indirectly interprete founding strategy as a tradeoff between the costs of staying and the costs of dispersal (Rosengren and Pamilo 1983; Rosengren et al. 1993; Reeve and Ratnieks 1993; Heinze 1993; Keller and Reeve 1994b; Bourke and Heinze 1994), and thus employ models which more generally explain dispersal polymorphisms (Hamilton and May 1977; Roff 1986; Johnson and Gaines 1990). Whenever dispersal and solitary founding is more costly than staying, selection favors queens which seek adoption into established colonies instead of founding their own colonies independently. An increase in dispersal costs may lead to a larger fraction of non-dispersing queens. Founding costs are affected by habitat characteristics, such as the availability of empty nest sites, climate, predators etc., whereas staying costs include decreased individual fertility (Wilson 1974; Mercier et al. 1985ab; Keller 1988; Vargo and Fletcher 1989), increased reproductive competition in multiply-queened societies (Rosengren and Pamilo 1983;

Reeve and Ratnieks 1993; Heinze et al. 1994), and increased local competition for resources such as food and nesting sites (Fortelius et al. 1987). Multiple queening may also decrease intracolonial relatedness (e.g., Rosengren et al. 1993).

Variation in queen number and female tactics can also be discussed in terms of life history strategies. For example, dispersal by budding may be favored if ant populations are unstable over longer periods of time and/or show fluctuations independent of nest density. In these cases, intrinsic growth rate (r-value) rather than lifetime reproductive success determines the fitness of a certain life history strategy (Tsuji and Tsuji in press). One can assume that if empty niches regularly become available in a habitat, a bud consisting of queens and workers can easily outcompete solitarily founding queens, both because they can quickly acquire and defend new nest sites and because they have a higher growth rate. Queens accompanied by workers have a higher initial fecundity and produce sexuals earlier than solitary queens. Hence, polygynous species may more quickly dominate new vacant habitat patches once they have been successfully reached by first founding individuals, provided that new empty nest sites are near enough to be reached by budding or nest sites are constructed by the ants themselves (Hölldobler and Wilson 1977; Rosengren and Pamilo 1983). Multiple-queening and budding can thus be considered to be r-selected and adaptive in short-lived habitats by an enhanced benefit of staying. Ant species characterized by a high propagation rate are indeed among the most successful cosmopolitan tramp species, i.e. *Monomorium pharaonis*, *Cardiocondyla nuda*, and *Linepithema humile* (formerly *Iridomyrmex humilis*). Their queens are incapable of solitary founding and often of flight, and new nests are founded mainly by budding (e.g., Hölldobler and Wilson 1977, 1990; Heinze et al. 1993). A survey of the ant fauna of Okinawa suggests that polygynous ants, especially tramp species, are more abundant in open country than in primary forests (Tsuji and Tsuji in press; Yamauchi and Ogata 1995).

Polygyny may also have evolved in stable habitats where density-dependent processes keep ant populations at an equilibrium close to saturation without large temporal fluctuations. Here, natural selection might favor strategies which increase population density or carrying capacity in terms of number of reproductive females per habitat patch. In saturated habitats, colony founding by a single dispersing queen might become difficult because of nest site limitation and strong competition with established colonies. The readoption of daughter queens in established colonies will thus become evolutionarily stable (see also Buschinger 1990a, who concluded that polygynous species are K-selected). If nest density and the number of workers per colony remain unchanged, the effective population size

will thus be increased by polygyny. Mathematical models for the evolution of polygyny in ants, which implicitly assume stable populations (Nonacs 1988; Pamilo 1991ab), are probably fully compatible with this explanation (Tsuji and Tsuji in press).

The two extremes outlined above may roughly correspond to the two polygyny syndromes described by Hölldobler and Wilson (1977), i.e. the opportunistic nesters in short-lived habitats and the patchy habitat dwellers. The theoretical distinction between these two types lies in the mode of population regulation in the relevant habitats or the strength of density dependent selection for alternative tactics.

Queen-polymorphism

As the term implies, solitarily founding queens do not have the support of workers to excavate a nest cavity, to forage, and to nurse the brood. Foraging is associated with high mortality in ants (e.g., Porter and Jorgensen 1981; Schmid-Hempel 1984; Hölldobler and Wilson 1990), and the success of solitary founding could be strongly increased if queens were endowed with enough body reserves to survive, lay eggs, and rear their first young without being provisioned with food over several weeks or months. Whereas especially in Ponerinae and Myrmeciinae, but also in several Myrmicinae, queens have to leave their founding cavity to forage (e.g., Wheeler 1933; Haskins and Haskins 1950, 1951; Peeters in press), in many of the "advanced" Myrmicinae and Formicinae foundresses seal themselves off in their nest cavity without ever returning to daylight (claustral founding; Wheeler 1933; Hölldobler and Wilson 1990). Queens adapted to dispersal and claustral founding are characterized by voluminous wing muscles and fat reserves, on which they at least in part rely during independent colony founding. The construction and provisioning costs could be economized when queens do not disperse. Several studies have indeed shown that queens in polygynous species are smaller and have less fat reserves than queens in related monogynous taxa (Buschinger 1974; Keller and Passera 1989; Passera and Keller 1990). Intraspecific size variation has likewise been thought to be associated with alternative dispersal strategies. In several *Myrmica* species, two discrete queen size classes exist; the smaller "microgynes" mate near the maternal nest, whereas "macrogynes" disperse and found solitarily (Brian and Brian 1949, 1955; Elmes 1991). Similarly, in *Pseudomyrmex venefica*, smaller queens are apparently more easily readopted into the maternal nest (Janzen 1973). In several *Formica* (e.g., Seifert 1991) and *Leptothorax* (Buschinger 1967), queens from monogynous colonies are on average larger than queens from polygynous colonies, and in *Formica truncorum* (Sund-

