Alternative reproductive tactics in females: the case of size polymorphism in winged ant queens

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Abstract:
Alternative reproductive tactics are common in males but rather rare in females. In this respect, ants are apparently an interesting exception. Ant queens can either start a new colony on their own or utilize the work force of existing colonies for dependent colony founding. As the success of these different options depends on body reserves of the queens, the finding of two different classes of alate queens in some ant species that differ only in size strongly suggests alternative modes of reproduction. Studies of queen size polymorphism from a number of ant species differ in scope and also in their results. Nevertheless, across taxa evidence exists that small queens found dependently while their larger conspecifics found colonies on their own. However, in most cases it is not clear whether the small queens exploit unrelated colonies (intraspecific "social parasitism") or return to their natal colonies. In some ant species the queen size polymorphism might constitute an evolutionary transition to either interspecific social parasitism or a morphologically more pronounced queen polymorphism linked to dispersal. In others, queen size polymorphism might be a stable phenomenon. Although it is important in this context whether queen size polymorphism is caused by a genetic polymorphism or phenotypic plasticity, so far no conclusive evidence about proximate mechanisms of size determination has been presented. Some considerations are made about the question why female alternative reproductive tactics correlated with morphological adaptations are comparatively widespread in ants.
Key words: Reproductive tactics, polygyny, social parasitism, ants, body size.

Article:
Introduction
In many animal species across the major taxa, males use alternative tactics to increase their reproductive success: some males attempt to monopolize mating with a large number of females by aggressively defending a harem against their rivals, whereas others engage in quick, unnoticed "sneak" copulations with females (Thornhill and Alcock, 1983; Andersson, 1994; Taborsky, 1994; Choe and Crespi, 1997). A famous example is provided by the marine isopod Paracerceis sculpta in which three alternative tactics coexist (Shuster, 1992): large α-males defend cavities in sponges (spongocoels) as territorial breeding sites to which females are attracted, middle-sized β-males mimic females in morphology and behavior to gain access to these and tiny γ-males are capable of sneaking into the spongocoels just because of their small

size. This system exemplifies well that body size might be considered as one of the most prevalent parameters for the adoption of alternative reproductive tactics (Clutton- Brock et al., 1979; Eberhard, 1980; Gross, 1985; Thornhill and Alcock, 1983; Crespi, 1988; Danforth, 1991): smaller males often follow sneak tactics while larger males are competitive and often territorial.

Alternative reproductive phenotypes are widespread among males, but much less is known about this phenomenon in females (Carroll and Loye, 1986; Gross, 1996; Cunningham and Birkhead, 1997). Although some purely behavioral alternative tactics in female reproduction have been reported (Caro and Bateson, 1986), very few alternative female morphotypes have been described. And even though there is considerable variability in female body size, typically the only biological significance that is related to it are fertility effects (Roff, 1992; Stearns, 1992; e.g., Kim, 1997). Recently, however, evidence is accumulating that in social Hymenoptera, particularly in ants, female alternative reproductive tactics are exceptionally abundant (Heinze and Tsuji, 1995) and that they often are correlated with differences in female body size.

Therefore, we will examine the significance of this parameter per se, reviewing the phenomenon of queen size polymorphism in ants (other polymorphisms are reviewed elsewhere: Buschinger and Heinze, 1992), after giving a short overview over alternative reproductive tactics in females that are related to morphology. It will be shown that ants in general and queen size-dimorphic species specifically might provide a particularly promising system for a detailed investigation of the evolution and the ecological significance of alternative reproductive tactics in females.

Most cases of female-specific polymorphism are as yet known from insects and they are related to a) the evolution of mimicry, b) dispersal polymorphism, or c) alternating life cycles. In some species of butterflies (Cook et al., 1994) and damselflies (Fincke, 1994 and references therein) male- mimicking females coexist with cryptic, ordinary females. This system of female polymorphism is probably stable because male-like females evade sexual harassment at high male concentrations but have lower mating chances when males are scarce (Hinnekint, 1987; for an alternative view see Johnson, 1975). The evolution of an alternative form of non-dispersing females in insects is often linked to the loss or the reduction of wings (aptery and brachyptery; Braune, 1983; Roff, 1986) but not always (e.g., Lindquist and Walter, 1988). In some cases, such as the cricket *Gryllus firmus* a central trade-off between fecundity and dispersion capability appears to be responsible for the reduction of wings (Roff, 1984). Finally, when species change their reproductive tactic between generations due to strong environmental fluctuations, this may also be correlated with differences in morphology, as shown in aphids (e.g., Moran, 1992), gerbils (Clark et al., 1986), waterfleas (Lynch, 1980) or rotifers (Gilbert, 1980). Still, examples of body size related differences in female reproductive behavior are few, apart from varying number (Parker and Begon, 1986) and sex (Clutton-Brock et al., 1984) of the offspring.

