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The ecology of communal breeding: the case of multiple-queen leptothoracine ants

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SUMMARY

Multiple-queen societies of ants are key subjects in the study of communal breeding. Societies of leptothoracine ants may be obligately monogynous (contain a single reproductive queen), functionally monogynous (only one of several mated queens lays eggs), or facultatively polygynous (some colonies contain more than one egg-laying, mated queen). This paper presents a framework for understanding these diverse social systems as a function of leptothoracine ecology. The framework is derived from a synthesis of empirical information – in particular, a link between the social system and the degree of habitat patchiness – with three bodies of theory. These are ecological constraints theory, ESS (evolutionarily stable strategy) models of dispersal, and kin selection models predicting the stable reproductive skew (allocation of reproduction). In contrast to several previous ecological hypotheses, multiple-queening in leptothoracines almost certainly results from high costs to single queens of dispersal and colony foundation (high ecological constraints), which select for queens to seek adoption in their natal colony. Factors raising these costs include nest-site limitation, cold climate, and habitat patchiness. ESS models suggest that high dispersal costs lead to a larger stable fraction of non-dispersers and hence to higher relatedness between queens. Skew models predict that high ecological constraints and high relatedness promote high skew (one or a few individuals dominate reproduction) and high within-colony aggression. Therefore, (i) extensive habitats with moderate costs of solitary colony foundation should promote multiple-queening with high dispersal levels, moderate queen relatedness, low reproductive skew, and low queen aggression. By contrast, (ii) patchy habitats should induce multiple-queening with less dispersal, higher queen relatedness, higher skew, and higher aggression. In addition, (iii) habitats with small or widely spaced nest-sites, or with low costs of founding colonies alone, should lead to universal dispersal without multiple-queening. These associations of traits occur in facultatively polygynous, functionally monogynous and obligately monogynous leptothoracines respectively. Therefore, the framework in this paper explains a substantial amount of the social and ecological diversity of leptothoracine ants.

1. INTRODUCTION

The evolutionary ecology of communal breeding is an important subject because of the theoretical interest in explaining how ecological factors and within-group kin conflict jointly determine social structure (e.g. Keller & Reeve 1994). In addition, communal breeding is widespread in both insects and vertebrates, and its evolution raises similar issues to those involved in the evolution of eusociality (Rosengren & Pamilo 1983; Keller & Vargo 1993). Multiple-queening in ants is a form of communal breeding in which there is also shared care of the young by a largely non-reproductive helper caste (workers). Therefore, to explain the observed variations in colony queen number (gyny) is a major challenge in evolutionary ecology and social insect biology (Keller 1993*a*).

Ants display great diversity in their social systems (Buschinger 1974; Hölldobler & Wilson 1977, 1990). In obligate monogyny, there is only ever one egg-laying, mated queen per colony. In functional monogyny, several mated queens coexist, but only one lays eggs. Polygyny describes the coexistence of several egg-laying queens in mature colonies. Primary polygyny arises from associations of colony founding queens that are, however, usually temporary. Secondary polygyny involves the adoption of young, mated queens into established colonies, and is described as facultative if only some colonies in a population are polygynous (Rissing & Pollock 1988; Hölldobler & Wilson 1977, 1990; Heinze 1993*a*; Herbers 1993).

Multiple-queening should arguably be unstable, because coexisting queens are expected to show reproductive competition (Hölldobler & Wilson 1977; Rosengren & Pamilo 1983; Herbers 1993).

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Nevertheless, secondary polygyny is common in ants (Buschinger 1974; Rissing & Pollock 1988; Hölldobler & Wilson 1990; Frumhoff & Ward 1992; Keller 1993*a*) and so has presumably been naturally selected under some ecological circumstances. Several studies have therefore sought to identify the ecological factors underlying social diversity (e.g. Hölldobler & Wilson 1977, 1990; Rosengren & Pamilo 1983; Brian 1983; Nonacs 1988, 1993; Rissing & Pollock 1988; Elmes & Keller 1993; Herbers 1993; Rosengren *et al.* 1993).

This paper aims to explain the diversity of social organization, and its ecological correlates, in the myrmicine ant tribe Leptothoracini. A starting point is the need to explain the association in this group of facultative polygyny with extended uniform habitats, and functional monogyny with patchy habitats (Heinze & Buschinger 1987, 1989; Heinze 1989*a*, 1992, 1993*a*,*b*). After examining some earlier ecological theories (§2), we argue that factors raising the costs of attempting to nest alone (increasing ecological constraints) are the principal ecological promoters of multiple-queening in the leptothoracines (§3). We also discuss the effect of ecological constraints – particularly habitat patchiness – on the evolution of dispersal in ants, drawing on insights from game theory models of dispersal (Hamilton & May 1977; Johnson & Gaines 1990). Section 4 reviews social and genetic factors that possibly promote polygyny in leptothoracines. Section 5 discusses the evolution of a stable reproductive skew (allocation of reproduction) (Vehrencamp 1983*a*,*b*; Reeve & Ratnieks 1993; Keller & Reeve 1994). In §6, we combine these elements to provide a framework for understanding leptothoracine social and ecological diversity. Section 7 describes how details of leptothoracine biology – including the link between social organization and the degree of habitat patchiness – fit into this framework. Lastly, predictions of these arguments are presented in §8.

Aside from showing ecological differences between their social systems, leptothoracines represent a useful group in which to study polygynous evolution for three main reasons. First, they are socially diverse, exhibiting obligate monogyny, functional monogyny and facultative polygyny. Second, focusing on one group partly controls for taxonomic differences. Third, the issue of how polygyny evolved is inseparable from general life history considerations (Hölldobler & Wilson 1977; Rosengren & Pamilo 1983; Heinze 1992; Reeve & Ratnieks 1993; Rosengren *et al.* 1993; Keller 1993*b*). Monogyny is typically associated with colony reproduction by the emission of sexuals, mating away from the nest, solitary colony foundation, and hence wide dispersal. By contrast, secondary polygyny is associated with colony reproduction by a mixture of sexual emission, mating away from the nest and dispersal on the one hand, and mating near the nest, queen readoption, colony budding and non-dispersal on the other (Hölldobler & Wilson 1977, 1990; Keller 1991). (Colony budding involves colony foundation by groups of emigrant queens and workers.) In addition, compared to queens in monogynous species, queens in polygynous species tend to have a smaller body size (Keller 1991; Keller & Passera 1989), fewer fat and glycogen reserves (Keller & Passera 1989; Passera & Keller 1990), shorter lifespan (Keller & Passera 1990), lower fecundity (Vander Meer *et al.* 1992; Elmes & Keller 1993), and an earlier first age of sexual production (Pamilo & Rosengren 1984; Keller & Passera 1990). So the comparison of monogyny and polygyny is the comparison of two distinct syndromes (Keller 1993*b*). Leptothoracine ants have been extensively studied for many years. Therefore a relatively large amount of the life history information needed to investigate the evolutionary ecology of multiple-queening is available in this group. However, we suggest that the ideas explored here in the leptothoracines apply widely among ants and communally breeding animals in general.