ström 1995) and *Vollenhovia emeryi* (K. Yamauchi and K. Tsuji unpublished), virgin queens produced in polygynous colonies are on average lighter or smaller than virgin queens produced in monogynous colonies and less prone to dispersal. In the fire ant, *Solenopsis geminata*, smaller queens reared in fall seek adoption in orphaned colonies, whereas larger queens reared in spring found solitarily (McInnes and Tschinkel 1995; W. Tschinkel personal communication). In *Solenopsis invicta*, queen weight and size differ significantly between conspecific monogynous and polygynous populations (Keller and Ross 1993). In contrast to *Myrmica*, where the gene pools of microgynes and
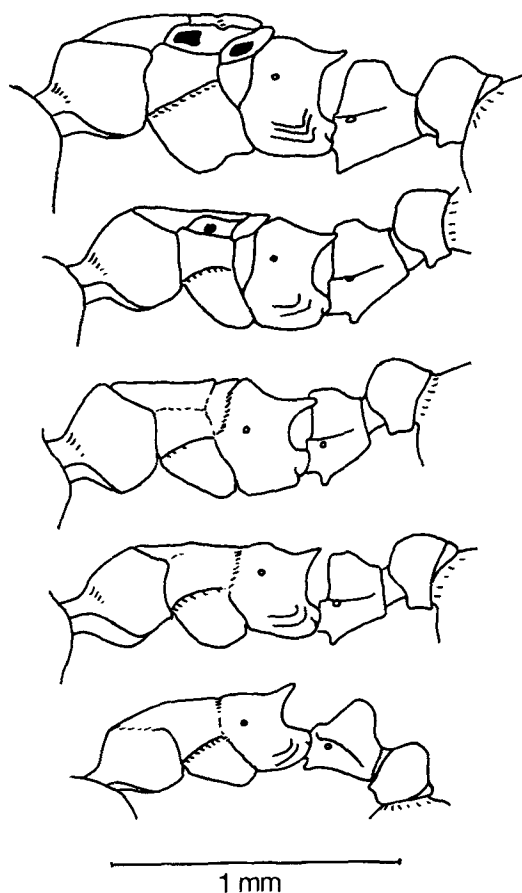

1 mm

Fig. 1. Schematical drawing of the alitrunk, petiole and postpetiole (in lateral view) of an originally winged queen (top), three wingless "intermorphic" queens with different degrees of reduction of thoracic sclerites, and a worker (bottom) of the ant *Leptothorax* sp. A from Québec. The black patches in the alitrunk of the originally winged queen indicate what remains of the wings when they are shed after mating. In the uppermost wingless queen, the black dot indicate strongly sclerotized vestiges of wings. Despite the enormous, highly heritable variation in external morphology, intermorphic queens and originally winged queens are indistinguishable in function and the structure of their ovaries (see also Heinze and Buschinger 1987, 1989).

macrogynes are at least partly separated and where in some species microgynes are considered to be distinct species (Elmes 1978, 1991; Seifert 1993), extensive gene flow exists between the monogynous and polygynous populations of *Solenopsis invicta* (Ross and Shoemaker 1993) and queen variation appears to result from phenotypic plasticity; offspring of polygynous colonies reared in monogynous nests developed into large queens and vice versa (Keller and Ross 1993).

The complete reduction of characters associated with dispersal and solitary founding, i.e. wings, ocelli, and thoracic sutures, is just one further step beyond size variation. In the weaver ant, *Polyrhachis doddi*, mesonotal structures are strongly reduced in smaller queens, though all sclerites and also the wings, though often degenerate, are typically retained (Heinze and Hölldobler 1993a), and *Vollenhovia emeryi* queens from polygynous populations often have degenerate wings (K. Yamauchi personal communication). Completely apterous, i.e. originally wingless, female reproductives with more or less greatly fused thoracic sclerites and reduced ocelli have been

known from some species for more than 100 years (Wasmann 1890, 1897; Forel 1904; Holliday 1903; Wheeler 1917, 1937; Ezhikov 1934), but only recent detailed studies have shown that wing reduction in ant queens is a rather wide-spread phenomenon (Peeters 1991a; Villet et al. 1991; Buschinger and Heinze 1992; Tinaut and Heinze 1992). Apterous female reproductives, also referred to as "apterogynes", "ergatoid queens", "ergatogynes", "reproductive intercastes", and "intermorphic queens", occur in almost every subfamily of the Formicidae, but are especially common in the "primitive" Ponerinae and Myrmeciinae and, among the higher ants, in army ants and the myrmicine genera *Monomorium*, *Megalomyrmex*, *Ocymyrmex*, and others (Bolton 1986; DuBois 1986, Brandão 1987; Forder and Marsh 1989; Table 1). They may differ enormously from workers in morphology, as in many ponerines and army ants, but may be virtually indistinguishable from workers in other species, distinct only in the anatomy of their ovaries, size, or the presence of feebly impressed thoracic sutures and vestigial ocelli, as in *Megalomyrmex* or *Leptothorax* (Fig. 1). In at least

Table 1. Occurrence of wingless reproductives in ants (based on Loiselle and Francoeur 1988; Buschinger and Heinze 1992; Tinaut and Heinze 1992; Peeters 1991ab, 1993, in press; Ito and Ohkawara 1994, and others).