Alternative reproductive strategies in ant queens
Like in other Hymenoptera, the general life cycle of ants leaves males with few options but death shortly after copulation (but see Fortelius et al., 1987; Kinomura and Yamauchi, 1987; Heinze et al., 1998). Females play the major role in reproduction facing the formidable quest of establishing a new reproducing unit, the ant colony. This can be achieved in two fundamentally different ways (Fig.1): the classic life cycle of all Formicidae is presumed to involve independent colony founding: mature colonies release sexuals into mating swarms to find a partner for

copulation. After being inseminated, the young queens disperse to suitable spots where they produce their first worker offspring in isolation. These independently and claustrally founding queens rely completely on their body reserves during the initial phase of colony growth and thus are typically well-equipped with fat, muscle tissue to histolyze, storage proteins and carbohydrates
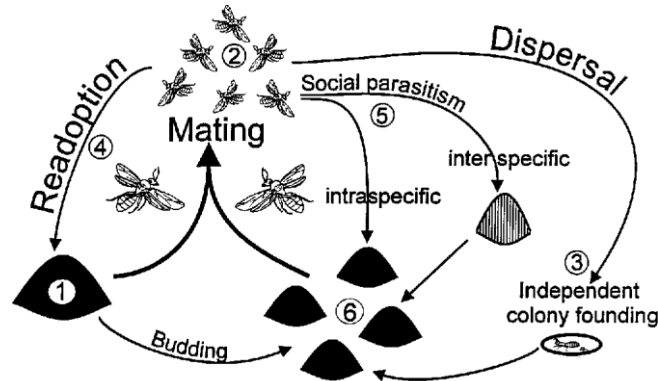

Figure 1. Ant queens have different reproductive options. The mature colony ① releases sexuals for the mating flight ②. Prevalently, the fertilized queen searches for a suitable spot, builds a nest chamber and rears the first worker offspring ③ (independent colony founding). After successful growth the colony enters the pool of mature, reproducing colonies ⑥. In contrast, there are several ways of dependent founding: the newly mated queen may be readopted into her natal colony ④ or seek adoption into an unrelated colony, in some cases coexisting with the original queen(s). The exploitation of an unrelated colony is referred to as inter- or intraspecific social parasitism ⑤

(Keller and Passera, 1989, 1990; Hölldobler and Wilson, 1990; Wheeler and Buck, 1995). In some species queens hold less body reserves which forces them to forage occasionally during the colony founding phase (independent, semi- and non-claustral colony founding), despite the high mortality risk. In any case, the success rate of solitarily founding queens typically appears to be low (Hölldobler and Wilson, 1990).

In contrast, in a broad variety of species colonies are founded in a dependent way (Buschinger, 1974; Hölldobler and Wilson, 1977). Here, young queens seek adoption into already established colonies, which they either join permanently as additional reproductives or subsequently leave to found a new colony assisted by workers from this colony (colony budding or fission). Although the costs of producing those queens are smaller because they need fewer body reserves and consequently a smaller body size (Buschinger, 1974; Keller and Passera, 1989; Stille, 1996), investment in those workers that join young queens in the budding process must at least in part be added to the reproductive investment (Trivers and Hare, 1976; Macevicz, 1979; Bulmer, 1983), thus considerably augmenting the per propagule cost of dependent reproduction. Socially parasitic species, where young queens invade alien colonies and temporarily or permanently exploit their work force to rear their own young, have the lowest investment cost per propagule because queens neither need large body reserves, nor assistance by workers of their mother colony.

To conclude, ant colonies invest their resources either into numerous queens or into a few propagules consisting of queens and workers, depending on environmental conditions and

demographic factors. Nowhere in the animal kingdom is this central life history trade-off between number and size of offspring as apparent as in ants: while a single mature fire ant colony consisting of 200000 workers releases thousands of virgin queens during one summer (Hölldobler and Wilson, 1990, p.145), an army ant colony of even greater size may split in only two units, each with a single queen (Hölldobler and Wilson, 1990, p. 583). Ants thus provide a promising study system for the investigation of the factors influencing parental investment and resulting female reproductive tactics. This seems particularly rewarding in species where queens may use both independent and dependent colony founding (e.g., Hölldobler and Carlin, 1985), because without genetic separation between the different forms, a dynamic equilibrium has to be stabilized by current selective forces.

The intraspecific degree to which individual queens are specialized for dependent or independent reproduction varies considerably: in several species, worker-like queens which have secondarily lost adaptations to independent colony founding, such as wings, ocelli and the bulky thorax with well-developed flight muscles, coexist with conventional, winged queens (e.g., *Monomorium* spp., Briese, 1983; *Leptothorax* sp. A, Heinze and Buschinger, 1987, 1989; Heinze, 1993; for a summary see Buschinger and Heinze, 1992). In the fire ant, *Solenopsis invicta*, externally indistinguishable queens may differ only in weight and behavior (Howard and Tschinkel, 1978; Tschinkel, 1996) and in the queens of some species no morphological correlates of differences in reproductive tactic have been reported (e.g., *Leptothorax acervorum*; Douwes et al., 1987; Stille and Stille, 1993). Intraspecific size dimorphism of ant queens might represent a (probably stable) intermediate stage in the evolution of a stronger morphological divergence between dispersing and non-dispersing forms. However, it may as well be the morphological manifestation of a facultative, intra- specific social parasitism: small queens might be efficient searchers of existing unrelated colonies without having the body reserves necessary for independent colony founding.

