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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). Monogyne (=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 semiclaustral 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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2008. The temperature was decreased to 15 °C for 1 week, then set at 8 °C for the rest of the hibernation time. In April 2008, the temperature was progressively raised to 25 °C. Colony growth (number and workers) and queen mortality were checked monthly until the end of the second summer, in September 2008. Queens were weighed at the start of the founding experiment, just before hibernation and at the end of the second summer.

In total, we obtained data on queen mortality and colony growth for 124 incipient colonies founded by a single queen (71 and 53 of monogyne and polygyne origin, respectively) and 159 incipient colonies founded by two queens (202 and 116 of monogyne and polygyne origin, respectively).

Statistical Analysis

Queen mortality was estimated as the proportion of dead queens, using one value per colony. Colony failure was characterized by the death of all queens in a colony. Queen mortality and colony failure rate were tested by logistic regressions with a quasibinomial error distribution. Three fixed factors and their interactions were tested: female social origin (monogyne or polygyne), male social origin (monogyne or polygyne), and mode of colony founding (one-queen or two-queen founding).

Worker production (square-root + 1 transformed) was tested using a three-way ANOVA with the following fixed factors and their interactions: female social origin, male social origin and the mode of colony founding. In cases of two-queen founding (pleometrosis), queen execution often occurs after worker emergence (Rissing & Pollock 1987; Sommer & Hölldobler 1995; Bernasconi & Strassmann 1999). As the timing of queen mortality is likely to be important for productivity, we made a distinction between two-queen colonies in which both queens survived (2Q), two-queen colonies in which one of the queens died in the early phase of colony founding before worker emergence (2 → 1Q early) and two-queen colonies in which one of the queens died after worker emergence (2 → 1Q late).

We tested for interactions between factors using likelihood ratio tests and sequentially removed all nonsignificant interactions ($P > 0.10$). Queen mortality, colony failure and worker production were compared after 5 months (just before hibernation) and after 15 months (at the end of the second summer). All statistical analyses were performed in R 2.8.0 (http://www.R-project.org).

RESULTS

Queen Mortality and Colony Failure

Five months after the start of the colony-founding experiment, queens originating from monogyne and polygyne colonies did not differ significantly in their rates of mortality or colony failure (mortality: $F_{1,282} = 1.1$, $P = 0.3$; colony failure: $F_{1,282} = 1.4$, $P = 0.2$; Table 1). There was also no significant effect of male social origin on queen mortality ($F_{1,282} = 1.4$, $P = 0.2$) or colony failure ($F_{1,282} = 1.8$, $P = 0.2$). Finally, there was no significant interaction between queen social origin, male social origin and mode of colony founding (all $P > 0.1$).

In contrast, queen mortality was more than two times higher in two-queen (56.3%) than in one-queen (23.4%) associations ($F_{1,282} = 36.6$, $P < 0.0001$). Colony failure was also higher in two-queen (42.1%) than in one-queen (23.4%) foundings ($F_{1,282} = 10.5$, $P = 0.001$). In 28.3% of the two-queen foundings, one queen died while the other successfully raised workers and survived until the end of the experiment. The social origin of queens did not influence the proportion of two-queen colonies in which one queen died before ($\chi^2_1 = 0.04$, $P = 0.8$) or after ($\chi^2_1 = 0.004$, $P = 0.9$) worker emergence. In two-queen foundings, the pattern of queen mortality was not random, as colonies in which both queens died or both queens survived were overrepresented (observed numbers of colonies in which both queens survived, one queen died, or both queens died: 47, 45 and 67, respectively; expected numbers if queens died independently of each other: 30, 79 and 50, respectively; $\chi^2_1 = 30.1$, $P < 0.001$; Table 1).

After 15 months, the interaction between queen social origin and mode of colony founding with respect to queen mortality was close to being significant ($F_{1,282}$, $P = 0.06$). This was because queens originating from monogyne colonies tended to have a higher mortality in two-queen foundings (68.3%) than queens originating from polygyne colonies (53.4%; $F_{1,158} = 5.0$, $P = 0.03$), whereas there was no significant difference between the two types of queens in one-queen foundings ($F_{1,123} = 0.6$, $P = 0.4$). Queen social origin had no significant effect on colony failure ($F_{1,282} = 1.6$, $P = 0.2$).

