The evolutionary fate of parthenogenetic ants' societies

Fabien Ravary
Laboratory of Sub-Tropical Zoology, Dept of Agriculture, University of the Ryukyus, Okinawa
Tel/Fax : +81 98 895 8797
E-mail : g056002@agr.u-ryukyu.ac.jp

Résumé :
Les insectes eusociaux parthénogénétiques (parmi les fourmis et les abeilles) combinent deux problématiques majeurs de la biologie évolutive: l'évolution de la reproduction sexuée d'une part, et l'évolution des comportements sociaux de l'autre. L'étude comparée de ces rares espèces, aux structures sociales différentes et parfois même "extraordinaires", peut permettre des avancées significatives, notamment dans l'identification des facteurs qui contribuent au maintien si paradoxal de la reproduction sexuée. En me basant sur de récentes découvertes de première importance, je présente ici l'hypothèse selon laquelle certains aspects de l'organisation sociale exerceraient des contraintes sur le développement d'une reproduction entièrement parthénogénétique, pourtant moins coûteuse. Ces mécanismes proximaux agiraient pour maintenir la reproduction sexuée (et donc la production des mâles!), indépendamment des avantages théoriques issus de la diversité génétique produite au niveau colonial. En effet, la structure sociale des hyménoptères sociaux est le siège de conflits permanents pour l'accès à la reproduction. Elle repose également sur une partition des tâches entre une caste sexuée et une caste ouvrière. Ces caractéristiques peuvent représenter d'importantes contraintes sociales permettant d'éviter la perte des individus sexués et apparaîtraient alors comme des moyens spécifiques et originaux de préserver la reproduction biparentale.

Abstract :
Parthenogenetic eusocial insects (among ants and bees) combine two lingering and exciting issues: the evolution of sex on the one hand, and the evolution of social behaviour on the other hand, undoubtedly the "Royal Couple" for evolutionists! Important insights may arise from the comparative study of these few species displaying different and sometimes extraordinary social structure. Notably, new and original factors contributing to the paradoxical maintenance of sex can be identified. Relying on recent major discovers in ants, I here venture the hypothesis that evolution towards parthenogenesis may be constrained by aspects of social organisation. These proximate mechanisms would act for the maintenance of sex, regardless of the theoretically advantageous genetic variance then provided at the colony level. Indeed, the social structure of eusocial hymenoptera is the locus of permanent kin conflicts and hinges on task partitioning between a sexual and a worker caste. These characteristics may represent important social constraints preventing the loss of sexuals and would then appear as specific and novel ways to save biparental reproduction.

Introduction:

The ubiquity of bisexual reproduction (amphimixy) in pluricellular organisms has long been considered "*the queen of problems in evolutionary biology*" [1]. It indeed seems difficult to explain the success of this strategy in view of its weak efficiency to promote genes, when compared to parthenogenesis and its theoretical two-fold advantage of coping without males (Fig. 1). Numerous hypotheses have been developed to shed light on this crucial issue [2]. Stressing a genetic viewpoint, some hypotheses focus on the efficient purge of the mutation load arising from recombination and amphimixy. Others advocate, in an ecological perspective, the constant shuffling of allelic combinations as a major advantage for sustaining varying selective pressures. Moreover, given that species incapable of retaining bisexual reproduction are likely to disappear after invasion by evolutionary dead-end parthenogens, an alternative standpoint may regard persistent amphimictic species as those that encounter constraints on parthenogenetic development [3]. This underlines the need to determine specific biological barriers that may influence the evolution of parthenogenesis in order to understand its current distribution. In this context, some promising new insights may come from eusocial Hymenoptera (ants and social bees) that developed parthenogenetic reproduction. The behaviour of these insects, thus, reflects two lingering and exciting issues: the evolution of sex on the one hand, and the evolution of social behaviour on the other hand, undoubtedly the "Royal Couple" for evolutionists! Basing on recent serendipitous discoveries [4, 5], I here venture the hypothesis that evolution towards parthenogenesis may be constrained by some aspects of social organisation that would act as proximate mechanisms for the maintenance of sex [6].