2. PREVIOUS ECOLOGICAL HYPOTHESES FOR THE EVOLUTION OF POLYGYNY

This section assesses the applicability to the leptothoracines of some of the ecological factors that have previously been proposed to select for polygyny.

(*a*) *Species rarity*

Wilson (1963) argued that polygyny, by raising the effective population size, acts as a buffer against population extinction. Therefore, in species at risk from extinction (rare species), between-population selection favours polygyny. However, the correlation between rarity and polygyny is poor. Many of Wilson's (1963) examples are social parasites, which may be polygynous for reasons unconnected with rarity (Buschinger 1986, 1990*b*; Bourke & Franks 1991). Furthermore, many non-parasitic, polygynous ant species are common (Rissing & Pollock 1988; Herbers 1993), including *Leptothorax acervorum* and *L. longispinosus*. Another problem is that between-population selection for population-beneficial traits is likely to be weak and slow compared to within-population selection for selfish behaviour by groups and individuals (e.g. Lewontin 1970). Therefore, polygyny is unlikely to evolve by this process alone (Herbers 1993).

(*b*) *Short-lived nest-sites*

Hölldobler & Wilson (1977) proposed that species using these sites ('nest-site opportunists') evolve polygyny to avoid harmful queenlessness that would otherwise arise from colony fragmentation. However, Herbers (1986*a*) did not find polygyny to be associated with short-lived nest-sites in *L. longispinosus*. In facultatively polygynous *L. acervorum*, nest-sites do not appear to be particularly short-lived (Douwes *et al.* 1987), whereas nest-sites are short-lived in the monogynous *L. congruus* (Yamaguchi 1992). So this idea is poorly supported (Herbers 1993), particularly in the leptothoracines.

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(*c*) ***Large, long-lived patchy habitats***

Hölldobler & Wilson (1977) also suggested that polygyny in species in these habitats ('isolated-habitat specialists') permits colony reproduction by budding, which in turn allows profitable domination of the habitat by a single colony or its descendants. This hypothesis seems most applicable to polygynous species with a unicolonial or polydomous social organization. (Unicoloniality is when neighbouring nests of the same species are mutually tolerant and intermix freely. Polydomy occurs when single colonies occupy several nests.) These species tend to be strong interspecific competitors that are able to dominate habitats in the way Hölldobler & Wilson (1977) envisaged. *Leptothorax* ants, however, are not unicolonial (e.g. Stuart 1987) and typically share their habitats with other species (e.g. Savolainen & Vepsäläinen 1989). So they are not true 'isolated-habitat specialists'.

(*d*) ***Interspecific social parasitism***

Rosengren & Pamilo (1983) and Herbers (1986*a*, 1993) suggested that polygyny could be a defence against socially parasitic ants. Polygynous colonies – with more queens and workers per colony – could be better at resisting the attacks of both parasitic queens and slave-raiding workers. Many leptothoracines are both polygynous and hosts to slave-making ants (Buschinger 1986). However, Herbers (1986*a*) found no positive correlation between the frequency of parasitism by slave-makers and the proportion of polygynous nests across populations of *L. longispinosus*. Similarly, *L. acervorum* is polygynous or functionally monogynous in parts of its range without social parasites, e.g. the British Isles (Bourke 1991), Japan (Ito 1990), and Alaska (Heinze & Ortius 1991). Furthermore, some host species of slave-makers are obligatorily monogynous, e.g. most hosts of *Epimyrma* slave-makers (Buschinger 1989). So, rather than being an evolved defence against parasitism, polygyny is probably associated with hosting social parasites because it makes species susceptible to them (Alloway *et al.* 1982; Buschinger 1986, 1990*b*; Bourke & Franks 1991). In sum, social parasitism may be rejected as a general factor selecting for polygyny.

3. THE COST OF SOLITARY COLONY FOUNDATION, STABLE DISPERSAL LEVELS, AND HABITAT PATCHINESS

The previous section argued that several ecological factors previously suggested to promote polygyny are unlikely to apply to leptothoracines. We now suggest that the major factor promoting polygyny in this group is the cost to young queens of attempting solitary colony foundation. A young queen has the choice of founding a colony alone, or seeking adoption in the natal nest. Solitary colony foundation leading to monogyny might entail higher queen productivity than adoption leading to polygyny. On the other hand, it almost certainly involves higher queen mortality than adoption, because singly founding queens lack the initial protection of a colony. Therefore, several authors (e.g. Crozier 1979; Rosengren & Pamilo 1983; Herbers 1993; Rosengren *et al.* 1993) have proposed that if solitary colony foundation is very costly, young queens should be selected to re-enter their natal colonies, resulting in multiple-queening. This is a version of the general idea that individuals should join communally breeding groups if their net gain exceeds that from solitary breeding (e.g. Vehrencamp 1983*a*).

This idea is subject to the qualification that there may be within-colony kin conflict between the natal colony and queens seeking admission, depending on the level of cost promoting adoption (Rosengren & Pamilo 1983; Nonacs 1988; Pamilo 1991; Herbers 1993; Seger 1993). However, above a certain cost all parties (resident queens, workers and young queens) should favour queen adoption, provided that adopted queens are on average related to the accepting colony (Seger 1993). From the residents' standpoint, this is because they have an evolutionary stake in the successful reproduction of related young queens. Therefore, ecological factors that increase the costs of solitary colony foundation will also promote multiple-queening. Ecological constraints on independent nesting have also been widely invoked to account for communal and cooperative breeding in other social insects (e.g. wasps: Queller & Strassmann 1988; Reeve 1991; Itô 1993), and in birds and mammals (e.g. Brown 1974; Koenig & Pitelka 1981; Emlen 1982*a*, 1991).

