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Multiple paternity or multiple queens: two routes to greater intracolonial genetic diversity in the eusocial Hymenoptera

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Abstract

Understanding the evolution of multiple mating by females (polyandry) is an important question in behavioural ecology. Most leading explanations for polyandry by social insect queens are based upon a postulated fitness benefit from increased intracolonial genetic diversity, which also arises when colonies are headed by multiple queens (polygyny). An indirect test of the genetic diversity hypotheses is therefore provided by the relationship between polyandry and polygyny across species, which should be negative if the genetic diversity hypotheses are correct. Here, we conduct a powerful comparative investigation of the relationship between polyandry and polygyny for 241 species of eusocial Hymenoptera (ants, bees and wasps). We find a clear and significant negative relationship between polyandry and polygyny after controlling for phylogeny. These results strongly suggest that fitness benefits resulting from increased intracolonial genetic diversity have played an important role in the evolution of polyandry, and possibly polygyny, in social insects.

Introduction

Although social insect colonies are classically thought of as being a simple family headed by a single mother (the queen) mated to a single male, their actual kin structure is often more complex. Colonies of many species of eusocial Hymenoptera (ants, bees and wasps) have multiple queens (polygyny) (Bourke & Franks, 1995; Crozier & Pamilo, 1996). In addition, the queens in around a third of species occasionally mate with multiple males (polyandry), although in only 13 genera do they do so commonly (Boomsma & Ratnieks, 1996; Crozier & Fjerdingstad, 2001). Why polygyny or polyandry should evolve is an ongoing puzzle, as both have costs. Polygyny requires a queen to share her colony's reproductive output with other queens. Polyandry involves energy expenditure and increased risks of predation, parasitism and damage by male partners.

Polygyny is believed to evolve primarily due to ecological pressures such as nest site limitation or particularly high risks associated with independent nest founding (Bourke & Franks, 1995; Keller, 1995). Explaining the evolution of polyandry is more problematic. Many hypotheses have been suggested. Several of the best supported are based upon the increased intracolonial genetic diversity that results from polyandry (although this effect may be mitigated by inbreeding). Greater intracolonial genetic diversity has been hypothesized to reduce costs from genetically incompatible matings, improve division of labour and make colonies more resistance to parasites (Boomsma & Ratnieks, 1996; Crozier & Fjerdingstad, 2001; Oldroyd & Fewell, 2007). There is now good empirical support from five species either for an overall beneficial effect of genetic diversity or the specific hypotheses (Oldroyd *et al.*, 1992; Baer & Schmid-Hempel, 1999; Cole & Wiernasz, 1999; Tarpy & Page, 2002; Hughes *et al.*, 2003; Tarpy, 2003; Hughes & Boomsma, 2004; Jones *et al.*, 2004; Wiernasz *et al.*, 2004; Hughes & Boomsma, 2006; Tarpy & Seeley, 2006; Goodisman *et al.*, 2007; Hughes & Boomsma, 2007; Mattila & Seeley, 2007; Seeley & Tarpy, 2007; Mattila *et al.*, 2008; Wiernasz *et al.*,

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2008). However, polygyny also increases intracolonial genetic diversity. If increased intracolonial genetic diversity is important in selecting for polyandry, therefore, then, given that both polyandry and polygyny are costly, there should be a negative relationship across species between the levels of polyandry and polygyny.

Previous studies of the relationship between polyandry and polygyny have given conflicting results. In the first investigation, Keller & Reeve (1994) found a negative relationship between polyandry and polygyny for 53 ant species. Subsequently, Boomsma & Ratnieks (1996) failed to find such an effect for 34 ant species, except when they restricted the analysis to 11 species with large colonies (> 10^4 workers) when the relationship was marginally significant. Neither of these analyses, however, controlled for phylogenetic relationships. A later analysis of ants which did use independent contrasts to control for phylogeny found no relationship for 68 species (Schmid-Hempel & Crozier, 1999). Here, we take advantage of the burgeoning literature on colony genetic structure to resolve the relationship between polyandry and polygyny in eusocial Hymenoptera.

