



Flexible colony-founding strategies in a socially polymorphic ant

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In social insects the number of queens per nest varies greatly. One of the proximate causes of this variation may be that queens produced by multiple-queen colonies are generally smaller, and might thus be unable to found new colonies independently. We examined whether the social origin of queens and males influenced the colony-founding success of queens in the socially polymorphic ant *Formica selysi*. Queens originating from single-queen and multiple-queen colonies had similar survival rates and colony-founding success, be they alone or in two-queen associations. During the first 5 months, queens originating from single-queen colonies gave rise to more workers than queens originating from multiple-queen colonies. Pairs of queens were also more productive than single queens. However, these differences in productivity were transient, as all types of colonies had reached a similar size after 15 months. Mating between social forms was possible and did not decrease queen survival or colony productivity, compared to mating within social forms. Overall, these results indicate that queens from each social form are able to found colonies independently, at least under laboratory conditions. Moreover, gene flow between social forms is not restricted by mating or genetic incompatibilities. This flexibility in mating and colony founding helps to explain the maintenance of alternative social structures in sympatry and the absence of genetic differentiation between social forms.

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One of the major transitions of life on earth is the monopolization of reproduction by a few members of a social group (Szathmary & Maynard Smith 1995). This partitioning of reproduction culminates in eusocial insects, where it primarily evolved by kin selection in simple families headed by one single-mated female (Hughes et al. 2008a, b). Secondary changes in colony social structure have been frequent, particularly in ants, which vary greatly in the number of breeders per nest, both within and between species (Keller 1993a; Bourke & Franks 1995). The shift from a single to multiple queens per colony seems paradoxical at first, as it decreases the relatedness among nestmates and the inclusive fitness of workers (Hamilton 1964). However, this shift is generally associated with profound changes in dispersal and life histories that may be beneficial in some ecological conditions (Hölldobler & Wilson 1977; Keller 1993a; Rosset & Chapuisat 2007).

Identifying the proximate and ultimate factors influencing the evolution and maintenance of alternative social forms has become a central question in studies of social evolution (Keller & Reeve 1994). In ants, variation in colony queen number is frequently associated with differences in queen dispersal and mode of colony founding (Hölldobler & Wilson 1977; Keller 1993b). Monogyny

(=single-queen) colonies are generally founded independently by queens (=haplometrosis). Young queens disperse on the wing, mate away from their natal nest and initiate a new colony alone (Hölldobler & Wilson 1977; Keller & Passera 1989; DeHeer et al. 1999). Haplometrosis can be claustral when queens stay in their lodge, or semiclastral when queens forage (Brown & Bonhoeffer 2003). Haplometrosis is a risky strategy, as lone queens are exposed to predation (Nichols & Sites 1991), nest usurpation and mortality from excessive dryness or humidity (Johnson 2000).

Young queens may also associate during colony founding and cooperate to raise their first workers (=pleometrosis, Helms Cahan 2001; Johnson 2004). Pleometrosis increases queen survival (Tschinkel 1998; Helms Cahan & Julian 1999) and worker production, which are critical for colony-founding success (Heinze 1993; Bernasconi & Keller 1996). Queen associations are often unstable: after the emergence of workers, queens generally fight until only one survives (Sommer & Hölldobler 1995; Bernasconi & Strassmann 1999). However, stable queen associations resulting in permanently polygyne colonies have been reported in several ant species (Kolmer et al. 2002; Johnson 2004).

Polygyny (=the presence of multiple reproductive queens) is often associated with restricted dispersal of queens (Bourke & Franks 1995; Chapuisat et al. 1997). As polygyne colonies readily accept additional queens, young queens have the option to stay within their natal colony or to seek adoption in a foreign colony (Heinze 1993; Bourke & Franks 1995). Polygyny is frequently

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associated with budding, a process whereby queens and workers walk away from their natal colony to establish a new colony in the vicinity (Peeters & Ito 2001). A similar process occurs in a few monogyne species such as army ants, in which the mother and daughter queens divide up the workforce to form two independent colonies (colony fission, Peeters & Ito 2001; Seppä et al. 2008).

The divergence between monogyne and polygyne social forms in their mode of colony founding is generally associated with a difference in size and relative fat content of queens (Keller & Passera 1989). Queens originating from single-queen colonies need large energy reserves to disperse and found new nests independently. In contrast, queens originating from multiple-queen colonies need fewer reserves if they mate close to their natal nest and found new nests with the help of workers. As a result, queens from polygyne species are generally smaller and have lower relative fat content than queens from monogyne species (Keller & Passera 1989; Howard 2006). Polygyne queens also tend to have shorter life span, lower fecundity and earlier age of first sexual reproduction (Bourke & Franks 1995; Keller & Genoud 1997). If, because of their smaller size and lower energetic reserves, queens originating from polygyne colonies are unable to found new colonies independently, a feedback loop may link queen number, queen size and mode of colony founding (Hölldobler & Wilson 1977; Keller & Passera 1989; Seppä & Pamilo 1995; Meunier & Chapuisat 2009).