The costs of solitary colony foundation have two components (e.g. Rosengren *et al.* 1993): namely costs arising from (i) the act of solitary colony foundation itself, and from (ii) mortality during dispersal to the new nest site.

(*a*) ***Factors raising the costs of successful solitary colony foundation***

An important contributor to a low chance of colony foundation in solitary queens is nest-site shortage arising, for example, through habitat saturation. This is especially likely in leptothoracines, which nest in preformed cavities including hollow twigs and acorns (Herbers 1986*b*). Consistent with this idea, Herbers (1986*b*) found that in *L. longispinosus* the degree of polygyny and the frequency of empty nest-sites were inversely related across populations, and that adding artificial nests reduced the mean number of queens per nest. Competition among cavity-nesting ant species for nest sites may also induce nest-site limitation for any one species (Herbers 1989), although such competition has not lead to polygyny in *L. congruus* (Yamaguchi 1992).

Another potentially important contributor to costly solitary nest founding is a cold climate that kills single queens attempting hibernation (Heinze & Buschinger 1988; Satoh 1989; Heinze 1991, 1992, 1993*c*; Heinze & Hölldobler 1994). In winter, leptothoracine ants form dense clusters in the nest even though they do not thermoregulate. This suggests an advantage of

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grouping during hibernation. In physiological terms, this could be because grouping protects overwintering ants against desiccation and inoculative freezing (Lee 1991). Direct evidence of increased mortality among single overwintering queens is lacking. However, *L.* cf. *canadensis* workers that hibernated in experimental groups survived better than those hibernating singly (Heinze 1992, 1993*c*; Heinze & Hölldobler 1994). The tendency for multiple-queening among leptothoracines to occur at high altitudes and latitudes (Heinze & Buschinger 1988; Heinze 1993*c*) is also evidence for the proposed effects of cold.

(*b*) *Factors increasing dispersal costs*

Factors that have been suggested to lead to costly dispersal include predation (Crozier 1979; Rosengren & Pamilo 1983; Bolton 1986; Herbers 1993) and resource shortage in arid climates. The latter factor makes it difficult for colonies to produce large numbers of dispersing queens rich in the fat reserves needed for solitary colony foundation (Briese 1983; Bolton 1986; Heinze *et al.* 1992*a*; Tinaut & Heinze 1992).

An additional factor influencing dispersal cost is habitat patchiness, which has previously been implicated in the evolution of multiple-queening by Hölldobler & Wilson (1977), Rosengren & Pamilo (1983) and, among leptothoracines, by Heinze (1992, 1993*a*,*b*) (see § 1). In the rest of this section, we argue that the degree of habitat patchiness affects dispersal costs and may covary with other contributors to these costs. Variable dispersal costs then lead to polymorphisms of non-dispersal (yielding multiple-queening) and dispersal by queens, with a variable balance between these two tactics. Our arguments draw on game theory models of evolutionarily stable dispersal strategies (Hamilton & May 1977; Johnson & Gaines 1990), as previously invoked in the context of polygyny by Rosengren & Pamilo (1983), Heinze (1989*a*) and Rosengren *et al.* (1993). The idea that habitat patchiness selects for non-dispersal has previously been applied to sedentary morphs among beetles (Darwin 1859, p. 136), socially parasitic ants (e.g. Heinze & Buschinger 1987, 1989), other insects (e.g. Wagner & Liebherr 1992), and plant seeds (e.g. Begon *et al.* 1990, p. 179). In ants, the connection between dispersal polymorphisms and multiple-queening has also been widely recognized (e.g. Heinze 1989*a*; Yamauchi *et al.* 1991; Rosengren *et al.* 1993). Rosengren & Pamilo (1983) and Rosengren *et al.* (1993) explicitly linked patch size, queen number and dispersal strategy in *Formica* ants.

Consider first the situation when the suitable habitat consists of very large uniform patches (Heinze 1992, 1993*a*,*b*), and where there is also a relatively low probability of colony foundation by single queens for whatever reason (e.g. nest-site limitation, cold climate). In leptothoracines, the co-occurrence of these features is likely, because nest-sites are probably easily limited in this group (see above), and because a typical habitat – extensive uniform pine forest – tends to be in northern areas. In these circumstances, queen readoption (leading to multiple-queening) would seemingly be favoured much more than dispersal. But queens dispersing far from the nest would still have an above-zero chance of founding a colony alone because they would tend to remain within the extensive habitat. Their exact chance would depend on the frequency with which empty nest-sites arise, through either colony mortality or the formation of new sites by the fall of twigs and acorns from trees.

In addition, game theory predicts that a species will never have completely non-dispersing young, because complete non-dispersal is not an evolutionarily stable strategy (ESS) (Hamilton & May 1977). This is because a strategy of complete non-dispersal could be invaded by a mixed strategy involving both non-dispersing and dispersing individuals. Sites occupied by non-dispersers could be taken over by mixed strategists, but the reverse could not occur, so all sites would eventually be occupied by mixed strategists (Hamilton & May 1977). Moreover, Hamilton & May's (1977) models suggest that the stable fraction of dispersers remains high even when the survivorship of dispersers is very low.

An alternative to readoption followed by remaining to breed in the natal colony is readoption followed by later departure with part of the workforce (colony budding). Departing in a bud avoids the low chances of founding colonies alone, especially since buds should be able to outcompete single queens for available sites. So conditions involving poor chances of solitary colony foundation that promote queen readoption, also promote colony budding.

For these reasons, an extensive habitat with low survivorship of solitarily founding queens should select for a mixed strategy of queen readoption and dispersal, with a relatively strong emphasis on dispersal. It should also lead to budding.

