

## SHORT COMMUNICATION

## The ecological benefits of larger colony size may promote polygyny in ants

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### Abstract

How polygyny evolved in social insect societies is a long-standing question. This phenomenon, which is functionally similar to communal breeding in vertebrates, occurs when several queens come together in the same nest to lay eggs that are raised by workers. As a consequence, polygyny drastically reduces genetic relatedness among nestmates. It has been suggested that the short-term benefits procured by group living may outweigh the costs of sharing the same nesting site and thus contribute to organisms rearing unrelated individuals. However, tests of this hypothesis are still limited. To examine the evolutionary emergence of polygyny, we reviewed the literature to build a data set containing life-history traits for 149 Palearctic ant species and combined this data set with a reconstructed phylogeny. We show that monogyny is the ancestral state and that polygyny has evolved secondarily and independently throughout the phylogenetic tree. The occurrence of polygyny is significantly correlated with larger colony size, dependent colony founding and ecological dominance. Although polydomy (when a colony simultaneously uses several connected nests) tends to occur more frequently in polygynous species, this trend is not significant when phylogenetic history is accounted for. Overall, our results indicate that polygyny may have evolved in ants in spite of the reduction in nestmate relatedness because large colony size provides immediate ecological advantages, such as the more efficient use of temporal food resources. We suggest that the competitive context of ant communities may have provided the conditions necessary for the evolution of polygyny in some clades.

### Introduction

High relatedness was crucial to the evolution of eusociality in insects. Several lines of evidence suggest that in Hymenoptera, social life arose from family groups composed of a singly mated reproductive female (the queen) and her daughters, who forewent reproducing themselves to rear their siblings (Hamilton, 1964;

Hughes *et al.*, 2008). Yet, the association of several queens in the same nest occurs relatively frequently in extant species (Hölldobler & Wilson, 1977; Ross & Carpenter, 1991; Keller, 1995). This social structure, which is functionally similar to communal breeding in some vertebrates (e.g. meerkats or warblers), considerably reduces genetic relatedness among colony members and thus raises the question as to which ecological factors compensate for this lower relatedness (Nonacs, 1988). It has been suggested that the harsh environmental conditions that limit the dispersal success of young queens may select for polygyny (Nonacs, 1988; Keller & Vargo, 1993; Keller, 1995; Oliveira *et al.*, 2011). For

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example, low nest site availability and elevated dispersal risk due to low temperatures and food limitations may favour newly mated queens being adopted by pre-existing colonies (dependent colony founding – DCF) as opposed to them founding new colonies alone (independent colony founding – ICF; Bourke & Heinze, 1994; Benschbach & Herbers, 1996; Herbers & Benschbach, 1998; Dalecky *et al.*, 2005).

Another, nonexclusive hypothesis is that the augmentation in colony size that potentially stems from the association of several egg-laying queens could provide a competitive advantage (Hölldobler & Wilson, 1977; Rubin *et al.*, 2013). However, this hypothesis has seldom been tested. Within ant communities, behaviourally dominant species are better at monopolizing resources than are behavioural subordinates (Cerdá *et al.*, 2013). The former are expected to be more territorial and to rely on group size in order to dominate resources (Savolainen, 1991; LeBrun, 2005). The latter, in contrast, are thought to be faster at discovering resources and their foraging efficiency is less dependent on group size (Cerdá *et al.*, 2013). As a consequence, if polygyny allows colonies to reach larger sizes and thus dominate local habitats, it may be more beneficial for dominant than for subordinate species (Rosengren *et al.*, 1993). In addition, populous polygynous colonies may be more likely to occupy several interconnected nests (polydomy), which may enhance food provisioning (Debout *et al.*, 2007; Boomsma *et al.*, 2014).

Polygyny and monogyny are predicted to be indirectly associated with differences in queen size as a result of different modes of colony founding (Keller, 1991, 1995). The solitary phase experienced by the queen during ICF imposes strong selection pressure on her morphology, and bigger, more resistant individuals are favoured (Ross & Keller, 1995; Wiernasz & Cole, 2003; Peeters & Molet, 2010). In contrast, the absence of a solitary phase during DCF relaxes selection pressure on queen morphology, which leads to relatively smaller queens. This prediction has been supported by studies conducted on species with conditional polygyny, which have revealed that polygynous queens are smaller than monogynous queens (Keller & Ross, 1993, 1999; Meunier & Chapuisat, 2009).