After 15 months, male social origin had no significant effect on queen mortality ($F_{1,282} = 3.1$, $P = 0.08$). However, an unexpected finding was that male social origin did influence colony failure ($F_{1,282} = 4.4$, $P = 0.04$). Specifically, colonies in which queens had mated with males from polygyne colonies had a higher failure rate (44.9%) than colonies in which queens had mated with males from monogyne colonies (31.5%), independently of the social origin of queens. There was no significant interaction between queen social origin, male social origin and the mode of colony founding with respect to colony failure (all $P > 0.08$).

The lower success of two-queen than one-queen foundings persisted over time. Indeed, queen mortality and colony failure rates over 15 months were higher in two-queen foundings than in one-queen foundings (mortality: $F_{1,282} = 44.4$, $P < 0.0001$; colony failure: $F_{1,282} = 13.4$, $P = 0.0003$; Table 1).

Table 1
Queen mortality and colony failure rate in the colony-founding experiment

	Queen mortality				Colony failure	
	One-queen founding		Two-queen founding		Two-queen founding	
	Monogyne queens	Polygyne queens	Monogyne queens	Polygyne queens	Monogyne queens	Polygyne queens
After 5 months						
Monogyne males	0.17 (34)	0.28 (25)	0.55 (40)	0.45 (28)	0.38 (40)	0.32 (28)
Polygyne males	0.24 (37)	0.25 (28)	0.64 (61)	0.53 (30)	0.54 (61)	0.33 (30)
After 15 months						
Monogyne males	0.20 (34)	0.32 (25)	0.60 (40)	0.46 (28)	0.40 (40)	0.32 (28)
Polygyne males	0.27 (37)	0.29 (28)	0.74 (61)	0.60 (30)	0.64 (61)	0.43 (30)

Queens originating from monogyne or polygyne colonies were experimentally mated with males originating from monogyne or polygyne colonies. Colony failure in two-queen foundings corresponds to the death of both queens. In one-queen foundings, colony failure is equal to queen mortality. These rates were measured 5 and 15 months after the start of the colony-founding experiment, that is, just before the first hibernation and at the end of the second summer, respectively. The number of colonies is indicated in parentheses.

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Worker Production

The social origin of the queens significantly influenced the number of workers produced by incipient colonies over the first 5 months of the colony-founding experiment ($F_{1,181} = 5.24$, $P = 0.02$; Fig. 1). Specifically, colonies founded by queens of monogyne origin produced more workers than colonies founded by queens of polygyne origin (Fig. 1). This higher productivity might be explained by the heavier weight of queens originating from monogyne colonies at the start of the colony-founding experiment (mean fresh weight of monogyne and polygyne queens ± SE = 38.6 ± 0.4 and 36.8 ± 0.5 mg, respectively; t test: $t_{169.5} = 2.8$, $P = 0.005$). In contrast, male social origin had no effect on worker production ($F_{1,181} = 0.007$, $P = 0.9$) and there was no interaction between queen social origin, male social origin and mode of colony founding (all $P > 0.4$).

The mode of colony founding had a strong influence on the number of workers produced over the first 5 months ($F_{1,181} = 17.7$, $P < 0.0001$; Fig. 1). Two-queen colonies in which one of the queens had died after worker emergence produced significantly more workers than one-queen colonies and two-queen colonies in which one of the queens had died at an early stage (Tukey honestly significant difference, HSD: 2 → 1Q late versus 1Q: $P < 0.0001$; 2 → 1Q late versus 2 → 1Q early: $P < 0.0001$). Two-queen colonies in which one of the queens had died at a later stage also tended to produce more workers than two-queen colonies (2 → 1Q late versus 2Q: $P = 0.05$). Two-queen foundings in which both queens survived produced more workers than one-queen foundings (Tukey HSD: 2Q versus 1Q: $P < 0.0001$) and than two-queen foundings in which one of the queens had died before worker emergence (Tukey HSD: 2Q versus 2 → 1Q early: $P = 0.0001$). These differences in worker productivity between various founding conditions were significant from 15 days after the first workers had emerged until the start of hibernation. In contrast, the different founding conditions, queen social origin and male social origin had no significant effect on the time of emergence of the first workers (Kruskal–Wallis test: all $P > 0.13$).

The differences in colony productivity were transient and had disappeared at the end of the second summer. After 15 months, monogyne and polygyne queens had produced similar number of workers ($F_{1,167} = 0.2$, $P = 0.6$; Fig. 1). Moreover, the differences in queen weight had also disappeared (mean fresh weight of monogyne and polygyne queens ± SE = 49.9 ± 0.8 and 49.2 ± 0.8 mg, respectively; $t_{126} = 0.13$, $P = 0.9$). This was due to a higher increase in weight for queens of polygyne origin (three-way ANOVA on queen weight difference between 5 and 15 months after founding, effect of female social origin: $F_{1,135} = 5.3$, $P = 0.02$).