Now consider a habitat consisting of small, scattered patches (Heinze 1992, 1993*a*,*b*). This kind of habitat will reduce a lone queen's chances of successful dispersal and colony foundation. Small patches are likely to become saturated more rapidly, leading to nest-site limitation (Rosengren *et al.* 1993). In addition, they can realistically be dominated by budding, so singly founding queens would be in competition with colony buds for nest-sites. Scattered patches also lead to greater costs of dispersal for queens attempting to leave patches, as these queens risk not finding another patch (Rosengren & Pamilo 1983; Heinze & Buschinger 1987, 1989; Heinze 1992, 1993*a*,*b*). The ESS dispersal models find that as the mortality of dispersers increases, the stable fraction of non-dispersers should rise, although complete non-dispersal remains unstable (Hamilton & May 1977). Finally, in leptothoracines in northern areas, small wind-swept patches of exposed rock – favoured by some species – are probably more hostile to solitary foundresses than surrounding woods because they receive less insulation from snow cover against the cold. For all these reasons, in habitats of small, scattered patches a mixed strategy of readoption (polygyny) and dispersal is still expected, but the

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emphasis on non-dispersal should increase as compared to the previous situation (Heinze 1992). Further, colony budding to dominate the patch should be prevalent.

Finally, if patches are so small that each can hold one nest only, i.e. each nest and its immediate neighbourhood constitute a 'patch', budding is not an option. The same applies if nest-sites are at low density. So dispersal should become correspondingly more important again. This will be especially the case if such a habitat is associated with a relatively high chance of solitary colony foundation.

4. SOCIAL AND GENETIC FACTORS PROMOTING POLYGYNY

As well as external, ecological effects (§§ 2 and 3), several social or genetic factors have been proposed to contribute to the maintenance of polygyny. They include: (i) enhanced genetic diversity in polygynous colonies (e.g. Shykoff & Schmid-Hempel 1991; Snyder 1992); (ii) greater colony longevity under polygyny (e.g. Wilson 1974*b*; Rettenmeyer & Watkins 1978; Bolton 1986); (iii) reduced colony mortality due to diploid male production under polygyny in *Solenopsis invicta* (Ross & Fletcher 1985, 1986; Ross 1988*a*); and (iv) greater winter survival of polygynous colonies in *L. longispinosus* (Herbers 1986*a*, 1993). We now discuss the relevance of these factors, emphasizing as before their applicability to leptothoracines.

(*a*) *Enhanced genetic diversity in polygynous colonies*

Although there is evidence for a genetic component to the division of labour in genetically diverse colonies (Stuart & Page 1991; Snyder 1992, 1993; Carlin *et al.* 1993), earlier studies failed to find many differences in the organization of work between monogynous and polygynous colonies of leptothoracines (Herbers 1982; Herbers & Cunningham 1983). However, it remains to be tested whether genetic diversity in task performance by workers enhances colony efficiency. Similarly, investigations are required to see if polygyny enhances a colony's genetically mediated resistance to parasites (Shykoff & Schmid-Hempel 1991).

(*b*) *Greater colony longevity under polygyny*

Colony longevity per se cannot be considered adaptive independently of other life history traits. However, long-lived colonies might be favoured through allowing lineages to retain their nests when these are costly to build or when nest-sites are scarce (Rosengren & Pamilo 1983; Rosengren *et al.* 1993). Thus, if leptothoracines are subject to nest-site limitation, this factor could promote the evolution of polygyny among them.

(*c*) *Reduced colony mortality due to diploid male production under polygyny in* **Solenopsis invicta**

Although diploid male production has been reported in leptothoracines (Buschinger 1989; Loiselle *et al.* 1990; Buschinger & Fischer 1991), there is no evidence that it promotes polygyny in this group. In other species, diploid male production is not unequivocally associated with polygyny (Pamilo *et al.* 1994), and in *S. invicta* its contribution to the maintenance of polygyny is almost certainly due to the unusual evolutionary history of this species in North America (Ross & Fletcher 1985, 1986; Ross *et al.* 1993).

(*d*) *Greater winter survival of polygynous colonies in* **L. longispinosus**

There is evidence that queen number is associated with higher survivorship of overwintering *L. longispinosus* colonies (Herbers 1986*a*, 1993). However, the causal mechanism is unknown, and an alternative explanation of this association is that those colonies strong enough to survive hibernation are also those that adopt many queens. On the other hand, the proposed effect of queens on colony survival is consistent with the link between polygyny and high latitude and altitude in leptothoracines (Heinze & Buschinger 1988; §3). So the search for this effect in other *Leptothorax* species would be valuable.

5. EVOLUTION OF STABLE REPRODUCTIVE SKEW

Nonacs (1988) and Pamilo (1991) showed that secondary polygyny involving the adoption of related queens is in principle consistent with kin selection theory, but that polygyny could also lead to kin-selected conflicts of interest within colonies. Another important set of kin conflict models deals with the evolution of a stable reproductive skew among communal breeders (Emlen 1982*b*; Vehrencamp 1983*a*,*b*; Reeve 1991; Reeve & Ratnieks 1993; Itô 1993; Keller & Reeve 1994). Reproductive skew means within-group variance in offspring number. High skew is when reproduction is dominated by one or a few individuals, and low skew is when it is evenly shared. The stable skew models are essential to understanding leptothoracine social organization, because a major contrast in this group is that between the functionally monogynous (high skew) and polygynous (low skew) species (Reeve & Ratnieks 1993).

The basic premise of the skew models is that multiple-breeder societies are unstable if subordinate individuals could receive greater payoffs from attempting to breed alone. The models therefore explain the stable skew in terms of the ecological constraints on joiner individuals, their relatedness with residents, and their relative fighting ability. So their general merit is to show how social structure is affected by both external, ecological factors and internal, conflict-related ones (Reeve 1991).

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The models of Reeve & Ratnieks (1993) make a number of assumptions. They are that: (i) polygynous groups contain two queens only; (ii) a dominant queen can control the reproduction of a subordinate; (iii) a queen that joins another can personally boost group productivity through helping raise brood; (iv) queens differ in their fighting ability; and (v) queens can monitor the skew in their colonies (and then adjust their behaviour if the skew is not balanced in their favour). In leptothoracines, assumption (i) is not always met. Multiple-queen colonies often have more than two queens, although average queen numbers are usually low (e.g. Herbers 1984; Stille *et al.* 1991). We therefore assume (cf. Vehrencamp 1983*a*,*b*; Keller & Reeve 1994) that the qualitative results of the skew models apply to larger groups. Assumption (ii) holds in leptothoracines, because dominance behaviour among queens has been recorded from this group (e.g. Heinze & Smith 1990). Assumption (iii) is taken to be effectively correct but requires qualification, since *Leptothorax* queens do not perform work. We assume that extra queens instead can enhance lifetime colony productivity either because polygyny is associated with an earlier first age of sexual production (see § 1), or because it increases the colony's genetic diversity (see § 4), or because it raises colony survivorship. For example, this could occur through the extra queens contributing to a larger workforce, or to greater overwintering success (cf. Herbers 1993), or to faster recovery from predation or other forms of queen loss (cf. Itô 1993). These effects are also taken to more than offset any negative influence of queens on productivity, because in leptothoracines, as in other polygynous ants, the average per capita offspring number of queens falls as queen number rises (table 2).