In the present study, we reviewed the literature in order to compare the life-history traits of monogynous and polygynous Palearctic ants and to test a series of predictions about the role of ecological conditions in the evolution of polygyny. First, we tested whether monogyny is the ancestral state in Palearctic ants. Moreover, if the benefits of polygyny lie in ecological dominance and group size, we would expect polygynous species to be behaviourally dominant in their communities, to form more populous colonies and to occupy several nests per colony. In contrast, monogynous species should occupy a lower rank in the dominance

hierarchy, have smaller colony sizes and live in single nests (monodomy). We would also expect DCF to prevail in polygynous species, and queens should be relatively smaller in polygynous than in monogynous species. Our results, which are based on a large number of species, provide the most comprehensive analysis of the ‘polygyny syndrome’ in ants (Keller, 1995) to date.

## Materials and methods

### Data collection

To create a life-history trait data set for Palearctic ant species, we conducted an exhaustive search of public databases (Web of Science, Google, Google Scholar and Formis) for scanning the scientific literature (more than 1000 articles or chapters in books and 1300 search hours) using as keywords the name of each ant species and the terms ‘Queen’, ‘Monodomy’, ‘Polydomy’, ‘Queen Size’, ‘Worker size’ and ‘Ecological dominance’. These data were complemented by personal observations and personal communications from various colleagues (see Data S1 for more details on the procedure of literature search). For each of 149 species, we described the breeding system (monogyny or polygyny), position in the behavioural dominance hierarchy (based on interspecific interactions at food resources), colony size, nesting patterns (monodomy vs. polydomy), colony founding mode and the queen/worker body length ratio. Primary polygyny or pleometrosis, in which 2 or 3 queens temporarily join up to found a colony, was considered as monogyny because the first workers that emerge often eliminate supernumerary queens, which leads to secondary monogyny. In addition, some species have a polymorphic breeding system in which a monogynous form coexists with a slightly to highly polygynous form (see Table S1 for the list of species and breeding systems). To reduce the uncertainty associated with such polymorphism, all statistical analyses were conducted twice. In a first series, polymorphic species were excluded and the analyses conducted on the remaining 127 species with monomorphic breeding system. In a second series of analyses, the monogynous forms of polymorphic species for which more data on life-history traits were generally available were included. Social parasites were also excluded from the data set. The descriptions, states and ranges of values for the different variables are given in Table S2.

### Phylogeny reconstruction

We constructed a composite phylogeny of the 149 species examined using the molecular genus-level phylogeny of Moreau *et al.* (2006) and Moreau & Bell (2013); furthermore, when a molecular within-genus phylogeny was available in the literature, it was also added to

the basal tree. When molecular data were not available, we reconstructed the species relationships within genera based on taxonomic data (Table S3). The tree was reconstructed using Mesquite version 2.75 (Maddison & Maddison, 2011); because of the composite nature of the tree, branch lengths were unknown and were therefore assigned a value of 1.0 (Purvis & Webster, 1999).

### Data analyses

We used the Ancestral State Reconstruction packages for Mesquite v. 2.75 (Maddison & Maddison, 2011) to trace the history of polygyny among the 149 species examined and to determine whether it is ancestral or derived. We first used the parsimony method to graphically reconstruct the most probable state of each node. We then estimated the corresponding likelihood using a Markov  $k$ -state 1-parameter model (Mk-1 model). In the latter, the likelihood of a state is considered to be significant if its log is at least two times higher than that of the alternative state. Finally, the phylogenetic signal of each life-history trait was estimated by calculating Pagel's  $\lambda$  values (Pagel, 1994) using the *fitContinuous* and *fitDiscrete* functions for continuous and discrete traits, respectively (R package *Geiger*, R Development Core Team, 2010).