Case studies
In a small number of species from at least eight different genera in four ant subfamilies queen size is reportedly dimorphic, with small "microgynes" and large "macrogynes", which only differ, almost isometrically, in size (e.g., Fig. 2). Apart from ants, female size polymorphism in social insects is also known from termites (Nasutitermes princeps (Isoptera: Termitidae), Roisin and Pasteels, 1985) and stingless bees (Imperatriz-Fonseca and Zucchi, 1995; Nogueira-Ferreira et al., 1996). In the following we examine the cases of size dimorphism in ants individually.

Myrmica
The myrmicine genus *Myrmica* probably provides some of the best studied examples of queen size polymorphism (Bourke and Franks, 1991): in *Myrmica rubra*, the micro- gyne form seems to parasitize the work force produced by macrogynes and is now considered to be a separate species,
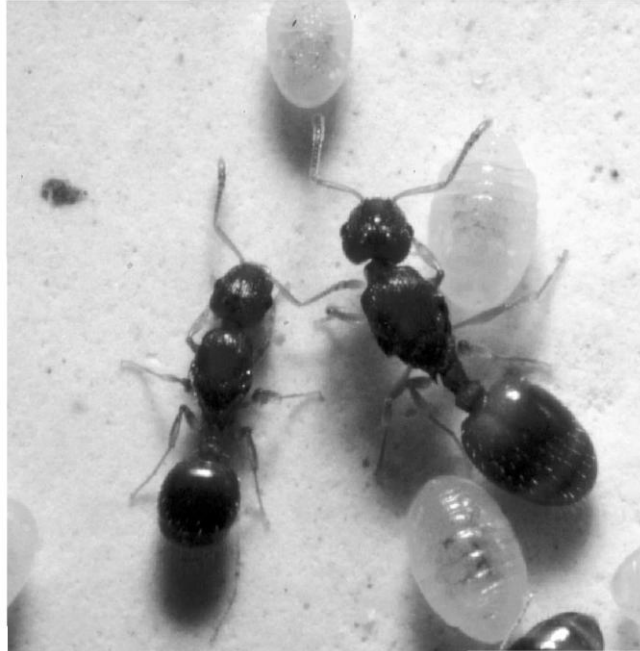
Figure 2. Queen size dimorphism involves an almost isometric size reduction in some of the queens. In *Leptothorax rugatulus* large and small queens occur within the same colonies, however most colonies contain only one queen morph

M. microrubra (Seifert, 1996; but see Buschinger, 1997): the gene pools are separated (Pearson and Child, 1980), thus the queen morph is presumably genetically determined, despite an effect of the queen/worker ratio in a colony on the size of queens it produces (Elmes, 1974). The microgynes generally co-occur with macrogynes and specialize in sexual reproduction (Elmes, 1976; Pearson and Child, 1980). They produce nearly forty times as many queens as macrogynes (Elmes, 1976) probably because microgynes induce gyne suppression while their daughters are immune to this effect (facilitated by their smaller size: Nonacs and Tobin, 1992). Complementary data on reduced survival of colonies with only microgynes and a distinct development of microgyne offspring have been collected from a Belgian population (Cammaerts et al., 1987).

By contrast, *Myrmica ruginodis* constitutes a single species in which the dichotomous queen size has been attributed to a dispersal polymorphism (Elmes, 1991b). Direct observation of the mating biology (Brian and Brian, 1955; Kasugai et al., 1983) and a close link between social structure and queen morph (monogynous macrogynous versus polygynous microgynous colonies) suggest that microgynes preferentially return to their mother colonies after mating in the vicinity (secondary polygyny). However, Elmes (1991 b) reports that microgynes are found in mating swarms without indication for assortative mating, and there is no evidence for a genetic differentiation between the two morphs (Seppä, 1992, 1994). In European populations the two forms show overlapping size distributions and occur sympatrically probably throughout the range of *M. ruginodis* (Elmes, 1991 b; Seppä, 1992). In Britain, about 25% of nests contain both queen types, however the majority of microgynes live and produce workers independently (Bourke and Franks, 1991). *M. kotokai* (considered a subspecies of *M. ruginodis* by Onoyama,

1989) also has macro- and microgynes (Mitzutani, 1981), and one population lacks macrogynes altogether (Kasugai et al., 1983).

Solenopsis

Alternative queen forms have been described in two species of fire ants, *Solenopsis geminata* (McInnes and Tschinkel, 1995) and *S. invicta* (Tschinkel, 1996), both, however, only from a single population. The two 'morphs' in *S. invicta* differ only in weight (30%), while in *S. geminata* true microgynes are found. As the social structure in both investigated populations is strictly monogynous, this case is fundamentally different from *Myrmica*: the authors suggest that the lighter or smaller queens are not capable of independent colony founding but instead take over orphaned colonies. As these will mostly be unrelated, this strategy amounts to an intraspecific, temporal parasitism (Tschinkel, 1996). Microgynes also might accidentally become unfertilized replacement queens in their natal colonies when their mother has died. In both *Solenopsis* species macro- and microgynes swarm in different seasons, however the timing of microgynous swarming flights differ between the two species, as does the extent to which the microgynous tactic is adopted: In *S. invicta* few lighter gynes are produced (Tschinkel, 1996) and the frequency of colony usurpation was estimated to be 0.7% per colony per year (DeHeer and Tschinkel, 1998), frequent enough for the authors to suggest that "the origin of polygyny in North-American *Solenopsis invicta* could be explained by the adoption of multiple replacement queens into orphaned monogynous colonies." In *Solenopsis geminata* the population allotment of energy to microgynes, as well as the percentage of colonies headed by them are as high as 35 %. Thus fitness payoffs for both alternative tactics may be equal (McInnes and Tschinkel, 1995) which has also been reported for *S. invicta*.