Assumption (iv) is almost certainly met in *Leptothorax* ants, but fighting ability is probably a relatively unimportant factor in determining differences in skew across species. In other words, it is unlikely that the skew differences shown between polygynous and functionally monogynous societies are due to variation in fighting ability among queens. Such variation as occurs, for example a larger Dufour's gland (part of the sting apparatus) in queens of the aggressive species *L.* species A and *L. gredleri* (J. Heinze, unpublished data), may have evolved as a consequence of fighting rather than vice versa. Finally, assumption (v) that queens can monitor skew is also plausibly met in leptothoracines, since fecund queens develop a conspicuous swelling of the abdomen (physogastry) and probably also emit chemical cues that indicate their reproductive status.

The first key finding of the skew models involves some of the ecological and social factors already discussed. Thus, Vehrencamp (1983*a*,*b*) and Reeve & Ratnieks (1993) found stable multiple-reproductive societies to be favoured by costly dispersal (high ecological constraints), and large group productivity relative to the productivity of singletons, since both these make joining a group relatively more profitable. Next, Vehrencamp (1983*a*,*b*) and Reeve & Ratnieks (1993) found that, in established multiple-breeder societies, a high reproductive skew is stable when there is: (i) a low chance of solitary breeding (because a joining queen tolerates lower personal reproduction in the group if its chances of success on its own are small); and (ii) high within-colony relatedness (because a subordinate queen accepts a smaller share of personal reproduction the more highly it is related to the dominant, since then its kin-selected gain via the dominant's offspring is also greater). In addition, Reeve & Ratnieks (1993) predicted that high skew should be associated with aggressive fighting behaviour by the dominant individual. If the prize is high, as under conditions of high skew, subordinates should be more inclined to challenge the dominant for supremacy, meaning the dominant must exert suppression more fiercely. When skew is low, the reward from winning the notional dominant's position is smaller, so queens should coexist relatively peacefully. This reasoning reverses the direction of causality implicit in explanations that regard high skew as a consequence of queen aggression.

In sum, the stable skew models predict an association between high skew and high levels of ecological constraints, fighting, and relatedness (Vehrencamp 1983*a*,*b*; Reeve & Ratnieks 1993; Keller & Reeve 1994). Although the link of high relatedness with high skew seems paradoxical, the point is that societies with low relatedness and high skew are unstable. Most queens in these societies would receive little fitness benefit from either their own or the dominants' reproduction. They would profit more from attempting independent colony foundation, leading to the break-up of the society. High skew and high relatedness are also mutually reinforcing in secondarily polygynous ants. This is because, if readopted daughters are offspring of just one or a few mothers, they will tend to be highly related to each other (Keller & Vargo 1993).

6. SYNTHESIS OF ECOLOGICAL CONSTRAINTS HYPOTHESES, ESS DISPERSAL MODELS, AND REPRODUCTIVE SKEW MODELS IN LEPTOTHORACINE ANTS

In this section we construct a synthesis from the arguments presented in the previous sections. These arguments derive from our consideration of the ecological constraints hypotheses (with habitat patchiness being a major constraint) (§ 3), the ESS dispersal models (§ 3), the stable skew models (§ 5), and existing information on leptothoracine biology, in particular the link between the social system and the degree of habitat patchiness (Heinze 1992, 1993*a*,*b*) (see § 1).

First consider again the case when the habitat consists of extensive uniform patches. In areas that are nest-site limited, or at high latitude, or both, this could be associated with significant but moderate costs of solitary colony foundation. Therefore some queens should seek adoption by their natal colony, leading to multiple-queening. But colony budding is also expected, and a sizeable proportion of queens should also be dispersers (§ 3). Furthermore, if some queens disperse and then seek adoption in foreign

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colonies (i.e. attempt intraspecific social parasitism), a fraction of queens gaining admission to nests are likely to be non-relatives. So although queens within colonies will be on average related (because the average adoptee is from the natal colony), the level of relatedness within colonies should be less than if fewer queens were dispersers.

According to the models of Reeve & Ratnieks (1993), both moderate costs of solitary founding, and reduced within-colony relatedness, select for a decrease in reproductive skew. This in turn should lead to a relative lack of between-queen aggression (§ 5). Therefore, nest-site limited and/or temperate uniform extensive habitats should select for: (i) moderate chances of single colony foundation, and hence some queen readoption and multiple-queening; (ii) a mixed mating and dispersal strategy with relatively many dispersers; (iii) above-zero but moderate queen-queen relatedness; (iv) a degree of colony budding; (v) low reproductive skew; and (vi) low queen–queen aggression (table 1). Reeve & Ratnieks (1993) themselves predicted low skew in non-aggressive, facultatively polygynous leptothoracines.

Now reconsider the case when the environment consists of small, scattered patches of suitable habitat. Here, colony foundation success for single queens is very low, leading to greater emphasis on non-dispersal, readoption and colony budding (§ 3). Consequently, adoptees will be from the home colony more frequently, so average within-colony relatedness should rise. Both low chances of solitary nesting and high relatedness select for high reproductive skew and hence relatively intense queen-queen aggression (§ 5).

Therefore, a habitat of small, scattered patches should lead to: (i) very low chances of single colony foundation, and hence (more pronounced) queen adoption and multiple-queening; (ii) a mixed mating and dispersal strategy with relatively fewer dispersers; (iii) relatively high relatedness; (iv) more colony budding; (v) high reproductive skew; and (vi) high between-queen aggression (table 1). Of course, traits (ii)–(vi) could also arise from high colony foundation costs due to factors independent of habitat patchiness.

Finally, when solitary colony foundation is not particularly costly, or the habitat consists of scattered patches so small that each can be occupied by only one colony (meaning budding is not feasible), or both, obligate monogyny with universal dispersal is expected to be stable.