1) Some extraordinary ants:

Original genetic systems were recently reported in two ant species. Queens of *Cataglyphis cursor* and *Wasmannia auropunctata* were found to reproduce alternatively by amphimixy and parthenogenesis to produce genetically diverse worker offspring and clonal gynes, respectively [4, 5]. One can wonder why *C. cursor* and *W. auropunctata* have not discarded amphimixy by queens despite its persistent cost. Alternating between both modes of reproduction may represent the optimal strategy for an ant species, as it leads to a more efficient promotion of genes through clonal gynes while a highly heterogeneous worker caste may provide the colony with some of the benefits usually advocated for genetic diversity. Decreased relatedness between workers might help to enhance colony homeostasis and division of labour, and ensure an invaluable lead in the arms race against pathogens. Nevertheless, though theoretically stimulating, these putative short-term advantages suffer weak empirical demonstration and it is not clear whether they could resist clonal reproduction by selfish individuals.

2) Worker policing as a possible social constraint upon parthenogenesis

In insect societies, selfish reproduction can be prevented by collective behaviours, such as

mutual policing [7]. Nestmates (queens and/or workers) may harass reproductive workers or selectively destroy worker-laid eggs. Theory predicts that worker policing will be selected when their selfish reproduction leads to a fall in colony efficiency and/or when the colony kin structure induces a decreased mean relatedness among workers [8].

A decreased relatedness may, indeed, enhance social cohesion by lessening potential kin conflicts over reproduction. This last point is crucial and may prove to mortgage the raising of a fully parthenogenetic reproduction in *C. cursor*, and by extension, the evolutionary fate of parthenogenetic societies in social hymenoptera (Fig. 2). Genetical analyses were conducted on 38 colonies of *C. cursor* using four highly polymorphic microsatellite loci (Table 1). They showed that queens had mated with an average of 5.6 ± 1.3 males (range 4 to 8) [5]. Then, the social structure of *C. cursor* clearly offers an opportunity for worker policing to emerge. Thus, amphimixy coupled with polyandry allows the queen to save her head and remain the unique reproducer within the colony, for the paradoxical greater genetic advantage of every nestmate, with males excluded as they gain no fitness any more. Consequently, the occurrence of social constraints in *C. cursor* signs away the further spread of parthenogenesis.

3) Caste determinism as another possible social constraint upon parthenogenesis

Nevertheless, the hypothesis of a constraint imposed by kin conflicts, as advocated here for the maintenance of amphimixy in eusocial hymenoptera, cannot apply straightaway to the late case of parthenogenesis just demonstrated in ants [4] (Table 2). This should stimulate the search for alternative specific constraints on parthenogenesis.

For instance, though caste determination in social hymenoptera is usually assumed to be environmentally induced, genetically determined caste differentiation was also recently demonstrated in two other ant species [9]. Here, the level of heterozygosity at a single locus governs the developmental fate of larvae towards the queen or worker caste (Fig. 3). A similar genetic process may also be at work in *W. auropunctata* (Table 2). It could explain, indeed, why workers agree to rear clonal gynes that are less related to them than sexually produced sisters. Given the partitioning between the male and female gene pools, workers that usually develop from fertilized eggs are likely to be heterozygous at the putative "caste" locus. On the contrary, parthenogenetic gynes are more prone to homozygosity. Since a colony composed of only gynes has no chance of survival, the absolute necessity of a worker caste, again regardless of the genetic diversity among individuals, would then be a pressing social constraint upon the loss of males. This hypothesis, of course, may also apply to *C. cursor* with the restriction that polyandry would then be unnecessary (see above).