From observations that queens produce mainly daughters of the same morph as themselves the authors conclude that there may be a genetic basis to the queen size dimorphism in *S. geminata* (McInnes and Tschinkel, 1995). However, this needs further testing, as one in seven colonies generated both morphs and maternal or social effects are known to play a role in the determination of queen phenotype in *S. invicta* (Keller and Ross, 1993).

Leptothorax

In addition to several cases of pronounced queen polymorphism in the subgenus *Leptothorax*(s. str.) (*L. sphagnicolus* from Québec, L. sp. A from northeastern North America, *Leptothorax*"muscorum" H from Colorado, and probably also *L. oceanicus* from East Siberia, Francoeur, 1986; Heinze
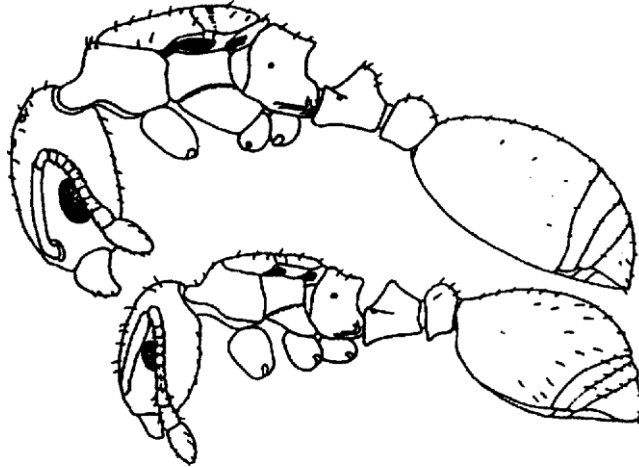
Figure 3. Many social parasites living permanently in the colonies of their host display a large reduction in queen size. The figure shows a queen of the social parasite *Leptothorax wilsoni* (below) compared to a queen of one of its host species *L. cf. canadensis* (top). In some cases, where the parasite queens co-occur with the host queen, they have initially been regarded as microgynes of the host species. (Drawing based on Heinze, 1991)

and Buschinger, 1987, 1989; Heinze, 1989; Kupyanskaya, 1990), the genus *Leptothorax* provides several examples of queen size polymorphism which have been investigated to various degrees. Microgyny has been claimed for several *Leptothorax* species (Wheeler, 1937; Stitz, 1939). However, it appears that in *Leptothorax* (s. str.) most, if not all microgynes are in fact separate socially parasitic species (e.g., Fig. 3), such as *L. faberi, L. goesswaldi, L. kutteri, and L. pacis* (in part previously considered to belong to an own genus, Doronomyrmex, Heinze, 1995) (Kutter, 1945, 1967; Buschinger, 1965, 1982).

Some data exist on microgyny in the European species *L.(M.) interruptus* and *L.(M.) corticalis* (Seifert, 1996; unpublished): while the small data set for *L. corticalis* only indicates high variability in queen size, the queen size distribution of *L. interruptus* seems to be bimodal and non-overlapping. As in *Myrmica ruginodis*, microgyny appears to be correlated with polygyny (Seifert, pers. comm.). Herbers (1984) presents some data on the highly variable queen size in *L. (M.) longispinosus*, yet the bimodality of the size frequency distribution is not clear. Furthermore, in a Mexican *Leptothorax* (Myrafant) species a strong queen size variability has recently been found (Rüppell, pers. obs.), however, no accurate data are available so far.