1. Wingless female reproductives

a) apterous and short-winged (brachypterous) queens

Cerapachyinae: several species of *Acanthostichus*, *Cerapachys*, *Sphinctomyrmex*

Dolichoderinae: several species of *Leptomyrmex* and *Technomyrmex* (a/w)

Dorylinae: all species

Ecitoninae: all species

Formicinae: *Proformica* spp., *Aporomyrmex ampeloni* (a/w), *Polyergus* spp. (a/w), *Cataglyphis* spp. (b, a)

Leptanillinae: all species

Myrmeciinae: *Myrmecia* spp. (a, a/w, b/w)

Myrmicinae: *Aphaenogaster* spp., *Blepharidatta brasiliensis*, *Calyptomyrmex* spp., *Crematogaster biroi*, *Ephebomyrmex* spp. (*imberbiculus* and *pima* [a/w], *huachucanus* [b]), *Forelomyrmex mayri*, *Formicoxenus* spp. (a/w), *Harpagoxenus sublaevis* (a/w), *Leptothorax* spp. (*paraxenus* [a/w], *wilsoni* [b/w]), *Lordomyrma* spp., *Megalomyrmex* spp. (a, a/w), *Monomorium* spp. (a, b, a/w), *Myrmecina* spp. (a/w), *Octostruma* spp., *Ocymyrmex*, *Pogonomyrmex* spp., *Stereomyrmex horni*, *Vollenhovia emeryi* (b), *Terataner*

Nothomyrmeciinae: *Nothomyrmecia macrops* (b)

Ponerinae: several species of *Discothyrea*, *Gnamptogenys*, *Heteroponera*, *Hypoponera* (a/w), *Leptogenys*, *Megaponera*, *Odontomachus* (a/w), *Onychomyrmex*, *Pachycondyla* (a/w), *Ponera*, *Platythyrea*, *Plectroctena*, *Prionogenys*, *Proceratium*, *Simopelta*

b) Gamergates

Ponerinae: several species of *Amblyopone*, *Diacamma*, *Dinoponera*, *Gnamptogenys*, *Hagensia*, *Harpegnathos*, *Leptogenys*, *Ophthalmopone*, *Platythyrea*, *Plectroctena*, *Rhytidoponera*, *Streblognathus*

2. Wingless male reproductives

Dolichoderinae: *Technomyrmex albipes*

Formicinae: *Aporomyrmex ampeloni* (a/w), *Plagiolepis xene*

Myrmicinae: *Anergates atratulus*, *Cardiocondyla* spp., *Crematogaster atitlanica*, *Formicoxenus* spp., *Pheidole neokohli* and *acutidens*

Ponerinae: *Hypoponera*

a, species with completely wingless, apterous reproductives; *b*, species with brachypterous reproductives; *a/w*, species with both apterous and winged reproductives.

two closely related species, the palaearctic slave-maker *Harpagoxenus sublaevis* and the nearctic *Leptothorax* sp. A, breeding experiments suggest that wing loss is caused by a dominant allele, E, (Buschinger 1975, 1978; Heinze and Buschinger 1989): the female progeny of a winged queen, ee, mated to the son of another winged queen, are winged, whereas female sexuals produced by a wingless queen mated to the son of another apterous queen are typically wingless "intermorphic queens" (Fig. 2). Similar single-locus, two-allele genetic mechanisms of wing morph determination are common in polymorphic non-social insects, and the allele causing wing loss or brachyptery is almost always dominant (Roff 1986, 1992, 1994a). It can thus be easily conceived that a "winglessness allele" can be carried from patch to patch by winged queens inseminated by male bearers of this allele. The loss of wings is associated with a reduction of thoracic sclerites. In *Leptothorax* sp. A, virgin queen offspring from crosses of a winged mother and the son of an intermorphic queen are wingless, but retain some of the thoracic sutures, which are more strongly reduced in homozygous intermorphic queens. Regression of the average thorax phenotype of female sexual progeny produced in 23 colonies against the midparent value (the mean of the phenotypes of the mother and the father's mother, as queen polymorphism does not affect male thorax morphology; remember here that males in Hymenoptera arise from unfertilized eggs) gives a heritability h_N^2 of 0.84, which, however, includes maternal effects (J. Heinze unpublished).

There is some evidence that queen polymorphism in non-parasitic ants is associated with alternative dispersal strategies and thus can be explained by the same models as wing dimorphism in non-social insects (Harrison 1980; Roff 1986) or queen number variation (Bourke and Heinze 1994). In *Leptothorax* sp. A, direct observations suggest that similar to *Myrmica* macro- and microgynes, the winged and apterous queens follow different dispersal and colony founding strategies: most winged queens mate only after extended ground swarming, whereas wingless queens mate in the immediate neighborhood of their maternal nest (Heinze 1993). Similarly, from two field observations, Briese (1983) concluded that colonies of an
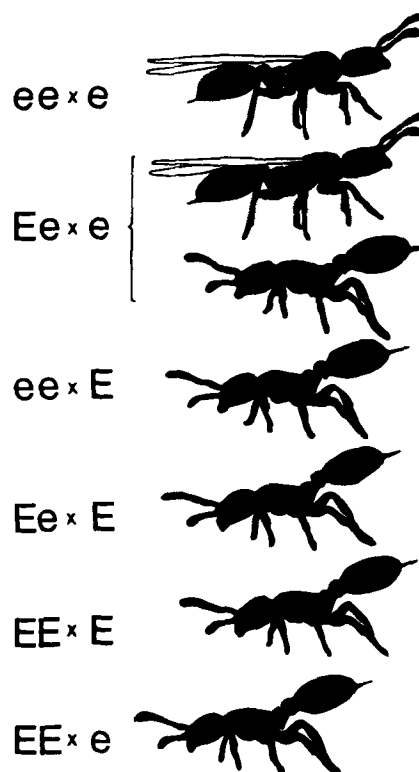

Fig. 2. Mating scheme illustrating how a single diallelic locus controls queen polymorphism in the ants *Harpagoxenus sublaevis* and *Leptothorax* sp. A. The schematical drawings show winged and wingless virgin queens in the sexual calling posture, in which they attract males with droplets of sex pheromone from the poison gland.

undescribed Australian species of *Monomorium* (*rothsteini* group) produce wingless queens, which found new nests by budding, under conditions of drought, but winged, dispersing queens when environmental conditions are favorable. In *Leptothorax* sp. A and several other species, indirect evidence further supports the idea that wingless reproductives are sedentary and winged queens are dispersers: colonies of *Leptothorax* sp. A, Australian *Monomorium* sp. 10, *Myrmecina graminicola* from Japan,

Table 2. Composition of colonies of several queen-polymorphic ant species, suggesting that queen morphs are associated with alternative dispersal strategies. Colonies containing both mated winged and wingless queens are not included. Not all queens were dissected (data from Ohkawara et al. 1993; Heinze 1993; Buschinger and Heinze 1992; J. Heinze and K. Schilder unpublished).