4) Conclusion and perspectives:

The social structure of eusocial hymenoptera provides a locus of permanent kin conflicts and

hinges on task partitioning between a sexual and a worker caste. Thus, social constraints preventing the loss of the sexual caste appear to be a specific and original way to maintain amphimixy in these insects. In order to test some of the proposed hypothesis, several experiments can be easily conducted. First, it appears important to check whether virgin queens can really lay thelytokous eggs. If not, that is if sperm is necessary to induce embryonic development, this would be a much more pressing constraint upon parthenogenesis than the proposed social constraint. Secondly, analysing the social structure of other populations belonging to both species but displaying classical sexual reproduction would help understanding the proximate factors involved there in the maintenance of sex. Finally, additional cases of parthenogenesis in ants, and the study of their social structure, will bring a robust test of the social constraint hypothesis. In that context, my project on the myrmecofauna of Okinawa (Japon - Ryukyus), especially the study of several species of *Monomorium sp.* (Figure 3) that were recently demonstrated also parthenogenetic (unpublished data), is likely to bring important insights. Behavioural observations and micrasatellite analyses are the main experiments planned for this project.

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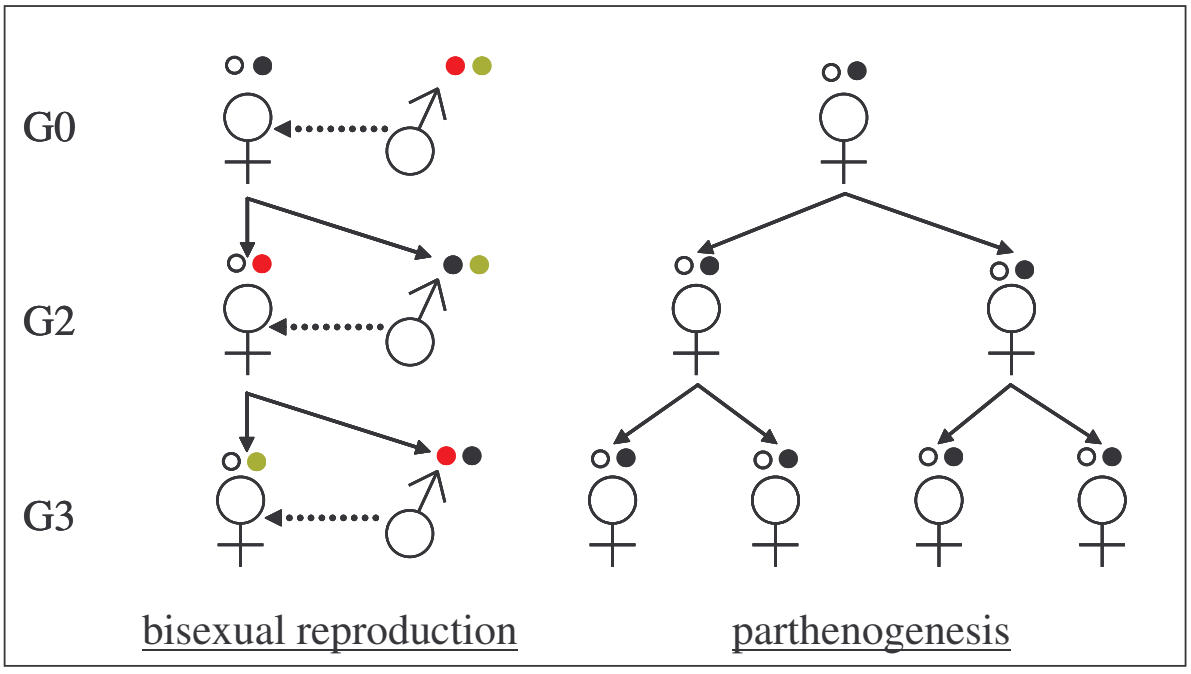

Figure 1. Illustration of the theoretical two-fold advantage of parthenogens (all female lineages). Points represent the hypothetical transmission of genes for diploid males and females, G = generation.