The best studied examples in this group are *L.(M.) spinosior* (Hamaguchi and Kinomura, 1996) from Japan and the North-American *L.(M.) rugatulus* (Rüppell et al., 1998): in both species the queen size is clearly bimodally distributed and fits two overlapping normal distributions (e.g., Fig. 4). Despite the fact that some colonies with both macro- and microgynes exist, most monogynous colonies are headed by a single macrogyne, while polygynous colonies most often contain several microgynes. In the population studied by Hamaguchi and Kinomura (1996) microgynes constitute
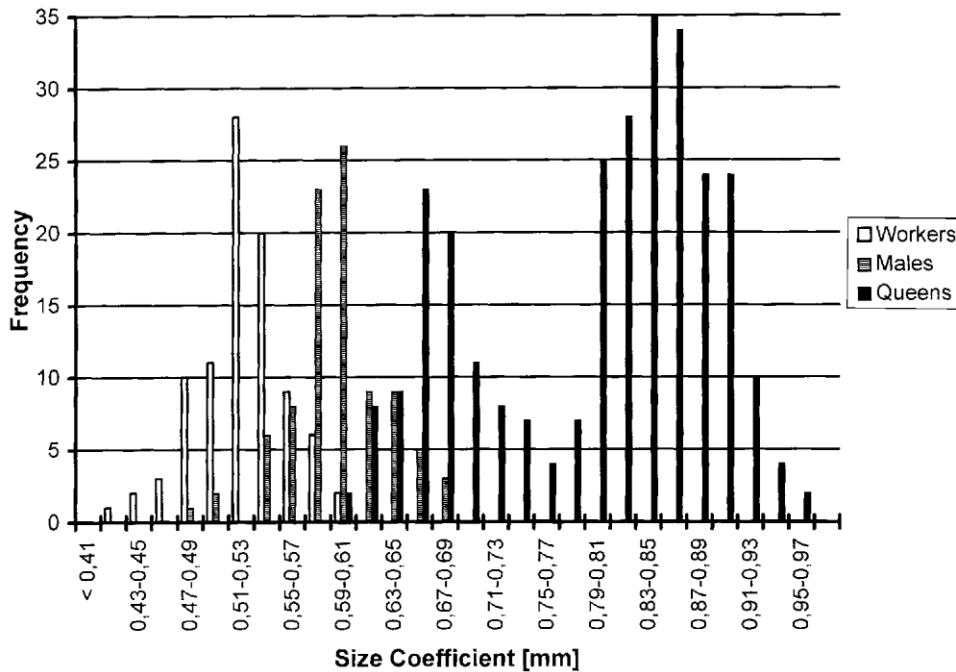
Figure 4. In *Leptothorax rugatulus* macro- and microgynes overlap in size. However, the size distribution is clearly bimodal, in contrast to worker and male size distribution (size measured as integrated maximal head width, thorax width and -length) Microgynes are intermediate in size between workers and macrogynes (modified from Rüppell et al. 1998). Similar overlapping, bimodal distributions of queen size were found in *Leptothorax spinosior* and *Myrmica ruginodis*. In *Ectatomma ruidum* and *Pseudomyrmex veneficus* no intermediates between the two morphs have been found

about two thirds of all queens collected. In *L. rugatulus*, the frequency distribution of queen size appears to be the opposite: averaged over 14 populations, macrogynes are twice as common as microgynes. However, in two sample sites, microgynes were found more commonly. While morphological investigations on *L. rugatulus* did not reveal any reductions of flight relevant structures in microgynes, preliminary microsatellite data in both species suggest restricted dispersal because queens within colonies are highly related (Hamaguchi and Kinomura, 1996; Rüppell, unpubl.). No genetic separation between the two morphs are reported. In *L. rugatulus* the ovaries of both queen morphs consist of a total of eight ovarioles, as opposed to two in workers and neither egg size differs between macro- and microgynes, nor does the size of workers and males they produce (Rüppell et al., 1998). Generally, there was a good correlation between mother and daughter size in both species, although occasionally microgynes matured in colonies with only macrogynes.

Other examples

Well established other examples of queen size polymorphism are taxonomically dispersed. Satoh (1989) presents a tri- modal pattern of queen sizes in the Camponotus nawai complex. However, the largest queens, found in monogynous nests only, represent a distinct species, Camponotus nawai (s. str.) (Terayama and Satoh, 1990). Still, queens from polygynous nests (= C. yamaokai) separate into two size groups, which differ over 10 % in their mean head width. Indiscriminately, Satoh (1989) suggests budding as the reproductive mode of the polygynous form and high levels of within- colony genetic relatedness (Satoh et al., 1997) support the hypothesis of secondary polygyny by readoption in this species. As the second documented example from the Formicines, the queens of an Australian weaver ant, *Polyrhachis cf. doddi*, have been reported as size-dimorphic (Bellas and Hölldobler, 1985). However, a subsequent study, found that thorax

structure and wing development varied strongly with size (Heinze and Hölldobler, 1993). Furthermore, bimodality of queen size distribution is not well substantiated.

Two other reports of queen size polymorphism exist from two further subfamilies: *Ectatomma ruidum* (Ponerinae) and *Pseudomyrmex veneficus* (Pseudomyrmecinae) are both clearly queen-dimorphic. Despite their worker-like size, the microgynes of *Ectatomma ruidum* seem capable of starting their own colonies independently because they forage during colony founding (semi-claustral colony founding), even if the success of macrogynes is probably higher (Schatz et al., 1996a). This is reflected in fecundity: macrogynes possess more ovarioles. On the other hand, microgynes are reported to have better flight abilities (Schatz et al., 1996b). Smaller colonies seem to produce microgynes while larger specialize on macrogynes, suggesting that the body size of queens is determined by non-genetic factors in this species. Schatz et al. (1996b) report functional monogyny in polygynous nests, however they do not convey any information about whether one of the morphs predominates reproduction in mixed nests. *Pseudomyrmex veneficus* might be only one species among several in its genus with size-polymorphic queens (Janzen, 1973; Ward, pers. comm). Like *E. ruidum* its both morphs do not overlap in size. Microgynes are believed to have advantages when entering the thorns of acacia trees which in this species are used as nest sites, and collection data suggest that microgynes explore the immediate surroundings, while macrogynes potentially specialize on long-range dispersal.
This could parallel the reproductive strategy of the acacia trees (Janzen, 1973).