Other statistical analyses were conducted in R. We carried out a series of generalized linear model analyses using the GLM function; polygyny/monogyny was the response variable and the life-history traits were explanatory variables. Each GLM was fitted using a binomial distribution and the logit link function. In addition, we conducted a series of analyses that accounted for autocorrelation due to phylogenetic non-independence. To do so, we used a generalized estimating equations (GEE) approach, which is similar to the generalized least squares (GLS) approach (Grafen, 1989), except that it can model non-normal errors in response variables (Paradis & Claude, 2002). Therefore, GEE models are suitable for data with discrete response variables through the specification of a binomial, rather than a Gaussian, error structure (Paradis & Claude, 2002; Paradis, 2006). A correlation matrix derived from the distances between terminal taxa in the phylogenetic tree was used to weigh variances in a generalized modelling framework. GEEs were carried out using the 'compar.gee' function in the APE package (Paradis *et al.*, 2004). The response variable was binary (monogynous: 0, polygynous: 1), and thus, binomial errors were specified with either logit or complementary log-log links, depending on which minimized residual variance the most. The independent variables were the different life-history traits. We ran one model for each trait. Species without trait values for a given variable were removed from that particular analysis.

## Results

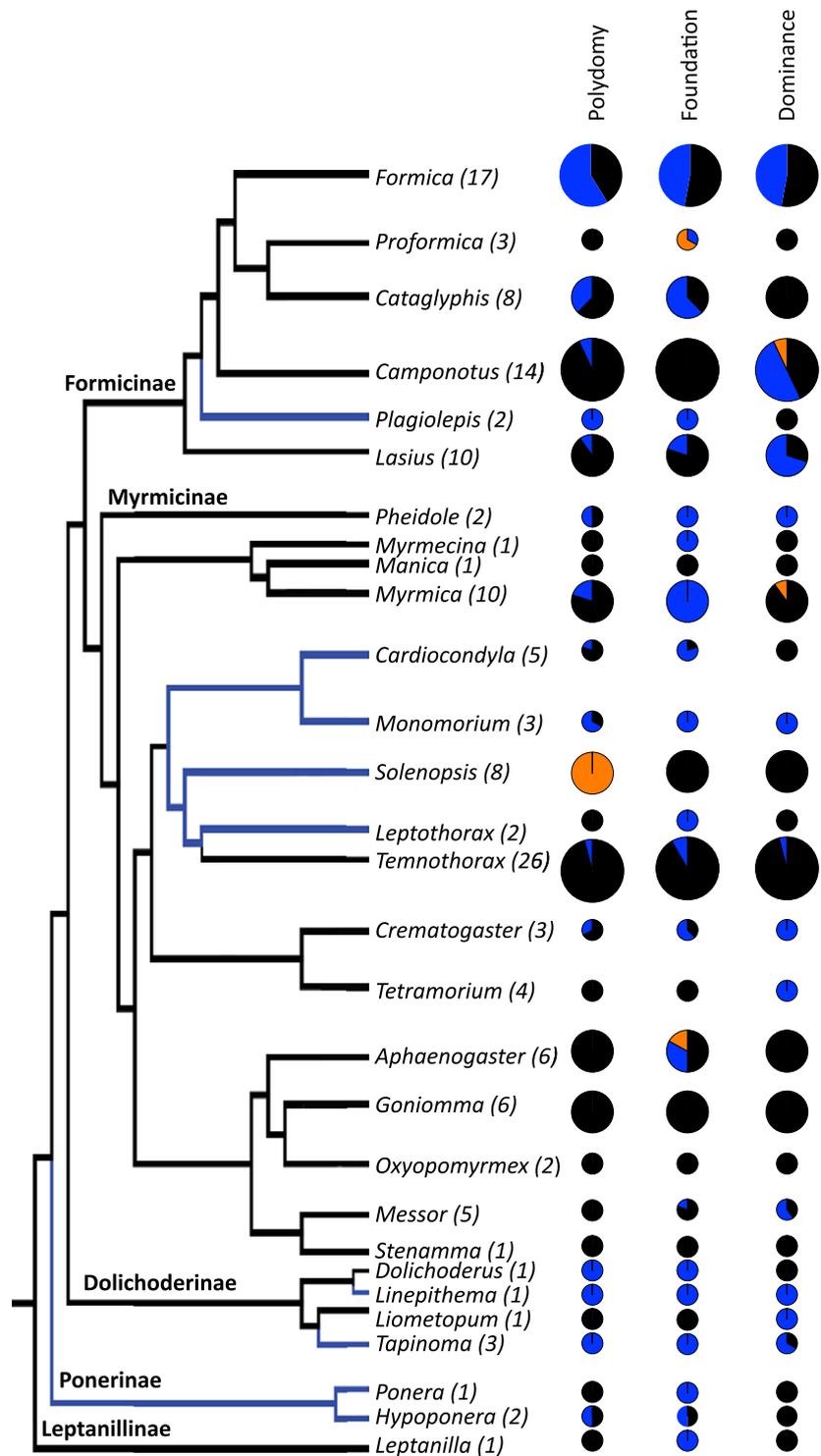
Forty-one (28%) of the 149 Palearctic ant species included in the data set were obligate polygynous, whereas 22 species (15%) were polymorphic for their breeding system. The reconstructed phylogeny indicated that the ancestral breeding system was monogyny and that polygyny had evolved secondarily in a few clades (Fig. 1). This conclusion was reached both when polymorphic species were included and excluded from the analyses. The corresponding proportional likelihood based on the Mk-1 model was 93% and 79%, respectively. This scenario was also supported when the two most speciose subfamilies, the Formicinae and Myrmicinae, were examined separately (proportional likelihood that monogyny was the ancestral state equalled 97% and 96%, respectively). The number of species in the other subfamilies (i.e. the Dolichoderinae, Ponerinae and Leptanillinae) was too small to provide meaningful likelihood estimates.