Materials and methods

We compiled a data set of 241 species of eusocial Hymenoptera from the literature for which data were available for both mating frequency and queen number (Table S1). We excluded three species which are obligate social parasites but included slave makers (see below). We assessed polyandry in two ways: as the effective mating frequency and as the proportion of females mating multiply. The former measure takes into account unequal sperm contributions of individual males and is thus the best estimate of the effect of multiple mating on intracolonial genetic diversity (Boomsma & Ratnieks, 1996). We also divided species into four polyandry categories: monandry, facultative low polyandry with effective mating frequencies of < 2, moderate polyandry with effective mating frequencies of 2–10 and extreme polyandry with effective mating frequencies of > 10. We assessed polygyny as the average number of reproductively active queens per colony and as the presence or absence of polygyny. For the latter trait, we scored species as polygynous if this occurs at least occasionally, although in practice almost all of the species included in the analysis were either monogynous or exhibited polygyny in > 10% of colonies examined. Similarly, the four species included which are monogynous in some populations and polygynous in others were all scored as polygynous. Species for which colonies typically contain multiple, mated females, but in which only a single female monopolizes egg laying at any one time, were classified as monogynous. The full data set included a number of species for which the data were somewhat uncertain (e.g. mating data based on behavioural observations rather than the genetic analyses used in most cases, mating data based on very few queens, species that were slave makers or species with colonies containing extremely high numbers of queens [hundreds or thousands] such as seen in unicolonial species; see Table S1 for the specific reasons for particular species). Therefore, we first ran the analyses with the complete data set of 241 species. We then removed all species for which either polyandry or polygyny data were in any way uncertain, and reran the analyses based on this more stringent data set of 180 species.

We mapped these data on to a phylogeny (Fig. S1) constructed based on that of Wenseleers & Ratnieks (2006). We modified this and added phylogenetic detail based on published phylogenies for social hymenopteran (Brothers, 1999; Carpenter & Wheeler, 1999), halictids (Brady *et al.*, 2006b), wasps (Hines *et al.*, 2007), polistine wasps (Arevalo *et al.*, 2004), vespine wasps (Carpenter, 1987, Carpenter & Perera, 2006), apid bees (Cardinal & Packer, 2007), bumblebees (Cameron *et al.*, 2007) and ants (Brady *et al.*, 2006a). The phylogeny of the apid bees is still controversial; so, while we followed that of Cardinal & Packer (2007), we confirmed that all results were robust to using the alternative phylogeny suggested by others (Thompson & Oldroyd, 2004; Kawakita *et al.*, 2008). The relationships between polyandry and polygyny were then compared using regressions of phylogenetically independent contrasts in the PDAP module of the Mesquite package (Midford *et al.*, 2003; Maddison & Maddison, 2006). The effective mating frequencies and the number of queens per colony were log transformed. The proportions of queens mating multiply were $\arcsin(\sqrt{x})$ transformed. The four categories of polyandry were assigned as 0 (monandry), 1 (facultative low polyandry), 2 (moderate polyandry) and 3 (extreme polyandry). Branch lengths were set as one and then transformed using Grafen's ρ (Grafen, 1989), with ρ set at 0.5, to satisfy the assumptions of independent contrast analysis (Midford *et al.*, 2003). Degrees of freedom were reduced by 34 and 22 in the complete and stringent analyses, respectively, to adjust conservatively for unresolved soft polytomies (Midford *et al.*, 2003). As there was a clear *a priori* hypothesis of a negative relationship between polyandry and polygyny, one-tailed P-values are presented throughout. The large sample size meant that statistical power of all tests was high for detecting a moderate effect (0.983–0.998 for detecting effect size $r = 0.3$), but quite low for detecting a small effect (0.33–0.415 for detecting effect size $r = 0.1$).

Results

All of the analyses used phylogenetically independent contrasts. There was a highly significant negative relationship between effective queen mating frequency and number of queens (complete data set: $F_{1,161} = 6.9$, $P = 0.0047$, $r = -0.19$; stringent data set: $F_{1,142} = 9.92$, $P = 0.001$, $r = -0.239$; Fig. 1). Species with monogynous

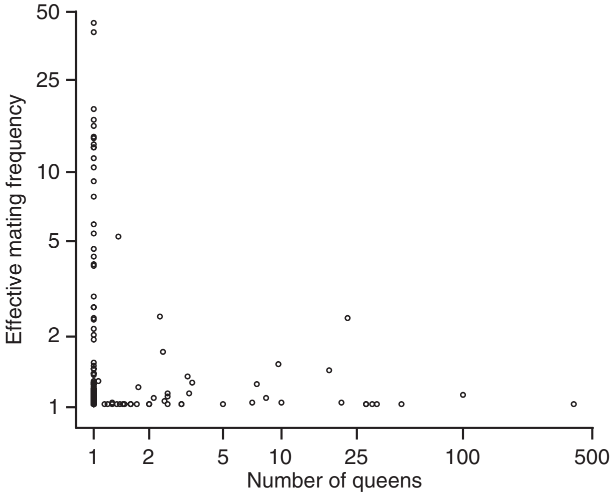

Fig. 1 The relationship across species of eusocial Hymenoptera between polyandry, measured as the mean effective mating frequency of queens, and polygyny, measured as the mean number of queens per colony. Raw data are presented uncorrected for phylogenetic effects. Unicolonial species are excluded.