Sundström (1995) reports that queens from polygynous and monogynous colonies of Formica truncorum differ in mating behavior and in head width. However, the latter difference is so small that a clear bimodality is unlikely. For some further ant species only minimal data exist, if at all. Some reports exist of occasional production of microgynes under aggression in *Acromyrmex crassispinus* (Fowler, 1977) or laboratory culture in *Atta cephalotes* (Jutsum and Cherret, 1978). The queens of the African pseudomyrmecine *Tetraponera tessmani* (formerly *Viticola tessmani*) were reported to be size-dimorphic (Wheeler, 1922; Bequaert, 1922 in Janzen, 1973) and the palaearctic formicine *Formica fusca* was mentioned by Donisthorpe (1927). Additionally, queen size in some *Tetramorium* species seems unusually variable (Sanetra, pers. comm.).

Conclusions
Queen size polymorphisms in ants clearly relate to alternative reproductive tactics which lead to different life histories of macro- and microgynes. However, the only common conclusion that emerges so far is that the microgynes preferentially employ some form of dependent colony foundation while macrogynes mainly found their colonies independently. The heterogeneity of findings beyond this point is partly explained by the heterogeneity of the underlying studies. Furthermore, the number of cases to be included is debatable, as data on the queen size distribution are not available for all species (e.g., Donisthorpe, 1927), or its bimodality has not been tested (e.g., Herbers, 1984). Moreover, microgynes might represent a distinct socially parasitic species co-occurring with the macrogyne host queens in some cases (Buschinger, 1990; Bourke and Franks, 1991). Nevertheless, we will discuss the evidence for the major hypothesis (dispersal polymorphism and social parasitism), draw some general conclusions and suggest where fruitful experiments might and need to be done.

Microgyny presumably has the potential to evolve to both social parasitism and a morphologically more pronounced dispersal polymorphism that might entail speciation into polygynous and monogynous sibling species (Hölldobler and Wilson, 1977; Brian, 1983; but see Ward, 1989). On the other hand, the co-occurrence of macro- and microgynes over a large geographical range in some species (*M. ruginodis* and *L. rugatulus*) suggests that in these cases the dimorphism is rather stable and not a mere transitory stage. A possible scenario is that mating occurs on the wing, but the mode of colony founding has changed, although it is difficult to see why dependent colony founding should not eventually entail a reduction of mating flight and wings in females, given the difficulty to relocate the natal colony and the flexibility of this trait (Sundström, 1995). In any case, that of a stable polymorphism or of an evolutionary switchpoint, we might be able to understand the involved selection pressures in more detail.

Microgynes as "intraspecific parasites"
Both studies in *Solenopsis* explicitly propose small body size of queens to be an adaptation to intraspecific social parasitism. A large-scale mark-recapture experiment or genetic investigations would provide unambiguous evidence that microgynes do not return (preferentially) to their natal colonies. This seems particularly important since, at least in *S. invicta*, queen morphology also differs between monogynous and polygynous colonies (Porter et al., 1988) and thus correlates with differences in dispersal. In contrast to other size-polymorphic species, different queen morphs in the two *Solenopsis* species swarm in different seasons. This mechanism of pre-mating isolation between different size classes might lead to sympatric speciation and to inter- specific parasitism (see Buschinger, 1990). In South America, *Solenopsis* is indeed parasitized by several workerless species which apparently are closely related to their hosts (Silveira-Guido et al., 1973; Wojcik, 1990). From theoretical considerations and the comparison between *S. invicta* and *S. geminata*, Tschinkel (1996) concludes that "a shift from independent to parasitic founding is driven by the degree of habitat saturation to which the species is typically exposed". However, exactly this line of argument has been put forward to explain the transition from monogyny to secondary polygyny (Herbers, 1986; Bourke and Franks, 1995; DeHeer and Tschinkel, 1998, see below).

The conclusion that microgyny is a likely stepping stone in the evolution of inquilinism has also been reached in the genus *Myrmica* (Pearson, 1981; Buschinger, 1990; Bourke and Franks, 1991): the abundance of small inquilines in this group provides suggestive evidence and the case of intra- specific social parasitism is well supported in *M. rubra/ microrubra*.

Size polymorphism as morphological correlate of alternative dispersal tactics
In *Myrmica ruginodis*, *Leptothorax*spinosior and *L. rugatulus*, no genetic differentiation between the two queen morphs could be shown. Moreover, some genetic evidence exists in these species and additionally in *Camponotus yamaokai* that in polygynous colonies queens are on average highly related. This strengthens the hypothesis that readoption of related queens instead of intraspecific parasitism is much more important for the establishment of polygynous (mixed) colonies in these species with size-polymorphic queens. However, a high average relatedness coefficient between queens does not exclude rare adoption events of unrelated queens (Stille and Stille, 1993). In order to evaluate the facultative tactic of parasitizing macrogynes it needs to be shown how often unrelated microgynes are adopted and whether they produce more than their proportional share of sexuals.