All the response variables had elevated Pagel's  $\lambda$  values, which were always close to 1 (Table 1). This is clear evidence that there was a strong phylogenetic signal for all the traits investigated. When phylogenetic history was not controlled for (the GLM models) and the polymorphic species excluded, four life-history traits were significantly associated with polygyny (Table 1). Polygyny occurred significantly more frequently (i) in dominant species; (ii) with large colonies; (iii) which occupied several nests; and (iv) were founded by DCF. Including polymorphic species from the analyses gave a similar result except that behavioural dominance was no longer significantly correlated to polygyny (Table 1).

The GEE models provided a slightly different perspective on the relationship between polygyny and life-history traits (Table 1). Hence, once phylogenetic history had been accounted for, polygyny was no longer significantly related to polydomy. However, there was still a highly significant association between polygyny and DCF, large colony size and behavioural dominance. Excluding species with a polymorphic breeding system from the GEE models did not alter these results (Table 1).

## Discussion

The results of our study show that monogyny is the ancestral breeding system of Palearctic ants, whereas obligate polygyny evolved secondarily throughout the phylogenetic tree and occurs in at least 28% of extant species. In our data set, 22 (15%) species are polymorphic for their breeding system (Rosengren *et al.*, 1993; Gyllenstrand *et al.*, 2005; Sundström *et al.*, 2005). These proportions are very close to those found by Boomsma *et al.*, 2014 at a more global scale (23% and 13%, respectively). What promotes such polymorphism and



**Fig. 1** Phylogenetic reconstruction of the evolution of polygyny among Palearctic ants based on a model employing parsimony. The ancestral state is monogyny (black), and polygyny evolved secondarily in several genus (blue). The pie charts indicate the following: (i) the proportion of monodomy (black), polydomy (blue), unknown mode of colony founding (orange); (ii) the proportion of species showing ICF (black), DCF (blue), and ICF/DCF or an unknown colony founding mode (orange); and (iii) the proportion of subordinate (black) vs. dominant (blue) species in each genus.