After 15 months, the differences in colony productivity between colony founding types (1Q, 2 → 1Q early, 2 → 1Q late and 2Q) had become nonsignificant ($F_{3,167} = 0.6$, $P = 0.6$; Fig. 1). The social origin of males had no effect on worker production ($F_{1,167} = 0.5$, $P = 0.4$) and there was no significant interaction between queen social origin, male social origin and mode of colony founding (all $P > 0.3$).

DISCUSSION

The proximate mechanisms contributing to the maintenance of colony queen number variation in ants remain poorly understood. We found a high degree of flexibility in mating and colony founding by *F. selysi* queens originating from monogyne as well as polygyne colonies. Young queens produced by monogyne colonies were significantly heavier than young queens originating from polygyne colonies (this study; see also Rosset & Chapuisat 2007; Meunier & Chapuisat 2009). However, queens originating from monogyne and polygyne colonies had a similar survival rate and colony-founding success, and both types of queens were able to found colonies without the help of workers. Hence, the results of our colony-founding experiment do not support the hypothesis that a feedback loop linking queen number, queen size and colony founding helps stabilize social structure variation in this socially polymorphic ant population (Hölldobler & Wilson 1977; Keller & Passera 1989; Meunier & Chapuisat 2009).

The queens had no access to food until the first workers had matured. Hence, queens of polygyne and monogyne origin are able

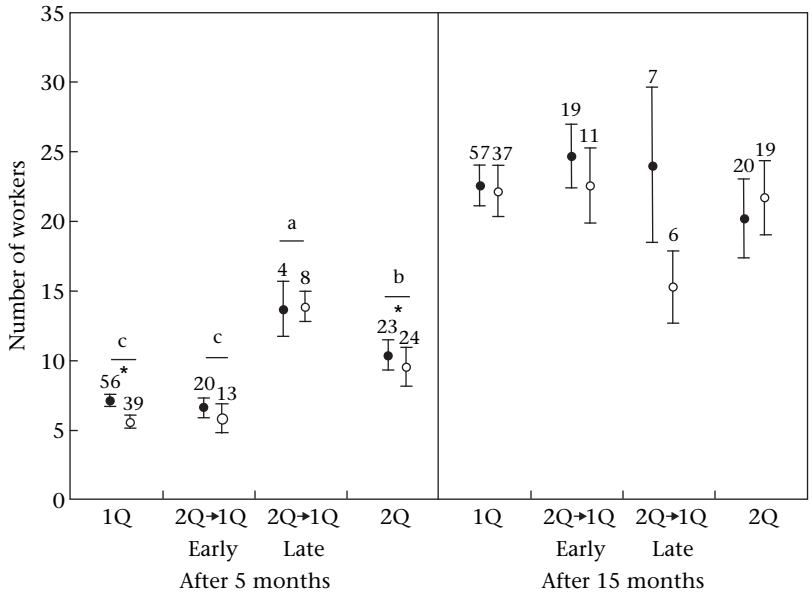

Figure 1. Mean ± SE number of workers produced by incipient colonies founded by queens originating from monogyne colonies (black dots) or from polygyne colonies (white dots). Incipient colonies were founded by a single queen (1Q), by two queens of which one died before worker emergence (2 → 1Q early), by two queens of which one died after worker emergence (2 → 1Q late), or by two queens that survived until the end of the experiment (2Q). The productivity is indicated after 5 months and 15 months. The number of colonies is indicated above the bars. Different letters (a, b, c) indicate significant differences between modes of colony founding in the number of workers produced. Asterisks indicate significant differences between queens of different social origin within the same mode of colony founding ($P < 0.05$).

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to rear a first cohort of workers by relying entirely on their energetic reserves, as required by claustral independent colony founding. Stable and protected laboratory conditions may have increased the survival and colony-founding success of queens, compared to natural conditions. However, the fact that queens of monogyne and polygyne origin had similar mortality and colony failure rates in the laboratory suggests that both types of queens have similar abilities for independent claustral colony founding in the field. Fire ant, *Solenopsis invicta*, queens originating from polygyne colonies were also able to start new colonies in isolation under laboratory conditions, but their success was lower than that of queens originating from monogyne colonies (DeHeer 2002).