colonies had a significantly higher effective mating frequency than those with polygynous colonies (complete: $F_{1,166} = 9.49$, $P = 0.001$, $r = -0.21$; stringent: $F_{1,145} = 12.02$, $P = 0.0004$, $r = -0.259$; Fig. 2a), although there was no significant difference in the proportion of females mating multiply (complete: $F_{1,177} = 0.19$, $P = 0.334$, $r = -0.03$; stringent: $F_{1,150} = 0.23$, $P = 0.316$, $r = -0.037$; Fig. 2a). When species were divided into four categories based on their level of polyandry, there was a consistent, although marginally nonsignificant, decrease in the number of queens per colony with increasing level of polyandry (complete: $F_{1,197} = 2.48$, $P = 0.059$, $r = -0.103$; stringent: $F_{1,152} = 2.27$, $P = 0.067$, $r = -0.113$; Fig. 2c). The levels of polyandry differed significantly in the number of species showing presence or absence of polygyny, with all species that had extreme polyandry being monogynous (complete: $F_{1,204} = 3.59$, $P = 0.029$, $r = -0.122$; stringent: $F_{1,155} = 4.57$, $P = 0.017$, $r = -0.159$; Fig. 2b).

Discussion

The recent expansion in the availability of genetic data on colony kin structure and phylogenetic relationships of eusocial Hymenoptera has allowed us to conduct a comprehensive test of the relationship between polyandry and polygyny. Based on 241 species with appropriate corrections for phylogenetic relationships, all of the analyses point in the same direction: there is a clear negative relationship between polyandry and polygyny. This contrasts with previous comparative investigations which produced mixed results but which were all limited to relatively few species and thus had limited statistical

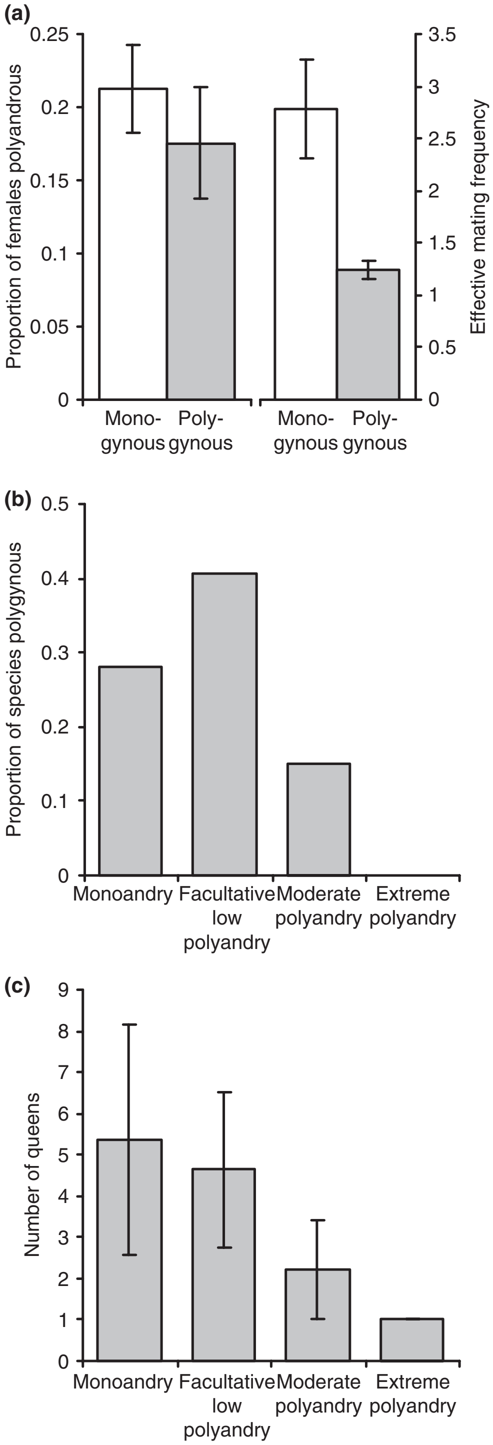

Fig. 2 (a) Mean (±SE) proportion of queens mating multiply and mean ± SE effective mating frequency of queens for monogynous and polygynous species. (b) Presence/absence of polygyny (0 or 1) and (c) mean ± SE number of queens per colony for species divided into the four categories of polyandry: monandry, facultative low polyandry (< 2 effective mates), moderate polyandry (2–10 effective mates) and extreme polyandry (> 10 effective mates). Raw data are presented uncorrected for phylogenetic effects.

power for detecting even moderate effect sizes (e.g. power of detecting $r = 0.3$ was 0.64 in Keller & Reeve, 1994, 0.56 in Boomsma & Ratnieks, 1996 and 0.45 in Schmid-Hempel & Crozier, 1999). Our analysis shows that species that have evolved polygyny tend to be monandrous and species that have evolved polyandry tend to be monogynous.