why it seems concentrated in some particular genera (e.g. *Formica*) is unclear. Polymorphic species may alternate between both forms depending on ecological conditions. Hence, it has been hypothesized that secondary

polygyny may predominate in homogenous habitats in which increasing queen number has a proportional positive impact on colony size and resource collection (Boomsma *et al.*, 2014). Removing these 22 species

**Table 1** Relationships between breeding system (monogyny or polygyny) and life-history traits in Palearctic ants both with (GEE) and without accounting for phylogenetic history (GLM). The *P*-values in bold denote that a significant (< 0.05) correlation exists between a given trait and the breeding system. For each trait, the upper line gives the statistical when considering facultative polygynous species as monogynous (*n* = 149). The lower line gives the same statistics when species with polymorphic breeding system are removed from the analysis (*n* = 127). DCF stands for dependent colony founding. Pagel's  $\lambda$  near 1 indicate a strong phylogenetic trace for the considered trait.

	Breeding system		Pagel's $\lambda$ (Log likelihood)	GLM		GEE	
	Monogyny	Polygyny		Z	<i>P</i>	<i>t</i>	<i>P</i>
Percentage of dominant species	26.2	37.5	1.00 (– 56.0)	1.34	0.181	2.17	0.041
	20.0		1.00 (– 49.3)	2.06	0.039	3.10	0.005
Colony size (Mean $\pm$ SE)	26382 $\pm$ 23132	69557 $\pm$ 33325	1.00 (– 267.7)	3.25	0.0012	4.10	0.0005
	1805 $\pm$ 333		1.00 (– 224.8)	3.95	< 0.0001	2.81	0.011
Percentage of polydomous species	14.8	45.5	0.91 (– 66.8)	3.54	0.0003	0.64	0.532
	8.1		1.00 (– 51.0)	4.25	< 0.0001	0.86	0.401
Percentage of DCF species	26.0	68.3	1.00 (– 70.5)	4.50	< 0.0001	4.01	0.0006
	15.9		1.00 (– 61.4)	5.39	< 0.0001	5.00	< 0.0001
Queen/worker size ratio (Mean $\pm$ SE)	1.65 $\pm$ 0.04	1.71 $\pm$ 0.10	1.00 (– 52.7)	0.73	0.465	0.21	0.833
	1.67 $\pm$ 0.05		1.00 (– 45.5)	0.43	0.67	0.67	0.512

from the statistical analyses did not alter the conclusion that monogyny is ancestral. This confirms previous studies conducted on a larger phylogenetic scale in hymenopteran societies (Ross & Carpenter, 1991; Hughes *et al.*, 2008). This finding also lends credence to the idea that kin selection has played a determinant role in the evolution of eusociality. The most likely route to eusociality was through certain females remaining in their natal nests and giving up their own reproduction to help their mothers (Hamilton, 1964). In most ant species, these sterile individuals then evolved into a morphologically distinct worker caste, whereas the queen caste specialized in reproduction.

Once sociality has evolved, polygyny may be selected for if short-term ecological advantages at the colony level compensate for the loss of inclusive fitness resulting from the erosion in relatedness among nestmates. One such ecological advantage may stem from larger colony size. As expected, polygynous colonies contain, on average, more workers than do monogynous colonies. Although comparative studies in facultative polygynous species show that individual polygynous queens are less productive, collectively, the queens lay more eggs and thus their colonies can reach larger sizes (Fletcher *et al.*, 1980; Mercier *et al.*, 1983). Several components of colony organization and productivity are directly dependent on the number of workers (Anderson & McShea, 2001; Dornhaus & Franks, 2006; Ruel *et al.*, 2012; Luque *et al.*, 2013). Thus, large colonies may be better at recruiting nestmates to food resources or collectively returning prey to the nest (Cerdá *et al.*, 2009; Ruel *et al.*, 2012). Large colony size may also enhance colony defence, homeostasis and labour capacity (Bourke, 1999). However, the benefits of large colony size may differ among species according to other life-history traits. We hypothesized that large colony size and thus, indirectly, polygyny would be

more beneficial to behaviourally dominant species that tend to monopolize and defend food resources than to subordinate species that rely on individual foraging strategies. This prediction was partially confirmed as a significantly higher proportion of dominant species were polygynous in the GEE models and in the GLM after removing polymorphic species. Although we classified all species as either dominant or subordinate, this categorization is relative and can slightly change depending on the environment, community composition, and the way it is measured in the field (using interactions at food baits or on naturally occurring food items).