Species	Colonies with originally winged queens		Colonies with wingless female reproductives	
	single queen	multiple queens	single queen	multiple queens
Myrmecina graminicola	50	0	20	10
Ephebomyrmex imberbiculus	3	0	22	22
Leptothorax sp. A	125	14	271	98
Monomorium sp. 10	46	2	21	80

and *Ephebomyrmex imberbiculus* from arid North America, mostly contained either a single originally winged queen or several apterous queens or intercastes (Heinze 1989; Buschinger and Heinze 1992; Ohkawara et al. 1993; J. Heinze and K. Schilder unpublished; Table 2).

Gamergates or Thelytoky

In many species of Ponerinae, all workers possess a spermatheca and are capable of mating and of laying fertilized eggs (Peeters and Crewe 1985; Peeters 1991b, 1993). Fertile, mated workers have been termed "gamergates". Which of the workers mate and reproduce and which do not may be determined by mutilation, overt aggression or ritualized dominance behavior (Fukumoto et al. 1989; Peeters and Higashi 1989; Peeters et al. 1992; Ito and Higashi 1991). Winged queens disperse whereas gamergates found new nests by budding (e.g., Ward 1983; Peeters 1993).

It is intriguing that in none of the numerous species with gamergates, apterous queens have been reported. If apterous queens and gamergates fulfill the same function (occupy the same functional niche), the evolution of species with both gamergates and apterous queens is unlikely. A possible exception is *Platythyrea punctata*, where in addition to mated queens, gamergates, and workers, which produce diploid offspring from unfertilized eggs by thelytokous parthenogenesis, morphological intermediates between queens and workers occur. Whether the latter have a reproductive function is as yet unknown (Schilder et al. 1995).

In a small number of species, workers do not have the capability to mate but nevertheless produce diploid, female offspring by means of thelytokous parthenogenesis. This opens the possibility that new colonies may be founded alternatively by winged queens or queenless worker groups. The co-existence of thelytoky and sexual reproduction was first demonstrated in the desert ant *Cataglyphis cursor* (Cagniant 1979, 1983), however, it is not known whether budding by queenless worker groups occurs in this species (Lenoir and Cagniant 1986; Lenoir et al. 1988). In contrast, in *Platythyrea punctata*, some 90 percent of all field-collected colonies were queenless and several contained only unmated workers. Isolation of unmated workers demonstrated that they are capable of raising female offspring, both workers and virgin queens, from unfertilized eggs. Both queens and workers may occasionally mate and thus increase genetic variation, which explains the formation of dominance hierarchies among the workers (Heinze and Hölldobler 1995; K. Schilder personal communication). In obligatorily thelytokous *Pristomyrmex pungens* and *Cerapachys biroi*, which at least in Japan also shows obligatory thelytoky, new colonies are frequently founded by bud-

ding or colony fission (Itow et al. 1984; Tsuji 1988ab, 1990; Tsuji and Yamauchi 1995).

The ecology of wing loss

In non-social insects, several studies indicate that genes causing winglessness will spread even when the probability to mate and reproduce is equal in winged and wingless forms. Wingless forms develop faster, start to lay eggs sooner and are more fecund than winged forms, probably because energy can be diverted to reproduction from flight and the construction and maintenance of the flight apparatus (Roff 1986, Zera and Mole 1995; but see Aukema 1991). This trade-off between reproduction and dispersal is less simple in social insects (Tinaut and Heinze 1992). Here, flight is a transient phenomenon, limited to the short period of mating, after which claustrally founding queens histolyze their flight muscles and use their body reserves to produce first batches of eggs and to nourish the first larvae, often without feeding during the whole period of solitary colony founding. After this phase has been completed, be it solitarily or in the case of colony fragmentation with the help of workers, the morphology of a queen's alitrunk is no longer important, and in the few ant species studied in this respect there is indeed little evidence for different egg laying rates in winged and wingless queens (Winter and Buschinger 1986; Heinze and Buschinger 1989).

Another trade-off exists on colony level. Where solitary founding has been completely or partially replaced by colony fragmentation or parasitic colony founding, a colony could produce more wingless queens with the same amount of energy than well-equipped winged queens. As resources invested in those workers which emigrate during budding must be counted as resources invested in the wingless queens, Villet (1989, 1991) questioned, whether energetic constraints alone are sufficient to cause winglessness in ant queens; instead, wings might be lost due to the unresisted accumulation of mutations in species which have switched to dependent founding, similar to the loss of eyes in cave-dwelling animals (Villet 1989). However, if colonies are founded by budding, it will always pay a colony to counterbalance some of the drain inflicted by emigrating workers by reducing the investment in queens.

