The Number of Queens: Causes and Consequences

A major feature of insect societies is the existence of reproductive division of labour, whereby reproduction is monopolised by one or a few individuals assisted by a non-reproductive worker caste. In ants, the existence of variations in the number of reproductives is a labile trait that has drawn much attention. The number of queens can be extremely variable among species as well as within species. It is now generally accepted that polygyny (a colony headed by more than one queen) is a derived trait and may be the predominant social structure in ants. The evolution of polygynous colonies from a single queen ancestor may challenge the evolutionarily explanation of reproductive altruism. Ant queens start new colonies in one of two basic ways. They can be either accompanied by workers (i.e. dependent founding) or found colonies independently, without the aid of workers. In the latter case, queens can either found alone (haplometrosis), or they may cooperate with other queens during colony foundation (pleometrosis). The maintenance of this initial cooperation between queens is relatively rare but it exists and can lead to the co-existence of several reproductives within the colony (primary polygyny). However founding associations are generally temporary and soon reduce to a single egg-laying queen (secondary monogyny), either before or shortly after the emergence of the first workers. The process of elimination of all but one co-founding queens is not clearly understood. In contrast to primary polygyny, secondary polygyny develops as a consequence of colony fusion or when established colonies adopt additional inseminated queens that can be daughters of the mother queen, or not, depending on the species and the ecological constraints. This richness and variability in the mode of colony foundation is unique to ants. The diversity of strategies of breeding systems, colony foundation and colony growth has drastic consequences on colony kin structure (within colony relatedness), and therefore on the delicate balance between cost and benefits of eusocial life, which typically underlines internal conflicts over reproduction.

In March 2016, a workshop entitled "*The number of queens - causes and consequences*" has been organized under the auspices of the Fyssen foundation in Paris. During two days, fifteen young and confirmed researchers presented and discussed their most recent findings about social organization in ants, with a particular emphasis on polygyny. With the aim of broadening the scope of this meeting, two additional speakers were invited to describe the state of the art in mammals. This small audience comprised experts in a variety of complementary fields ranging from genomics to ethology to ecology and evolution.

In an introductory lecture, **Koos Boomsma** addressed semantic and conceptual issues in the definition of eusociality and polygyny. He focussed about the abundant evidence that life-time monogamy is ancestral throughout eusocial lineages and that physically differentiated castes evolved in core single-mother families. He argued that there is a fundamental difference between multi-queens societies in lineages with morphologically differentiated castes from those having castes that are based on phenotypic plasticity, a distinction that is fundamental for an operational definition of eusociality.

In polygynous societies, nestmate queens share reproduction more or less evenly (various degrees of reproductive skew), leading eventually to the development of functional monogyny. **Jürgen Heinze** examined how ecological constraints affect the magnitude of reproductive skew. Low skew is associated homogeneous habitats and high skew is favoured by limited nest availability and strong limitations to dispersal. In addition, he provided evidence that reproductive skew is a plastic trait as queens can adjust their reproductive strategies in response to social changes (i.e. variations in queen-worker ratio).

Lotta Sundström examined the mechanisms underlying reproductive partitioning in the polygynous ant *Formica fusca*. She showed that queens ovipositing earlier in the season get more sexual pupae and she provided evidence that larger worker entourage increases the fecundity and influences the chemical signature of queens. She also reported evidence that worker reproduction increases as the average relatedness between nestmate queens decreases.

Cristian Lorenzi presented an overview of social organization in wasps. Paper wasps show certain similarities with some life-history traits documented in ants, including the existence of solitary and group-founding strategies. In foundress associations, wasps form a linear dominance hierarchy with dominant females monopolizing reproduction and subordinates foraging (thus acting as helpers). One likely explanation for the presence of helpers, despite their low relatedness to dominant females, lies in the prospective of nest inheritance.

After their nuptial flights, queens can either found their colony solitarily or seek adoption into another colony or in their natal nest. In *Leptothorax gredleri*, **Abel Bernadou** investigated the decision-making processes of young mated queens. He demonstrated that young queens show a preference for substrates marked with chemical cues laid by their nestmates over unmarked substrates and that they can be adopted, to some extent, in their maternal nests.

In some ant species, founding queens can cooperate during the initiation of new colonies and, soon after in the emergence of workers, all but one queen die after they engage in fatal fights. Using the black garden ant *Lasius niger* as a model organism, **Kévin Berthelot** examined what mechanisms are involved in the onset of aggression between queens. His approach suggests that queens can use olfactory cues and compare their fertility status to their rival's one before engaging in agonistic interactions.

Populations of the Alpine silver ant *Formica selysi* contain a mix of monogynous and polygynous colonies. Using genomic approaches, **Michel Chapuisat** demonstrated that this social polymorphism relies on the existence of a supergene, which is a large cluster of tightly linked genes preserving the associations of alleles. Interestingly, the genetic architecture underlying social polymorphism in *F. selysi* resembles that of fire ants, suggesting that chromosomal rearrangements are important for the shift between social organizations in ants.

Raphaël Jeanson proposed a comparative approach between populations of the ponerine ant *Odontomachus hastatus* that are strictly monogynous in French Guiana and facultatively polygynous in Brazil. He showed that nestmate recognition and the aggression toward unrelated individuals do not vary between monogynous and polygynous colonies and that the cuticular profiles of both social forms do not differ substantially.

Raphaël Boulay reviewed the literature to compare the life-history traits of monogynous and polygynous Palearctic ant species. His analysis revealed that monogyny is the ancestral breeding system in European ants and that polygyny evolved secondarily throughout the phylogenetic tree and occurs in about 30% of extant species. He also provided evidence that polygynous species are more frequently dominant than monogynous species, thereby bringing support to the prediction that one benefit of polygyny lies in ecological dominance.

Serge Aron examined whether the variation in reproductive traits (including mating frequency, queen number and asexual thelytokous reproduction) in the desert ant genus *Cataglyphis* results from a single evolutionary transitions or from multiple independent transitions, per trait. Using phylogenetic analyses based on the analysis of DNA variation at four loci, he showed that multiple evolutionary changes occurred for the three reproductive traits studied and that monogyny and polyandry are the ancestral states of the genus.

In ants, new colonies can be founded by a queen alone (independent colony foundation) or by a queen assisted by workers (dependent colony foundation) and these strategies have different costs and benefits associated to competitiveness and colonisation efficiency. **Thibaud Monnin** developed a theoretical approach to simulate spatially explicit environments differing in patch quality and colony density to identify the environmental conditions favouring either strategy. His work reveals the importance of the interaction between dispersal and landscape structure on the ecological success of either strategy and suggests that the competition-colonisation trade-off can explain the co-existence of both strategies.

Elise Huchard reviewed social and mating systems in mammals. Using long-term field data collected in Namibia, she reported the existence of intense intra-sexual competition in Chacma baboons, a polygynous primate, where females compete over males.

Across species, conflicts are inherent to group life and reconciliation between former opponents limit the occurrence of further conflicts and reduce anxiety. **Christine Webb** showed that stable individual variations in reconciliation behaviour exist in chimpanzee and she also stressed that further work is now required to explore the relationship between post-conflict behaviours and fitness.

This inspiring workshop offered a comprehensive picture of our current knowledge of the mechanisms underlying polygyny and opened new avenues for future, collaborative research. The perfect logistics organization and the dynamic and at the same time relaxed atmosphere of the Fyssen foundation headquarter, located in a beautiful historical building in central Paris, significantly contributed to the success of this

workshop. We therefore would like to thank again the Fyssen administrative staff and the scientific board for making this workshop possible.

The organizers

Raphael Jeanson and Patrizia d'Ettorre