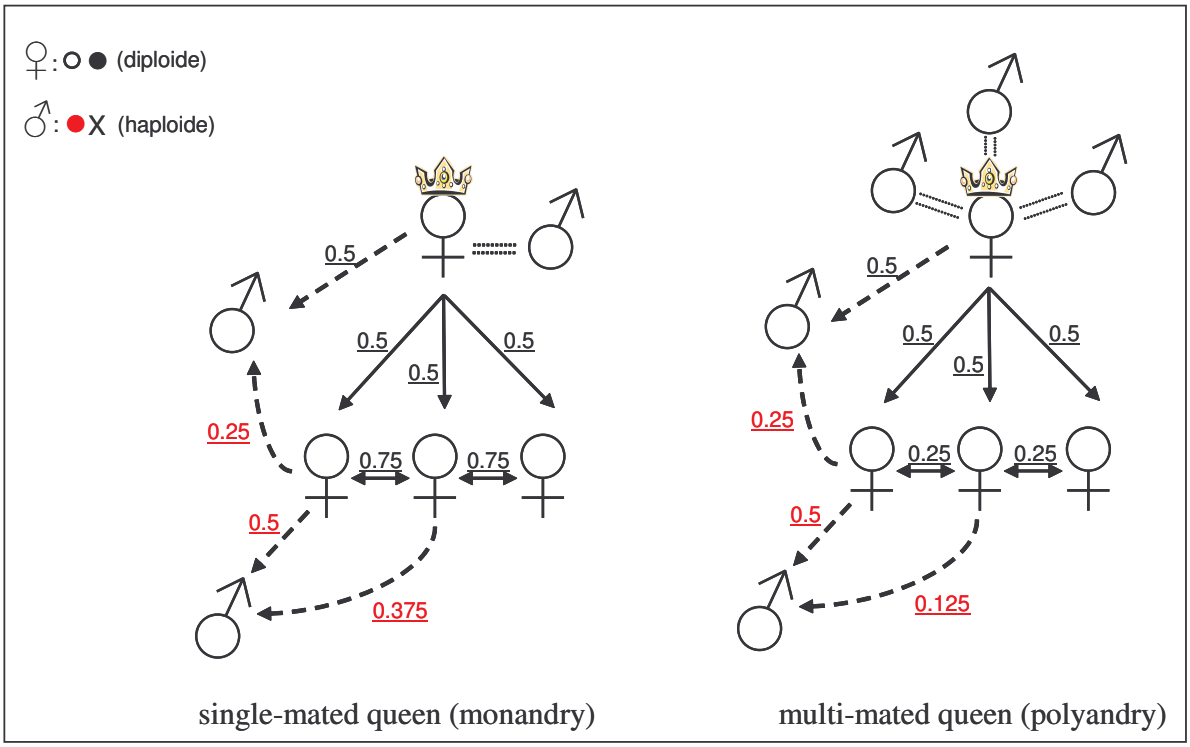

Figure 2. Synopsis of average relatedness between individuals in monandrous and polyandrous colonies.

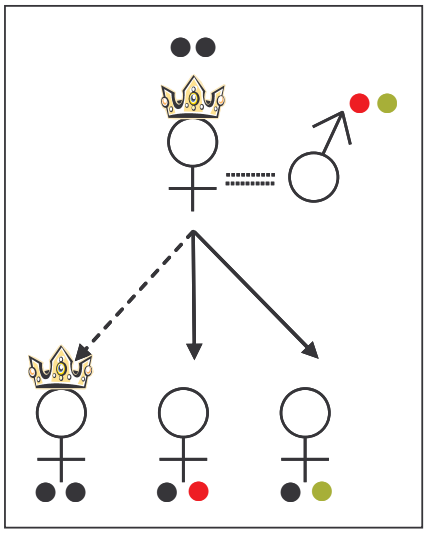

Figure 3. Genetic caste determination as a possible explanation for the maintenance of sex in *Wasmannia auropunctata*: queens are homozygous at the "sex-locus", whereas workers are heterozygous.