Table 1. *Expected features of facultative polygyny and functional monogyny in leptothoracine ants*

facultative polygyny	functional monogyny
extensive uniform habitat with moderate costs of solitary colony foundation	habitat of small, scattered patches (leading to high costs of solitary colony foundation)
mixed dispersal strategy with relatively many dispersers	mixed dispersal strategy with relatively many non-dispersers
above-zero but moderate queen–queen relatedness	high queen–queen relatedness
colony budding	more frequent colony budding
moderate to low reproductive skew	high reproductive skew (by definition)
low to absent queen–queen aggression	high queen–queen aggression

7. THE SOCIAL SYSTEMS, GENETIC STRUCTURE AND LIFE HISTORY ATTRIBUTES OF *LEPTOTHORAX* ANTS

This section is a systematic examination of leptothoracine biology showing how the detailed features of this group fit into the framework described in the previous section. Because this framework was derived both from theoretical arguments and from some of the existing data on leptothoracines, the predictive power of our arguments is confined to those traits that are currently unknown. These are discussed in the following section. As background to the current discussion, table 2 sets out relevant traits common to all leptothoracine species. Table 3 shows features of the group that are expected to differ among species on the present arguments.

Comparative analyses should ideally take account of phylogeny, since species may share traits through common ancestry (e.g. Harvey & Pagel 1991). There is a major phylogenetic dichotomy within *Leptothorax* between the subgenera *Leptothorax* (*Leptothorax*) and *Leptothorax* (*Myrafant*) (Buschinger 1981; Douwes & Stille 1987). Multiple-queening is known from all *Leptothorax* (*Leptothorax*) and a number of *Leptothorax* (*Myrafant*) species. The polygynous *Leptothorax* (*Myrafant*) belong to two species groups: the eleven-jointed species from North America (e.g. *L. ambiguus*, *L. curvispinosus*, *L. longispinosus*), and the *tubero-interruptus* group (e.g. *L. tuberum*, *L. nigriceps*, *L. interruptus*). However, existing phylogenies based on allozyme data (e.g. Douwes & Stille 1987, 1991; Heinze 1989*b*) are not well-established enough for a rigorous application of comparative method in the leptothoracines. But the within-group lability shown by ants in their social systems (Ross & Carpenter 1991; Frumhoff & Ward 1992) suggests that queen number is not subject to strong phylogenetic constraints.

With this reservation, the available information on leptothoracines (table 3) suggests that they fit the framework set out in the previous section (see also Heinze 1992, 1993*a*,*b*). Species occupying extensive uniform boreal or alpine habitats are facultatively polygynous, tend to have wide dispersal, and lack queen-queen aggression. Examples are *L. acervorum* (in Europe), *L. muscorum*, *L.* cf. *canadensis*, and the North American facultatively polygynous *Leptothorax* (*Myrafant*) species (table 3). By contrast, species in small-patch habitats are functionally monogynous (have high skew), show less dispersal, and exhibit queen aggression. Examples are *L. gredleri*, *L.* species A,

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and *L. sphagnicolus* (table 3). Species in the leptothoracine 'guest ant' genus *Formicoxenus* (Francoeur *et al.* 1985) also fit this pattern, as they are functionally monogynous, live in a patchy habitat (the nests of other ant species), and show limited dispersal (intermorphic queens: see below) and queen aggression (Heinze 1993*a*; Heinze *et al.* 1993).

Table 2. *Shared traits of leptothoracine ants*

nest type

All species nest in preformed cavities such as plant cavities (e.g. in hollow stems, dead twigs, or acorns), under bark, under stones, or between rocks (Collingwood 1979)

colony size

Colonies contain low numbers of workers and (if polygynous) queens, compared to other taxa. Typically, 1–10 queens plus 10–100 workers (Collingwood 1979)

genetic structure

In the few species examined genetically to date, queens are believed to mate singly (Herbers 1986*c*; Bourke *et al.* 1988; Heinze & Buschinger 1989; Stille *et al.* 1991; J. Heinze, N. Lipski, B. Hölldobler & A. F. G. Bourke, unpublished data on *L. acervorum*)

In all multiple-queen species, cohabiting queens are probably related on average (because of queen readoption). Relatedness estimates from allozyme analysis support this conclusion (table 3). *L. acervorum* colonies probably also adopt some non-relatives (Stille & Stille 1992, 1993) (table 3)

There is no genetic evidence for inbreeding in multiple-queen species (Heinze & Buschinger 1989; Stille *et al.* 1991; J. Heinze, N. Lipski, B. Hölldobler & A. F. G. Bourke, unpublished data). It is probably avoided despite mating near the nest by wide dispersal of males. Costs of inbreeding as a penalty of non-dispersal (Johnson & Gaines 1990) are therefore probably unimportant in leptothoracines

In *L. acervorum*, genetic subdivision of populations exists in that neighbouring colonies tend to be related matrilineally. This probably arises through colony budding, and so may occur in other species as well (Stille & Stille 1992, 1993)

queen productivity

In several facultatively polygynous species, per capita brood and adult production by queens fall with rising queen number (Wilson 1974*b*; Herbers 1984; Buschinger 1990*a*; Bourke 1991, 1993)

colony foundation

There are four modes: (1a) independent (without workers) by single queens (haplometrosis); (1b) independent by multiple queens (pleometrosis); (2a) dependent by adoption (queens enter existing nests); and (2b) dependent by budding (queens leave existing nest with some workers). Solitary foundation (1a) is rarely successful, as populations contain few monogynous, incipient colonies. But the production of numerous winged queens suggests it is attempted frequently. It may be attempted in spring following hibernation in the natal nest. Pleometrosis (1b) is rare. Both dependent modes (2a,2b) are common, but their relative frequencies are unknown. In polydomous species (having multiple nests), budding (2b) may occur through nests losing contact (Buschinger 1968; Alloway *et al.* 1982; Heinze & Buschinger 1988; Heinze 1993*b*, *c*; Stille & Stille 1993)

mating and dispersal

Leptothorax (*Leptothorax*) species have female calling (females release male attractant pheromones from a stationary position on the ground). In winged forms, this can occur after flight. *Leptothorax* (*Myrafant*) species have nuptial flights. In all multiple-queen species, some queens presumably mate near nests (to account for queen–queen relatedness). This definitely occurs in some species with female calling. But in most species the exact balance between mating near the nest and readoption, and mating far from the nest and dispersal, is unknown (Buschinger 1971; Buschinger & Alloway 1979)

Intraspecific variation in gyny systems is also explicable with the current ideas. For example, *L. acervorum* is facultatively polygynous in homogeneous habitats throughout Europe (Buschinger 1968; Bourke 1991) (table 3), but functionally monogynous in northern and patchy habitats (sun patches in wood or tundra) in Japan (Ito 1990) and probably Alaska (Heinze & Ortius 1991).