Despite generally similar abilities to found colonies independently, there were some subtle differences between *F. selysi* queens of monogyne and polygyne origin. The rate of colony failure appeared to be slightly higher for monogyne queens in two-queen foundings at the end of the experiment, albeit not significantly so. It is thus possible that monogyne queens are less tolerant towards the presence of other queens. Monogyne queens also produced more workers than polygyne ones during the first 5 months of colony founding, which is probably a consequence of their heavier initial weight. However, the difference between monogyne and polygyne queens in colony productivity was transient, as all types of colonies had reached a similar size at the end of the second summer.

Colonies founded by two queens produced more workers than colonies founded by one queen during the first 5 months of the experiment, independently of the social origin of queens. Reaching higher worker number during the first months of colony life may considerably increase the success of incipient colonies, as it improves hunting efficiency, brood care, task partitioning or colony competitiveness in the field (Rissing & Pollock 1987; Vargo 1988; Heinze 1993; Bernasconi & Keller 1996; Helms Cahan 2001). Again, in our experiment these differences in colony productivity between one-queen and two-queen colonies were only observed during the first few months of colony life, at a time when the queens' energetic reserves are important for worker production. After 15 months, the two types of colonies had reached a similar size, which might be caused by variation in queen fertility and reproductive skew over time.

The frequency of pleometrosis in the field is unknown for *F. selysi*. Our results indicate that queens in two-queen associations suffer from higher mortality and colony failure rates than single queens. Moreover, the nonrandom pattern of queen mortality suggests that queens either fight, which results in a high probability of death for both queens, or do not fight at all. The lower rate of success of two-queen associations suggests that cooperative colony founding may be rare or nonexistent in the field. However, associative colony founding by queens of monogyne or polygyne origin might still be favoured if nest sites are rare or if joint colony founding increases the nest resistance to disease, usurpation or predation in the field (Johnson 2002; D'Ettorre et al. 2005; Reber et al. 2008).

We found no sign of mating avoidance or genetic incompatibility between social forms. Males and females originating from different social forms readily mated in the same experimental conditions and in the same amount of time as individuals belonging to the same social form. Moreover, queens that had mated with a male of the same or of the other social form had similar productivity. These results suggest that there is no morphological or behavioural barrier to mating between social forms, and that the social forms are genetically compatible. In our study site, monogyne and polygyne colonies occur in close proximity (Chapuisat et al. 2004) and produce queens and males in synchrony (Rosset & Chapuisat 2006), further suggesting that mating between social forms may be frequent.

An unexpected result of our study was that colonies in which queens had mated with males of polygyne origin suffered from higher colony failure over 15 months than colonies in which queens had mated with males of monogyne origin, and this was independent of the social origin of queens. However, this effect was weak and only marginally significant, and should thus be considered with caution. Speculative explanations for the observed pattern might be that males of polygyne origin transfer toxic products during mating, or produce brood of lower quality.

Flexible colony founding and mating between individuals originating from polygyne and monogyne colonies probably help maintain gene flow between social forms in *F. selysi*, which is in line with the lack of genetic differentiation between social forms at nuclear microsatellite markers in our study population (Chapuisat et al. 2004). Significant and apparently bidirectional gene flow between social forms has also been documented in populations of *F. fusca* and *F. podzolica* (DeHeer & Herbers 2004; Bargum et al. 2007). These *Formica* species with high gene flow between social forms and presumably plastic social structures occupy ephemeral, open or discontinuous patches of habitat that undergo frequent disturbance (Chapuisat et al. 2004; DeHeer & Herbers 2004; Sundström et al. 2005; Bargum et al. 2007).

Formica selysi is a pioneer species that lives in open habitat along alpine rivers. At our study site, rare but severe floods markedly change the soil topology and create patches that are free of resident colonies. In contrast, colonies occur at high density in parts of the site that have not been recently flooded (Rosset & Chapuisat 2007). Heterogeneous and disturbed environmental conditions probably contribute to the coexistence of alternative social forms in sympatry, as new areas to colonize should favour independent colony founding by single queens, while densely populated areas should favour polygyne colonies and colony budding (Ross & Keller 1995). The observed flexibility in colony founding by *F. selysi* queens of monogyne or polygyne origin is in line with the hypothesis that variable and unpredictable environmental conditions select for plastic responses in dispersal, colony founding and queen number (Herbers 1986; Feldhaar et al. 2005).

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