With some notable exceptions (e.g. Cerdá *et al.*, 2002), polygyny is often associated with polydomy, whereas monogyny is associated with monodomy (Hölldobler & Wilson, 1977; Debout *et al.*, 2007; this study). However, this association became insignificant after controlling for phylogeny. Although it is possible that the smaller number of contrasts in GEE models meant that power was reduced, a more likely explanation is that phylogeny constrains the evolution of polydomy. Maintaining several nests is probably costly for a colony in terms of predation, desiccation, and the loss of brood and workers during transfer between nests. These costs may be countered by ecological benefits if the number of workers is sufficiently large, a condition that is more likely to be fulfilled in polygynous colonies (Debout *et al.*, 2007). Hence, one advantage of polydomy may be that colonies are better able to monopolize stable food resources that are spread out over a larger area by decentralizing their foraging network and thus reducing the travelling costs between their nests and food items (Pfeiffer & Linsenmair, 1998; Holway & Case, 2000; Lanan *et al.*, 2011).

Our results show that polygyny is closely linked to DCF. This was true even after controlling for the

phylogenetic relationship among species and after removing polymorphic species from the analysis. A large majority of colonies containing more than one queen result from newly mated queens that either remain in their natal nests or are adopted by pre-existing nests (Keller, 1991, 1995). Moreover, the mode of colony founding is thought to condition queen morphology and physiology (Keller & Passera, 1989; Wierasz & Cole, 2003), which suggests that an indirect relationship exists between these variables and the number of queens per colony. This hypothesis is supported by a few studies that have shown that, within species with plastic social structure, polygynous queens are smaller than monogynous queens (Keller & Ross, 1993, 1999; Ruppell & Heinze, 1999; Meunier & Chapuisat, 2009). In *Solenopsis*, this difference has a genetic origin (Keller & Ross, 1999; Wang *et al.*, 2013), which may also be the case for *Formica* (Meunier & Chapuisat, 2009). Our results do not confirm this pattern at the interspecific level. Overall, queens were not bigger (relative to workers) in monogynous than in polygynous species. However, the queen/worker size ratio as estimated from total body length, which is the most frequently available measure in the literature, may not be the morphological measurement that is most affected by the transition from monogyny to polygyny. Instead, fine-scale measurements, such as of thorax size or fat-body reserves, might better estimate queen survival capacity during the founding phase (Keller & Passera, 1989; Peeters & Molet, 2010). Moreover, the relationship between colony founding mode, polygyny, and queen size may be blurred by the fact that species that perform colony fission (Amor *et al.*, 2011; Cronin *et al.*, 2013) have small queens but maintain monogyny.

Although the use of comparative analyses based on published data has some limitations and can only roughly reveal functional relationships, the amount of data and the resolution of the phylogeny for some groups of animals are beginning to provide enough information for hypothesis testing. Here, we have demonstrated that, in ants, polygyny has evolved concurrently with other important life-history traits, namely ecological dominance, dependent colony founding and increased colony size. The highly competitive context of ant communities may have provided a selective landscape in which increasing the number of workers in a colony was sufficiently beneficial to compensate for the erosion in nestmate relatedness in some but not all species. More generally, short-term ecological advantages may explain the composition and structure of societies of both invertebrates and vertebrates. Further comparative studies should be conducted using a higher degree of resolution to test this hypothesis. Moreover, other regions of the world should also be investigated to test the effect of present and past environmental conditions and habitat harshness on the evolution of polygyny.

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### Supporting information

Additional Supporting Information may be found in the online version of this article:

**Data S1** Search procedure and literature sources from which life trait data of ant species were obtained.

**Table S1** Breeding system of all the species considered in this study and references from which this information was obtained.

**Table S2** Description and range of the variables analysed in this study.

**Table S3** List of references used to build the European ants phylogeny.

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