The conclusion from this broad analysis matches that for a recent direct comparison between closely related species. All army ants are monogynous and highly polyandrous, with the single exception of *Neivamyrmex carolinensis* which is highly polygynous and monandrous (Kronauer & Boomsma, 2007). The negative relationship does not match intraspecific comparisons in three ant species: *Formica paralugubris*, *Myrmica sulcinodis* and *Pogonomyrmex pima* (Chapuisat, 1998; Pedersen & Boomsma, 1999; Holbrook *et al.*, 2007). However, this is most probably because the range of polyandry found within these species (one to two effective mates) is very limited compared with that exhibited by the army ants or the full comparative data set.

An alternative explanation for the negative relationship between polyandry and polygyny is that the evolution of one or both is driven by sperm limitation. Arguments both for (Cole, 1983; Kraus *et al.*, 2004) and against polyandry evolving to gain more sperm, and thus increase a queen's reproductive output, have been outlined elsewhere (Koeniger & Koeniger, 1991; Oldroyd *et al.*, 1992; Boomsma & Ratnieks, 1996; Crozier & Fjerdingstad, 2001; Kronauer & Boomsma, 2007). Polygyny also increases the total sperm stored per colony, but, importantly, individual queens will not gain as much direct fitness benefit as under polyandry. If polygyny and polyandry evolve to increase reproductive output, then there should still be selection on queens in polygynous species to evolve polyandry, but results indicate that they generally do not. This is not due to the costs of polyandry preventing polygynous species evolving the trait because most polygynous species are notable for mating in or close to their natal nest and returning to it afterwards (W.O.H. Hughes, unpublished data). The potential costs of polyandry are therefore probably in fact lower for most polygynous species than for monogynous species. Furthermore, the per capita reproductive output of queens actually decreases as level of polygyny increases (Bourke & Franks, 1995), making it improbable that polygyny has evolved to increase this variable. In addition, there is now excellent experimental evidence that offspring genetic diversity improves the fitness of queens when the quantity of sperm is either controlled or not a factor (Oldroyd *et al.*, 1992; Baer & Schmid-Hempel, 1999; Cole & Wiernasz, 1999; Tarpy & Page, 2002; Hughes *et al.*, 2003; Tarpy, 2003; Hughes & Boomsma, 2004; Jones *et al.*, 2004; Wiernasz *et al.*, 2004; Hughes & Boomsma, 2006; Tarpy & Seeley, 2006; Goodisman *et al.*, 2007; Hughes & Boomsma, 2007; Mattila & Seeley, 2007; Seeley & Tarpy, 2007; Mattila *et al.*, 2008; Wiernasz *et al.*, 2008).

The most probable explanation for the negative relationship between polyandry and polygyny is thus that intracolonial genetic diversity is involved in the evolution of one or both traits. It seems unlikely to be the only factor because polygyny increases genetic diversity to a greater extent than polyandry. There should therefore be selection on polyandrous species to evolve polygyny, yet the results indicate that they generally do not and there is no obvious reason why polyandrous species should not be able to evolve polygyny if genetic diversity was all that mattered. Instead, there is good evidence for direct ecological factors, specifically the high cost of independent nest founding, driving the evolution of polygyny in many species (Bourke & Franks, 1995; Keller, 1995). For polyandry, in contrast, the genetic diversity hypotheses are currently the leading explanations (Boomsma & Ratnieks, 1996; Crozier & Fjerdingstad, 2001; Oldroyd & Fewell, 2007). The most parsimonious model given this current state of knowledge is therefore that polygyny evolves for direct ecological reasons and that the benefits of intracolonial genetic diversity select for polyandry. Where species do not already achieve increased intracolonial genetic diversity through polygyny, and where these benefits outweigh the costs of the trait, polyandry then evolves.

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Supplementary material

The following supplementary material is available for this article:

Figure S1 The phylogeny used in the comparative analyses. Please note that this figure needs to be viewed electronically to be fully readable.

Table S1 The full data set of polyandry and polygyny for the eusocial Hymenoptera.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1420-9101.2008.01532.x