Which environments promote the loss of dispersal? In non-social insects, temporal stability (Darlington 1943; Southwood 1977; Roff 1986, 1994a), spatial patchiness of habitat (e.g., den Boer 1970), and the high energetic costs of flight in cold or wind-exposed areas (Heppner 1991; Wagner and Liebherr 1992) are thought to favor the non-dispersing, wingless forms. Dead trees, both patchy and temporally stable resources, appear to be especially rich in

wing-polymorphic species (Hamilton 1978). In ants, numerous ecological conditions have been identified which appear to favor budding over solitary founding, including cold climate, limitation of food or nest sites, habitat patchiness and nest site instability (for reviews, see Hölldobler and Wilson 1977, 1990; Herbers 1993; Bourke and Heinze 1994). Winglessness in female reproductives is therefore expected to occur predominantly under conditions which decrease the relative success of solitary founding. Previously proposed hypotheses, which explain the evolution of winglessness in certain species by specialization to prey which cannot be handled by solitary queens (Villet 1989), obligate mutualistic relationships to symbionts, which require the help of workers (Maschwitz and Hänel 1985), or high colony founding costs in patchy habitats (Heinze and Buschinger 1989; Buschinger and Heinze 1992) and deserts (Bolton 1986; Tinaut and Heinze 1992) can probably be subsumed under these more general models.

Those queen-polymorphic species, whose life histories have been studied to some extent, live predominantly in medium-sized habitat patches, isolated by stretches of habitat unsuitable for colony founding. This is especially clear in Formicoxenus, which live as "guests" semi-parasitically in the nests of other ants. One single nest of a host ant, e.g., a wood ant colony, can contain dozens of the tiny Formicoxenus colonies, but the next mound may be hundreds of meters away (Buschinger and Winter 1976; Francoeur et al. 1985). Long-range dispersal is of little success and most queens found their own colonies within the host nest. The retainment of winged queens is probably necessary to colonize new host nests. Though generally little is known about the temporal stability of ant habitats, according to numerous observations, Formica mounds may exist for several dozen years (e.g., Henderson et al. 1989). Wing reduction might be a similar adaptation to patchy host ant populations in slave-makers, such as Polyergus rufescens (Viehmeyer 1908; Zaayer 1967) and Harpagoxenus sublaevis, and several workerless parasites, where the chance to encounter a host nest suitable for founding is higher on foot than by long-range dispersal.

Leptothorax sp. A, a non-parasitic relative of Formicoxenus, is similarly specialized to patchy habitat (Heinze 1993). Wingless queens are especially common on wind-exposed rocky outcrops along the shores of St. Lawrence and Saguenay Rivers in Québec. These patches measure several dozen squaremeters, are isolated by dense, humid forest or the sea, and according to old photographs have persisted for more than one hundred years. The low frequency of winged queens in these patches (<10%) probably results from the net emigration of winged queens and a low life expectancy of dispersers. Leptothorax sp. A also occurs in homogeneous coniferous woodland, but here only along the forest edge or on sunny patches, which

often are too small to house more than a single colony and probably are also temporally instable. In these forests, winged queens clearly outnumber wingless queens (Heinze 1993). A similar habitat structure might promote queen polymorphism in L. sphagnicolus, an endemic species in dry patches in Québec sprucebogs (Buschinger and Francoeur 1991), in Australian Monomorium sp. 10, which lives in insular groups of scattered rocks (Buschinger and Heinze 1992), and wing reduction in the living fossil ant Nothomyrmecia macrops (Taylor 1978).

In the majority of species in which winged and apterous queens co-occur, the former are quite rare. In the slave-maker Harpagoxenus sublaevis, e.g., winged queens were found in less than 1% of all colonies in southern Germany (Buschinger 1966) and are probably completely absent from Scandinavian populations (Adlerz 1896; Peeters 1991a). According to ESS models on dispersal (Hamilton and May 1977), even in temporally and spatially homogeneous environments a certain percentage of an organism's offspring should retain the capability of long-range dispersal. Nevertheless, there is firm evidence that in such different taxa as army ants, with colony sizes of several million individuals, and various Ponerinae and Myrmicinae, with colonies averaging less than a few dozen or hundred individuals, winged queens have been completely replaced by wingless reproductives, be it apterous queens, gamergates, or thelytokous workers. In army ants and other legionary ants, dispersal capacity is retained by the migratory life history of the complete colony. Other species apparently can adapt to a broad variety of different habitats and thus might avoid to be trapped in a dwindling habitat patch. Among these generalists are Diacamma, a genus with gamergates (Peeters 1991b, 1993), and Pristomyrmex pungens (Tsuji 1988, 1990) and Cerapachys biroi (Tsuji and Yamauchi 1995), in which sexual reproduction has been completely replaced by thelytoky. All three taxa are often found in anthropogenic, disturbed habitats.

A third group of species with only or predominantly wingless queens live in stable, uniform habitats, such as deserts. In arid areas of North Africa and southern Spain, flightless queens are known from some 5 to 8% of all species, and apterous queens have also been reported from numerous genera in other desert ant faunas (Bolton 1986; Heinze et al. 1992a; Tinaut and Heinze 1992). Dry, seasonal habitats probably also favor queen loss and propagation by gamergates (Ward 1983; Peeters 1990).

In addition to ecological factors, sociometric and phylogenetic constraints might lead to the replacement of winged queens by apterous female reproductives. Small colony size, solitary foraging, or the lack of trophallaxis might restrict the resources available for the production of large queens with enough body reserves for claustral founding (Bolton 1986; Tinaut and Heinze 1992; Peeters in

press). If the mortality of queens which forage during non-claustral colony founding is indeed very high, as is generally assumed though empirical data are lacking, natural selection might favor the evolution of queen adoption, budding, and winglessness.