Leptothoracines in areas with mild winters and hence probably low costs of solitary colony foundation tend to be obligately monogynous as expected. Examples include the monogynous *Leptothorax* (*Myrafant*) species of the Mediterranean, Central Europe, and temperate and subtropical North America (e.g. Heinze & Buschinger 1988; Frumhoff & Ward 1992; Heinze 1993*c*).

Further details of the expected associations are as follows.

(*a*) *Queen–queen relatedness*

The expectation that relatedness among queens should be higher in functionally monogynous species has not been directly tested because relatedness estimates (from allozyme data) are currently only available from facultatively polygynous *Leptothorax*. Among these, estimates of queen-queen relatedness vary from moderate to high depending on the population (table 3), although it needs noting that they typically have large standard errors. In *L. acervorum*, mitochondrial DNA analysis suggested that 15% of colonies may contain unrelated queens (Stille & Stille 1992). Laboratory experiments have also shown that nests of facultatively polygynous species occasionally accept non-nestmate queens (Bruckner 1982; Stuart *et al.* 1993). Therefore relatedness in these species may indeed be reduced by the adoption of unrelated queens. However, Heinze (1992) suggested on preliminary evidence that queens are equally highly related in facultatively polygynous and functionally monogynous leptothoracines. From the earlier arguments, this could only be the case if the greater costs of dispersal and solitary colony foundation among the functionally monogynous species were alone sufficient to induce high reproductive skew.

(*b*) *Balance between dispersal and non-dispersal*

Evidence exists for the relatively recent evolution of widespread dispersal in the facultatively polygynous *L. acervorum*. A mating system involving mainly 'female calling' near the nest seems to be the ancestral trait for the European members of the subgenus *Leptothorax* (*Leptothorax*) (Buschinger & Alloway 1979; Lipski *et al.* 1992) (tables 2 and 3).

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Table 3. *Features of leptothoracine ants varying between species*

species[a]	social system	habitat	mating and dispersal system[b]	queen aggression[c,d,e]
Leptothorax (*Leptothorax*)				
L. acervorum (Europe)	facultative polygyny	pinewoods, moorland, bogs	female calling after flight to distant swarm	absent
L. gredleri	functional monogyny	forest edges, thickets	female calling	present
L. muscorum	facultative polygyny	pinewoods	female calling near nest; plus dispersal on wing	absent
L. species A	functional monogyny (or monogyny with gynomorph queen)	isolated rocky hilltops, woods	queen polymorphism; female calling near nest (intermorphs) or after flight (gynomorphs)	present
L. cf. *canadensis*	facultative polygyny	woodlands, bogs	female calling, following flight	absent
L. sphagnicolus	functional monogyny	moss hummocks	queen polymorphism; no data on mating	no data
Leptothorax (*Myrafant*)				
L. ambiguus	facultative polygyny; polydomy	deciduous woods	no data	no data
L. curvispinosus	facultative polygyny; polydomy	deciduous woods	nuptial flight	absent
L. longispinosus	facultative polygyny; polydomy	deciduous woods	nuptial flight; hilltop swarming	absent

[a] *Leptothorax* species A and *L.* cf. *canadensis* are two as yet undescribed North American species.

[b] In species with queen polymorphism, queens are either 'gynomorphs' (initially winged) or 'intermorphs' (permanently wingless).

[c] Queen aggression refers to fighting between queens within nests. Several species exhibit egg cannibalism (Wilson 1974*a*; Bourke 1991; Heinze *et al.* 1992*b*), but it is unlikely to alter reproductive skew (Bourke 1994).

[d] Queen–queen relatedness estimates (from allozyme analysis) are only available from facultatively polygynous species, as follows. *L. acervorum*: 0.40 (mean from nine populations: Douwes *et al.* 1987), 0.33, 0.60 (two populations respectively: Stille *et al.* 1991), 0.26, 0.63 (two populations: J. Heinze, N. Lipski, B. Hölldobler & A. F. G. Bourke, unpublished data); *L. muscorum*: 0.27 (one population: N. Lipski, unpublished data); *L. ambiguus*: 0.21 (one population: Herbers 1993); *L. longispinosus*: 0.46, 0.55 (two populations: Herbers & Stuart 1990; Herbers 1993). Worker–worker relatedness in the functionally monogynous *L. gredleri* was estimated at 0.41 (Heinze *et al.* 1992*b*). In *L. acervorum*, mitochondrial DNA studies suggest that 15% of colonies contain wholly unrelated queens (Stille & Stille 1992, 1993).

[e] References: *L. acervorum*: Collingwood (1958); Buschinger (1968, 1971); Douwes *et al.* (1987); Bourke (1991, 1993); Franks *et al.* (1991); Lipski *et al.* (1992); Stille *et al.* (1991); Stille & Stille (1992, 1993). *L. gredleri*: Buschinger (1968); Buschinger & Alloway (1979); Heinze & Lipski (1990); Heinze *et al.* (1992*b*); Lipski *et al.* (1992). *L. muscorum*: Buschinger (1968); Buschinger & Alloway (1979); Lipski *et al.* (1992); J. Heinze (unpublished observations of flying queens). *L.* species A: Heinze (1989*a*, 1990, 1993*b*); Heinze & Buschinger (1987, 1988, 1989); Heinze & Smith (1990). *L.* cf. *canadensis*: Heinze & Buschinger (1987, 1989); Heinze (1993*b*). *L. sphagnicolus*: Francoeur (1986); Buschinger & Francoeur (1991). *L. ambiguus*: Alloway (1980); Alloway *et al.* (1982). *L. curvispinosus*: Headley (1943); Talbot (1957); Wilson (1974*a*,*b*); Alloway (1980); Alloway *et al.* (1982); Stuart (1985); Stuart *et al.* (1993). *L. longispinosus*: Headley (1943); Alloway (1980); Alloway *et al.* (1982); Herbers (1982, 1984, 1986*a*,*b*,*c*, 1989, 1990); Herbers & Cunningham (1983); Herbers & Tucker (1986); Herbers & Stuart (1990); Leprince & Francoeur (1986).