Readoption of daughter queens was also suggested for *Polyrhachis doddi* (Bellas and Hölldobler, 1985) and Pseudomyrmex veneficus (Janzen, 1973), though genetic data are missing, and hostile, intrusive behavior was observed in the former (Bellas and Hölldobler, 1985). Nevertheless, *P. doddi* might classify as an intermediate between species with wing-dimorphic and size-dimorphic queens and hence could provide in future studies excellent evidence for the hypothesis of a causal link between the two.

The data currently available on *Ectatomma ruidum* do not allow any firm conclusion about the underlying life history tactics: the microgynes certainly have the potential for independent (semiclaustral) colony founding, however it remains to be shown whether this is their preferred mode of reproduction. We would like to note that a more favorable wing load (= body mass per unit wing area) of microgynes (which has also been found in *L. rugatulus*: Rüppell et al., 1998) does not necessarily imply a better dispersal capability because absolute as well as relative physical parameters account for flight performance (Ellington, 1984; Vogel, 1994). The relationships between relative queen size and the mode of colony founding across species (Buschinger, 1974; Stille, 1996) and between social system and queen size within many species (Brian and Brian, 1949; Sundström, 1995; Hamaguchi and Kinomura, 1996; Rüppell et al., 1998) argue otherwise: small queens are typically found where dependent founding is common, and larger queens presumably disperse and attempt independent founding. Some queen size-dimorphic species in which macrogynes may also be found in polygynous nests (e.g., *Myrmica ruginodis*: Wardlaw and Elmes, 1996; *Leptothoraxrugatulus*: Rüppell et al., 1998) provide a rigorous test system for comparing dispersal behavior of the different morphs, irrespective of social structure.

Dispersal polymorphisms are expected to evolve in spatial and/or temporal heterogeneous habitats in which it is highly successful for the offspring to stay at home (Emlen, 1991) and profit from the local environment, but dispersers have the potential to colonize uninhabited areas. When both behavioral options are successful, disruptive selection is caused leading to a distinct dispersal polymorphism with two (or more) selective optima. These, if existing long enough, will eventually be reflected by correlated phenotypes. This reasoning explains the evolution of wing polymorphisms in insects in general (Roff, 1986) and in some ant species in particular (Buschinger and Heinze, 1992; Heinze and Tsuji, 1995). It can be extended to queen size polymorphisms in ants, with microgynes providing the means for successfully exploiting the local patch by budding, as do wingless, intermorphic queens in wing-polymorphic species (Briese, 1983; Heinze, 1993a). Budding is particularly important when competitive pressure on young colonies is strong due to high population density.

Dependent colony founding commonly leads to polygyny by philopatry (Keller, 1991) and to potentially immortal colonies. This space-perenniality (Nonacs, 1993), increasing the habitat saturation even further, might create a positive feedback loop on local social structure. However, certain authors (Sundström, 1995; Hölldobler and Wilson, 1977) stress that local habitat saturation (i.e., high colony densities) should favor dispersal, like in some other, non-social organisms (Begon et al., 1991). Interestingly, this is a question of whether selection is stronger within a patch (favoring depen dent colony founding) or between patches (favoring independent colony founding and dispersal to reach new patches), assuming metapopulation structure

(Olivieri et al., 1995). In uniform habitats (many of which are man-made), selection between patches is weak or absent, and hence dependent colony founding is strongly favored. This hypothesis is supported by the fact that tramp species, which mainly found new colonies by budding, displace the native ant fauna in many parts of the world (e.g., Yamauchi and Ogata, 1995), following the "homogenization" of habitats by man.

To summarize, a positive correlation between population density and microgyny cannot be taken as evidence for either, microgynes as adaptation to secondary polygyny or social parasitism, as both might be favored by habitat saturation.

Intraspecific parasitism and philopatry
In the end, secondary polygyny and intraspecific parasitism might not be so different as it is commonly perceived: one may evolve from the other (Bourke and Franks, 1991; Bourke and Heinze, 1994; Ross and Keller, 1995; DeHeer and Tschinkel, 1998) and both processes, colony usurpation and queen readoption, might co-occur in one species. In fact, the latter largely facilitates the former as secondary polygyny involves by definition readoption of young queens. The difference to social parasitism is simply the degree of relatedness, and an alien queen might overcome the colony recognition more easily in species where the behavioral repertoire of acceptance of newly mated queens exists at all. Likewise, the adoption of unrelated queens in polygynous colonies of *Solenopsis invicta* might be explicable in proximate terms only, i.e., by their genetic homogeneity in North America. Viewed under a population perspective, both pure tactics might represent only ends of a continuum. In this case, the distinction between readoption and intraspecific social parasitism would only be quantitative. However, it would be insufficient to ask whether more queens are adopted into alien or natal colonies, but (at least in theory) the question has to be answered which phenomenon has the higher evolutionary (fitness) impact in the population.

The co-occurrence of readoption and intraspecific social parasitism is also likely from a mechanistic point of view. If microgynes perform mating swarms as is suggested by their flight capability (Elmes, 1991; Schatz et al., 1996a; Rüppell et al., 1998), the mother colony might be difficult to relocate but other nests might accidentally be found. This is probably also the case in oligogynous ant species (Gadau et al., 1999).