The sociogenetic consequences of winglessness

The consequences of winglessness on the social and genetic structure of ant colonies and populations have as yet not been fully investigated. Polygyny generally tends to decrease nestmate relatedness and may thus strongly affect the reproductive interests of nestmates concerning sex allocation, allocation in colony maintenance and reproduction, the origin of males, and the partitioning of reproduction among queens (e.g., Nonacs 1988; Pamilo 1991ab). Species with multiple wingless reproductives will be no exception: In *Rhytidoponera confusa* and *R. chalybea*, workers in nests with a single, originally winged queen were on average fullsisters, whereas worker relatedness was as low as 0.3 in colonies with multiple gamergates (Ward 1983). In wing-polymorphic *Leptothorax* sp. A, on the other hand, a dilution of nestmate relatedness in colonies with multiple queens is partially prevented by the monopolization of reproduction by a single, dominant queen ("functional monogyny", Buschinger 1968; Heinze and Buschinger 1989; Heinze and Smith 1990). Kin selection predicts that if solitary founding is extremely costly and queens therefore return into the maternal colony, stable dominance hierarchies among nestmate queens may evolve (Reeve and Ratnieks 1993; Bourke and Heinze 1994). In *Leptothorax*, species adapted to a broad variety of boreal habitats are typically polygynous and have winged queens, whereas species specialized on patchy boreal habitats, in which dispersing queens face both cold climate and nest site limitation, are functionally monogynous and queens are polymorphic (Heinze 1992; Bourke and Heinze 1994). In functionally monogynous species, nestmate relatedness as estimated from the frequency of genetic markers in worker brood appears to be higher than in polygynous species, but due to frequent exchange of the top-ranking queen, the relatedness of adult workers may be significantly lower than 0.75 (Ortius and Heinze 1995; Heinze 1995).

Genetic heterogeneity among populations was found to be larger in wingless than wing-polymorphic waterstriders (Zera 1981). In ants, winglessness of female reproductives might affect the genetic structure of populations in a similar way by increasing the spatial variation of allele frequencies, however, as males are usually winged, genetic drift is probably not very strong. Preliminary data suggest that allele frequencies differ more strongly between

populations of wing-polymorphic *Leptothorax* sp. A than in sympatric *L.* cf. *canadensis*, where all virgin queens are winged (J. Heinze unpublished).

Finally, if the morphology of female reproductives is determined by the amount of food the larvae receive during their development, as appears to be the case in *Technomyrmex albipes* (Yamauchi et al. 1991), conflict may arise about the investment in the various types of reproductives. The optimal investment ratio in the various types of reproductive and non-reproductive females may differ between workers and the mother queen, because they differ in their genetic relatedness to the females (Nonacs 1988, Pamilo 1991ab). Conflicts also exist between female larvae and workers, as larvae might attempt to grow into reproductives (Nonacs and Tobin 1992; Tsuji in press). As yet no detailed data are available to conclude who is in control of the production of female sexuals.

Nest inheritance and wing loss without budding

Though there is ample evidence that wingless queens and gamergates may be important in colony propagation by budding, an alternative hypothesis seems plausible at least in a number of species. In these species, colonies are typically founded by single winged queens, which after their death are replaced by wingless secondary reproductives, either apterous queens or gamergates. In *Technomyrmex albipes*, apterous female reproductives ("intercastes") mate with their wingless brothers or nephews and after significant colony growth winged female and male sexuals are reared from the progeny of these replacement reproductives. Colonies may become extraordinarily large (more than six million workers) and may simultaneously inhabit different nesting sites, but true "budding", leading to completely separate colonies, does not occur (Yamauchi et al. 1991; Tsuji and Yamauchi 1994).

In *Harpegnathos saltator*, gamergates probably have the same function as the *Technomyrmex* "intercastes". Here, too, budding apparently does not occur. The nest is a highly valuable and probably long-lived structure (Peeters et al. 1994), which after the founding queen's death is thus inherited by her gamergate offspring (Peeters and Hölldobler in press).

These two species may be examples of space perennial polygyny (Nonacs 1988, 1993). At least in *Technomyrmex albipes* the dispersing success of queens by flight and the opportunities for budding appear to be extremely low. The polydomous mother colony occupies the only available habitat patch, which, however, is very stable.

Whereas replacement reproductives or nest inheritance

are common phenomena in termites and honey bees, they appear to be rare in ant societies headed by a single, winged queen, excepting the two examples cited above and probably *Solenopsis invicta* (Tschinkel and Howard 1978). In many cases, the death of the foundress queen is followed by male-production by egg-laying workers until the last workers die, or a short boom of sexual production from the queen's last brood if the workers themselves are completely sterile.This raises the question why nest inheritance is not more common, i.e., why does not one of the last female sexuals to be reared always take over the nest after mating (Tsuji 1990; Hölldobler and Wilson 1990)?

One might speculate that in most monogynous species the maternal nest is not stable or costly enough to counter-balance the risks that the old colony has already exploited the surrounding habitat or that it is infested with parasites or diseases. Alternatively, however, it might well be that colony takeover occurs far more frequently but has been overlooked as it is typically detected only by long-term assays of a colony's worker genotypes (e.g., Pamilo 1991c).

One special case of nest inheritance is probably "oligogyny", where workers tolerate the return of young queens into their maternal nests, but queens are mutually intolerable and space out. Oligogyny is known from carpenter ants, *Camponotus ligniperda* and *C. herculeanus*, which build elaborate, long-lived nests in dead or living trees. The huge, complex nests and their territories are valuable resources (Hölldobler 1962, personal communication).

The evolution of parasitic colony founding

In some 3 percent of all ant species, queens invade the colonies of other species, which they permanently or temporarily exploit to rear their young. Most parasite queens kill or expel the resident queen and in some cases also the adult workers of the host colony, while others coexist with host workers and queens.

The evolution of socially parasitic ants has been extensively discussed (see, e.g., Buschinger 1970, 1990; Wilson 1971; Hölldobler and Wilson 1990; Bourke and Franks 1991), but which ecological factors might promote parasitism and why some parasites are queen-intolerant whereas others are queen-tolerant has as yet not been investigated. The parasitic ways of life of ants—slavery, xenobiosis, and temporary parasitism, are remarkably diverse. However, in this review we will focus only on two aspects which might be related to dispersal, namely the evolution of parasitic founding and the loss of the worker caste.