However, *L. acervorum* has apparently re-evolved the trait of mating away from the nest, since unlike its congeners it mates principally in distant swarms, while still retaining female calling at the site of mating (Collingwood 1958; Buschinger 1971; Douwes *et al.* 1987; Franks *et al.* 1991).

By contrast, an emphasis on non-dispersal in the functionally monogynous, patchy habitat dwellers is very strongly shown by the fact that *L.* species A, *L. sphagnicolus* and *Formicoxenus* (but not *L. gredleri* or the functionally monogynous populations of *L. acervorum*) display a queen polymorphism in which some queens are wingless 'intermorphs' instead of orthodox, initially winged 'gynomorphs' (Heinze & Smith 1990) (table 3). This indicates powerful selection for non-dispersal (Heinze & Buschinger 1987, 1989; Heinze 1992, 1993*a*,*b*). Furthermore, the association of non-dispersal with habitat patchiness is found intraspecifically in *L.* species A. This species has colonies that tend to be either monogynous with a single gynomorphic queen, or functionally monogynous with wingless, intermorphic queens (Heinze 1989*a*, 1993*b*). Populations with a high proportion of gynomorph-headed colonies are found in extended habitats (woods), whereas those with a high proportion of colonies containing intermorphs occur in

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patchy ones (rock outcrops) (Heinze & Buschinger 1987, 1989; Heinze 1993*b*). Furthermore, the fact that the gynomorphic colonies are usually not polygynous could stem from the low density of nest sites in the woods they inhabit (Heinze 1989*a*; Heinze & Buschinger 1989). However, colonies are occasionally polygynous with several gynomorphic queens (Heinze 1993*b*).

(*c*) *Relative amount of colony budding*

Maternally related neighbouring colonies in *L. acervorum* (Stille & Stille 1993), stereotyped emigration behaviour (Möglich 1978), seasonal fluctuations of queen and worker number (Heinze *et al.* 1992*b*), the occurrence of very small colonies in the field (Heinze 1993*c*), and laboratory observations (Heinze 1993*b*) all suggest that budding is a regular feature of *Leptothorax* biology. Polydomy in North American *Myrafant* could also promote a sort of budding, since units of a polydomous nest may become cut off from the 'mother' nest (Alloway *et al.* 1982). However, although colony budding is therefore suspected in all species, the relative amount of budding in the different social forms is unknown (table 2).

(*d*) *Reproductive skew*

Dissections and observations clearly show that in facultatively polygynous species almost all queens within colonies typically lay eggs (e.g. Buschinger 1968; Wilson 1974*a*; Herbers 1984; Bourke 1991), whereas in functionally monogynous species only one queen does so (by definition) (Buschinger 1968; Heinze & Buschinger 1988; Heinze & Smith 1990). Reproductive skew may be quantified with Reeve and Keller's skew index (Keller & Vargo 1993; Reeve & Ratnieks 1993). This equals $(N_b v + N_n)/(N_b + N_n)$, where N_b is the number of breeders in the colony, N_n is the number of non-breeders, and v is the ratio, observed variance among breeders in proportionate share of reproduction within colony:maximum value of this variance. Hence v equals $\Sigma(p_i - 1/N_b)^2/(N_b - 1){:}(1/N_b)$, with p_i being the fraction of offspring produced by the ith breeder. The skew index varies between 0 (no skew) and 1 (maximum skew). In the facultatively polygynous *L. acervorum*, its average value across four colonies, based on egg-laying rates (Bourke 1991), is 0.12 (range 0.01–0.19). However, although this value is low as expected, egg production is probably a poor measure of queen reproductive success because eggs may be inviable, may be eaten, or develop into non-reproductive workers (Ross 1988*b*; Bourke 1991). Another indicator of skew comes from comparing observed queen numbers with effective queen numbers deduced from relatedness data (Queller 1993; Ross 1993). In *L. acervorum* this method suggests that not all queens within nests contribute to adult worker production (Stille *et al.* 1991), and hence that a degree of skew exists.

However, reproductive skew should ideally be measured from the variance in the production of adult sexuals by queens (Ross 1988*b*, 1993). In multiple-queen leptothoracines, worker production can be excluded because it is unlikely that workers contribute many eggs in colonies containing queens (e.g. *L. acervorum*; Bourke 1991). In addition, workers probably do not promote a queen's reproductive success through nepotistic brood rearing, because within-colony kin discrimination appears either weak or absent in polygynous ants (Carlin 1988; Carlin *et al.* 1993; Snyder 1993; Bourke 1994). But the precise measurement of within-colony variance in sexual production is technically hard because of the difficulty of assigning parentage, which requires molecular methods of high resolution (Ross 1988*b*). So reproductive skew among sexual progeny is presently unknown for facultatively polygynous leptothoracines.

8. CONCLUSIONS

This paper has combined empirical data on leptothoracine polygyny with three relevant bodies of theory. The first is the set of ecological constraints hypotheses that explain polygyny in terms of dispersal and colony founding costs, to which cold climate and habitat patchiness are major contributors. The second is represented by game theory models predicting stable dispersal levels as a function of dispersal costs. The third comes from kin selection models predicting the stable reproductive skew and degree of between-queen aggression as a function of ecological constraints and relatedness.

The conclusions from this synthesis are that it helps explain the existence and nature of the diverse social systems of leptothoracines, as well their ecological correlates. Existing data (table 3) are consistent with the framework provided by the present arguments (table 1). In addition, our synthesis makes several predictions.

1. The features of undiscovered or uninvestigated leptothoracine species should fit the framework described above. This also applies to gaps in knowledge of otherwise well known species (i.e. the missing data in table 3).
2. By implication, certain types of society should not exist, for example functionally monogynous colonies in non-patchy habitats with cheap dispersal.
3. Functionally monogynous species should have higher between-queen relatedness than polygynous ones, unless the costs of solitary colony foundation are exceptionally high.
4. Facultatively polygynous species should exhibit a low skew in their sexual production.

Therefore, future work should test these predictions and also assess whether similar arguments to these apply to other ant species, and to totally different taxa of communal breeders (cf. Vehrencamp 1983*a*, *b*; Keller & Reeve 1994).

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