Proximate factors underlying size polymorphism
Apart from the ultimate factors, the proximate causation of alternative tactics is of general interest (Austad, 1984; Gross, 1996): queen size and related to it the mode of reproduction could be based on a genetic polymorphism, environmental effects, or a combination of both. As mentioned above, the weight of queens in *Solenopsis invicta* is mainly due to the social structure of the nest in which they are raised, hence this "cultural transmission" can be viewed as adaptive phenotypic plasticity. This is in sharp contrast with reports on species where wing dimorphism in queens is brought about by the inheritance of a single locus or a closely linked set of loci as demonstrated both by breeding experiments and quantitative genetic analysis (Buschinger, 1975, 1978; Heinze and Buschinger, 1989; Heinze, 1998). Generally, body size is considered a quantitative trait to which environmental factors as well as numerous loci contribute (Stearns, 1992; Roff, 1997). So far, in queen size-dimorphic ant species the knowledge on proximate determinants of queen size is only based on occasional observations: McInnes and Tschinkel

(1995) conclude a genetic basis from the fact that queens produce daughters of the same morph as themselves. While this is also true for *Leptothoraxspinosior* and *L. rugatulus*, in these cases the same conclusion is not drawn, because of high variability in offspring size from single colonies in *L. spinosior* and some exceptional small queens produced in large- queened colonies in *L. rugatulus*. The high overall correlation of body size in mothers and offspring in natural colonies (Hamaguchi and Kinomura, 1996; Rüppell et al., 1998) might result from genotype-environment covariance, i.e., relatives sharing not only genes, but also the same micro-environment (Falconer, 1989), or from maternal effects (Bernardo, 1996). The fact that gyne size seems to be related to colony size in *E. ruidum* gives some support for the hypothesis that queen size is a plastic response.

In particular this area of research should be emphasized in the future, as quantitative, carefully controlled investigations on mechanisms not only are virtually absent, but also may allow for inferences on ultimate causation and might be of general interest in the current discussion of adaptive phenotypic plasticity (Sakwinska, 1997; Callahan et al., 1997). Furthermore, it provides an excellent study system to re-evaluate the importance of body size in female caste deter-mination in ants.

Alternative reproductive tactics in social insects
Social insects, and ants in particular, exhibit many different examples of alternative reproductive tactics in females (Hölldobler and Wilson, 1990; Bourke and Franks, 1995; Heinze and Tsuij, 1995). Apart from socially parasitic queens that enter foreign colonies and exploit their work force to gain a headstart in reproduction (Buschinger, 1986) and flightless queens that mate near their natal nest and return to it (e.g., Buschinger and Heinze, 1992; Heinze and Tsuji, 1995), some species have lost the queen caste altogether (Peeters, 1991 a), again others even reproduce unisexually by (thelytokous) parthenogenesis (Pristomyrmex pungens, Itow et al., 1984; Tsuji, 1988). However, the most variable trait of ant reproduction is the number of queens per colony (Keller, 1993). An ever increasing number of species is reported that show, at least to some extent, intraspecific variation in this trait. As demonstrated, not only the number of queens but also their size varies in some species. This is particularly interesting because a central trade-off between offspring number and size occurs, which has to be balanced by different selective forces acting upon the alternative reproductive tactics that the different morphs are specialized for.

Why are alternative reproductive tactics in post-copulatory female life history more common in ants than in other animals? Ant colonies can be compared to sedentary organisms (superorganism concept), which show an almost ubiquitous pattern of alternative modes of dependent (asexual) and independent reproduction (e.g., Harvell, 1994). The longevity and "somatic productivity" of ant colonies renders philopatry and social parasitism a rewarding, although certainly frequency-dependent alternative in reproduction. Queens on the other hand, are highly specialized dispersing units which are probably comparable to dispersal stages in complex life cycles (Wilbur, 1980). Compared to females of solitary animal species, the selection pressure on an ant queen's performance in everyday maintenance is relatively weak because these tasks are largely provided by workers. Thus, selection is less conservative and evolutionary response to a varying environment may be faster and more flexible (compare to Gadagkar, 1997).

The reproductive specialization "liberated" in turn the workers from the necessity to disperse and consequently they could adapt efficiently to an edaphic life style (loss of bulky thorax, wings and large optic apparatus). This morphological differentiation based on phenotypic plasticity constitutes a pre-adaptation to the evolution of ergatoid queens as the genetic programs necessary for this developmental pathway are already existing in the genome. The fact that the subsequent modifications of queen phenotype by recombining parameters of the worker and queen developmental program are cheap in an evolutionary sense is reflected by the occurrence of accidental intercastes in most ant species (Peeters, 1991b; Heinze, 1998).

Even without bimodality the considerable variability of queen size in some species (e.g., Liebig, 1995), needs to be studied in more depth since it presumably is of general biological relevance. While enforcement of dichotomies upon more or less continuous variation has to be avoided (Caro and Bateson, 1986), a continuous morphological variation may well translate into discrete behavioral tactics. This variation is found across taxa and although ants might provide particularly promising case studies for the reasons above, the general relevance of female body size apart from pure fertility effects needs to be elucidated.

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