The association between colony social structure and queen dispersal has mostly been studied by comparing species or populations that are geographically separated and differ in ecological conditions. However, in some species the monogyne and polygyne social forms coexist in sympatry (Fournier et al. 2002; Fritz & Vander Meer 2003; Chapuisat et al. 2004; DeHeer & Herbers 2004; Seppä et al. 2004; Gyllenstrand et al. 2005; Bargum et al. 2007). Such populations are particularly interesting to investigate the causes and correlates of social structure variation.

Formica selysi is a socially polymorphic species in which monogyne and polygyne colonies are interspersed within the same population (Chapuisat et al. 2004). Queens produced by polygyne colonies are smaller, and polygyne colonies invest less in reproductive individuals and more in workers (Rosset & Chapuisat 2007; Meunier & Chapuisat 2009), which suggests that queens originating from polygyne colonies might be constrained to found new colonies with the help of workers. A recent cross-fostering experiment has shown that queen size is influenced by genetic or maternal effects transmitted to the eggs (Meunier & Chapuisat 2009), further indicating that queens originating from monogyne or polygyne colonies might differ in their colony-founding ability. However, the lack of genetic differentiation between social forms at microsatellite markers suggests that mating between social forms or flexibility in dispersal and colony founding maintain gene flow between social forms (Chapuisat et al. 2004).

There is very limited information on mating and colony founding by *F. selysi* queens in the field. We have occasionally observed young queens flying away from their natal colonies and joining nuptial flights around pine trees. We have also observed dealated queens walking on the ground, and incipient colonies with very few workers. These anecdotal field observations do not allow us to assess whether queens originating from monogyne and polygyne colonies differ in their colony-founding strategies.

To get insight into the mechanisms contributing to the maintenance of alternative social structures in sympatry, we experimentally investigated the reproductive options of *F. selysi* queens. First, we compared the colony-founding ability of queens originating from monogyne and polygyne colonies, alone or in association. Second, we assessed whether mating between males and females belonging to alternative social forms was possible and resulted in genetically viable offspring. These experiments will

allow us to determine whether colony founding is plastic or influenced by the sociogenetic origin of queens, and more generally whether gene flow between social forms is restricted by differences in colony-founding strategies or mating incompatibilities.

METHODS

Sampling of Ants

The ants came from a population of *F. selysi* located between Sierre and Susten along the River Rhône in central Valais, Switzerland. We sampled males and females from 46 monogyne and 19 polygyne colonies from which we already had detailed genetic data (Chapuisat et al. 2004; Schwander et al. 2005). Males and females were collected in June 2007 under flat stones placed on each field colony. Ants were brought back to the laboratory in plastic boxes (13.5 × 15 cm and 5 cm high) lined with Fluon to prevent escape.

Experimental Mating

Queens were crossed with males originating from either monogyne or polygyne colonies. Experimental mating took place outside, in the morning, at a temperature between 20 and 25 °C. Pairs of queens from the same colony were placed in plastic containers (35 × 22 cm and 15 cm high) lined with Fluon and covered with a net. We added 5–10 males from several colonies, using separate containers for males originating from monogyne or polygyne colonies. We isolated each queen immediately after mating.

Colony Founding

In June and July 2007, we placed 456 mated queens in glass test-tubes (15.5 cm long × 6 mm diameter). The queens were either alone (one-queen founding, which involved 74 and 54 queens of monogyne and polygyne origin, respectively) or in pairs originating from the same colony and mated on the same day (two-queen founding, which involved 103 and 61 pairs of queens of monogyne and polygyne origin, respectively). The bottom of the test-tube was filled with water retained by a small cotton wool plug, and the tube opening was closed with cotton wool (Bernasconi & Keller 1998). Founding queens were maintained at 25 °C under a 12:12 h light:dark regime, without food. Test-tubes were inspected daily until the first workers were 5 days old. At this point, the tubes were opened and placed in plastic boxes (13.5 × 15 cm and 5 cm high) lined with Fluon. These incipient colonies were then provided with ad libitum supplies of water and protein-rich jelly made of honey, chicken egg, beef meat and agar.

The growth of incipient colonies was recorded over 15 months, until the end of the second summer (September 2008). Eighty-two queens died during the first phase of colony founding, before worker emergence. These queens were dissected to check their mating status. None of them had an empty spermatheca, which indicates that they had successfully mated. Fourteen queens were still alive but had not produced any brood after 5 months. These queens were killed and 11 of them were successfully dissected, which revealed that six had no sperm in the spermatheca. The proportions of broodless queens and unmated queens were not significantly affected by the social origin of queens (broodless: $F_{1,455} = 0.7$, $P = 0.4$; unmated: $F_{1,455} = 0.3$, $P = 0.6$) or the social origin of males (broodless: $F_{1,455} = 0.2$, $P = 0.7$; unmated: $F_{1,455} = 1.2$, $P = 0.3$), and there was no interaction between the two factors (broodless: $F_{1,455} = 0.6$, $P = 0.4$; unmated: $F_{1,455} = 0.01$, $P = 0.9$).

Five months after the start of the experiment, we placed the colonies in hibernation, which lasted from November 2007 to April

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