We suggest that parasitic colony founding has evolved in

habitats which pose extraordinarily high costs on other founding strategies. This follows from an extension of a model for multiple-queening in Formicoxenini, a myrmicine tribe very rich in social parasites (Bourke and Heinze 1994). As mentioned above, cold climate and nest site limitation apparently increase dispersal costs enormously and may lead to the evolution of functional monogyny, i.e., dominance hierarchies among nestmate queens. Queens in these functionally monogynous species are behaviorally and also morphologically preadapted to parasitic colony founding. Though nestmate queens in *Leptothorax* are typically closely related, some queens occasionally succeed in entering an alien colony (Stille and Stille 1991; Heinze et al. 1992b) and might usurp the α-position. From this "preparasitism" (e.g., Buschinger 1990b) it is perhaps a short step to genetic isolation and speciation of a parasite, especially if associated with host transfer as suggested in the workerless parasite *Leptothorax paraxenus* (Heinze 1991; Heinze unpublished.).

The common occurrence of social parasites in boreal and alpine habitats—some 30% of all ant species in Switzerland are social parasites (e.g., Kutter 1968)—might thus reflect the difficulties of colony founding in areas with short summer periods and long, cold winters, but could also be related to the high density of host ants. Models relating the evolution of social parasitism to the adoption of queens and reproductive conflict among nestmate queens have been proposed by Baroni-Urbani (1967) and Buschinger (1991), but do not explicitly connect social parasitism to ecological constraints (but see Nonacs 1993).

Transmission rate, virulence, and workerless parasites

In many parasites, the parasite queen lays eggs from which workers develop, which either step by step replace the host workers or pillage host-pupae from neighboring colonies. In other species, however, no workers are produced and the parasite queen completely focusses her reproductive efforts on the production of sexual progeny. This is perhaps not surprising if the host queen survives and produces new generations of workers. However, in several species, workerlessness co-occurs with the parasite queen's intolerance of host queens, i.e., the parasite queen eliminates or expels the only source of new workers.

Game theory predicts that if a parasite is transmitted easily from one host to another, it will turn the host's resources more selfishly to its own purposes (e.g., May and Anderson 1983; Herre 1993). Thus, if the colony founding success of the parasite's offspring is comparatively high or if the survival rate of a parasitized colony is low, the parasite queen should exploit the existing workforce in the host colony to produce one or a few large broods con-

sisting exclusively of sexuals. On the other hand, if new parasite colonies are predominantly founded by "vertical transmission", i.e. through fragmentation of the host colony into buds each containing parasite queens, the parasites would benefit from the prduction of new host workers and should leave the host queen alive. In what is probably a similar idea, Hamilton (1972) concluded that harmless "symphiles" should be more commonly associated with sedentary ant colonies than with mobile bee colonies.

In ants, the observed pattern of colony founding and tolerance towards the host queen among socially parasitic ants fits these predictions better than those made by alternative theories, such as coevolution of host and parasite towards a more benign relationship (J. Heinze unpublished). Colony founding success of queen-tolerant *Plagiolepis xene* (Passera 1964) and *Doronomyrmex kutteri* (Allies et al. 1986; A. Buschinger personal communication) appears extraordinarily low at least in the laboratory, whereas queen-intolerant *Leptothorax wilsoni*, *L. paraxenus* (J. Heinze unpublished), and *D. goesswaldi* (A. Buschinger, personal communication) can be more easily introduced into host colonies. At least in *Plagiolepis xene*, queen-tolerance is associated with propagation by budding (Passera 1964). A simple determinant of whether workerless parasites are queen-tolerant or queen-intolerant might thus be host queen number and the occurrence of budding in the host species. Firstly, it might be easier for a parasite queen to kill one queen than several queens, and secondly, vertical transmission by budding will occur predominantly in multiply-queened host species. However, queen-tolerant *Doronomyrmex kutteri* and queen-intolerant *Doronomyrmex goesswaldi* both parasitize the same host species, facultatively polygynous *Leptothorax acervorum*. Whether the two parasites exploit colonies with different queen numbers is not known.

As host populations at least in boreal habitats are typically dense and widespread, one might expect long-range dispersal to be reduced in parasitic queens and it is generally believed that winglessness is a common feature associated with parasitic life (Wilson 1971; Baroni-Urbani 1967, Hölldobler and Wilson 1990). However, more commonly parasitism leads to a miniaturization of queens (e.g., Nonacs and Tobin 1992) but not to wing loss, and in fact, in some taxa, e.g., the *Monomorium minimum* group (DuBois 1986), wingless queens are known from non-parasitic species but are rare among parasites.

Male polymorphism

Polymorphic males are far less common in ants than wingless female sexuals and also less well studied (Loiselle and Francoeur 1988). In some species, size variation oc-

curs among winged males which probably reflects differential dispersal and mating strategies. Size polymorphism in queens is associated with a similar polymorphism in males in *Myrmica ruginodis* (Elmes 1991), and in *Leptothorax* sp. A, the sons of originally winged queens are larger than those of wingless queens (Heinze and Buschinger 1989). In *Formica exsecta*, males from colonies which occupy multiple nests (polydomy) are smaller and disperse more efficiently than males from monodomous colonies (Fortelius et al. 1987).

Wingless males occur only in half a dozen of genera. Their scarcity is probably connected to the aversive affects of inbreeding in Hymenoptera, which results in sterile, diploid males (e.g. Cook 1993). Loss of flight capability in female reproductives does not necessarily lead to inbreeding, as queens mate either in the neighborhood of the colony, as in *Leptothorax* sp. A, or alien males may enter the nest (Peeters 1991b; Passera and Keller 1994). In most species, however, queens cannot enter an alien colony to mate and will also be attacked in its surroundings. Hence, winglessness in ant males is typically associated with intranidal mating between closely related males and females as in non-social insects (Hamilton 1967, 1979). In only a few ant species are the detrimental effects of inbreeding somehow avoided.

We have already mentioned the wingless replacement males in *Technomyrmex albipes*. Other wingless males are known from social parasites and guest-ants, e.g., *Anergates atratulus*, *Aporomyrmex ampeloni* and *Formicoxenus*, the queenless ponerine *Hagensia saldanhae* (H. Robertson and C. Peeters personal communication), several species of *Hypoponera*, and the cosmotropical tramp genus *Cardiocondyla*. In the two latter cases, male morphology is associated with male fighting (Hamilton 1979; Stuart et al. 1987; Yamauchi and Kinomura 1987, Heinze et al. 1993). By killing other males, wingless *Cardiocondyla* males may monopolize the female sexual progeny of a colony for weeks, if not months. Histology has shown that in contrast to other Hymenopteran males, in which spermatogenesis is completed by the time they reach sexual maturity, in wingless *Cardiocondyla* males spermatogenesis continues throughout the adult life (Heinze and Hölldobler 1993b). Surprisingly, in several *Cardiocondyla* species both peaceful, dispersing, winged males with completed spermatogenesis and wingless fighting males co-occur. An undescribed Japanese species of *Hypoponera* has a similar polymorphism as *Cardiocondyla*, with winged dispersing males and wingless fighting males, but in addition shows also a queen polymorphism (Hashimoto et al. 1995, K. Yamauchi, pers. comm.). *Hypoponera bondroiti* has small and large wingless males. The large males fight and monopolize all eclosing queens in an area of the nest, while small males are less aggressive and apparently mimic workers or queens (K.

Yamauchi personal communication). In *Cardiocondyla emeryi* from Barbados, in addition to winged males and workerlike, wingless males, apterous males with the thorax structure of winged males have been observed, and all three male morphs attempt to copulate in the nest (J. Heinze unpublished).

The significance and the proximate causes of male polymorphism are by far less well understood than in polymorphic queens. A first explanatory attempt in form of a mathematical model for wing dimorphism in *Cardiocondyla* was based on the assumption that because wingless males are smaller than winged males they eclose earlier and thus have the opportunity to kill other male pupae and to inseminate eclosing queens. A stable polymorphism can result if, among others, wingless males have a reduced behavioral ability to copulate compared to winged males (Tsuji et al. 1994).

Conclusion and prospects

Many of the described peculiarities in ant reproduction appear to be related to changed dispersal strategies. Wherever the costs of solitary colony founding and dispersal outweigh their benefits, alternative reproductive strategies might evolve, which result in colony propagation by budding. Winged queens then might be supplemented or replaced by miniaturized or apterous queens incapable of long-range dispersal, by mated workers, or unmated workers which reproduce by thelytokous parthenogenesis. Which of the various strategies has evolved in adaptation to low founding success of dispersing queens is probably determined by developmental or phylogenetic constraints. Flightlessness, e.g., can evolve only where mating flights have been replaced by ground-bound copulation, which is probably more frequently the case in species with small-sized colonies (Hölldobler and Bartz 1985). To clarify the causes underlying complete winglessness or wing polymorphism it will be necessary to take phylogenetic relationships into account: winglessness in army ant queens has probably arisen only once in a common ancestor (see also Roff 1994b). Only workers possessing a spermatheca can successfully mate and produce fertilized eggs, limiting the potential occurrence of gamergates to Ponerinae, *Nothomyrmecia*, and *Myrmeciinae*, several parasitic Myrmicinae and the apparently queenless species *Eutetramorium mocquerysi* (G. Alpert, J. Heinze and B. Hölldobler unpublished) Thelytokous parthenogenesis is widely distributed among many hymenopteran lineages, but the conditions favoring its evolution are poorly understood. In the wasp genus *Trichogramma*, e.g., thelytoky is caused by cytoplasmatically inherited bacteria and can be "cured" by antiobiotics (Stouthamer et al. 1990, 1993), but nothing is known yet on the proximate fac-

tors underlying thelytoky in ants. Male polymorphism in ants is also little understood.

First mathematical approaches, which examine conditions for the evolution of dispersal by solitary foundresses or its various alternatives, have been made (Nonacs 1988, Pamilo 1991, Reeve and Ratnieks 1993, Tsuji and Tsuji in press). As we have shown, the key ecological factors appear to be spatial distribution and temporal fluctuation of nest sites and other resources available, and the type of density dependence of population regulation. Data on the success of alternative founding strategies in different types of habitat are still lacking, and though plausible, the suggested correlations between wing loss and founding cost must be considered hypothetical. Detailed field studies are strongly needed to test these assumptions. Future investigations should also address the effects of winglessness on the sociogenetic colony and population structure.

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Glossary

polygyny: reproduction by several inseminated female reproductives within a single colony. To avoid confusion with the same term denoting mating of males with multiple females, Choe (1995) suggested to refer to multiple-queening as "plurimatry".

monogyny: reproduction by the only inseminated female reproductive present within a single colony (also unimatry, Choe 1995).

functional monogyny: monopolization of reproduction by one of several inseminated female reproductives present within a single colony.

monandry: single insemination.

polyandry: multiple insemination (also pluripatry, Choe 1995)

queen: several definitions exist which define the term either based exclusively on function (inseminated, fertile female reproductive), morphology (female which differs in its morphology or anatomy from typically non-reproductive workers), or both, leading occasionally to conflicting or ambiguous descriptions. We here use the term "queen" for all females capable of mating and the production of fertilized eggs, which differ in their morphology or anatomy from the non-reproductive workers.

gamergate: fertile, mated worker.

thelytoky: parthenogenetic production of diploid offspring from unfertilized eggs.