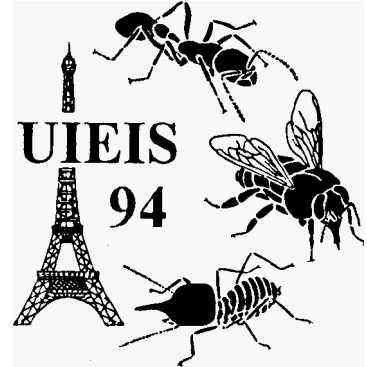# LES INSECTES SOCIAUX

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THE EVOLUTION OF EUSOCIALITY

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Eusocial insects are defined as those that show cooperative brood care, reproductive caste differentiation and overlap of generations. I argue that this definition is rather restrictive and has often prevented the simultaneous consideration of some-what less social insects and cooperatively breeding birds and mammals which exhibit levels of altruism comparable to that exhibited by many eusocial species of bees and wasps. I suggest therefore that the definition of eusociality be broadened to permit the inclusion of all species showing substantial levels of altruism towards group members (Gadagkar, 1994).

The evolution of eusociality has two components, the origin of eusociality - concerned with the conditions under which altruists can invade a population of selfish, solitary individuals and the maintenance of eusociality - concerned with the conditions under which selfish mutants cannot invade a population of altruists. Hamilton's inclusive fitness theory provides a powerful unifying framework to explore both the origin and maintenance of eusociality. However, the problem of the maintenance of eusociality is not as easily amenable to investigation because it may simply be difficult for mutations to take highly eusocial species back to the solitary, non-social condition. As for the origin of eusociality, the inequality in the inclusive fitnesses of workers and solitary nest builders may be brought about by a number of factors leading to genetic, physiological, ecological and demographic predispositions to eusociality.

Genetic predisposition implies that workers have access to more closely related brood than solitary foundress do. Physiological predisposition implies that workers are less fertile compared to solitary foundresses. Ecological predisposition implies that due

to the advantages of group living, workers are more productive than solitary nest builders. Demographic predisposition implies that demographic factors such as mortality rates and time taken to attain reproductive maturity affect workers differently than they do solitary foundress.

I have explored the possibility of each of these kinds of predispositions in the primitively eusocial, old world, tropical polistine wasp *Ropalidia marginata,* a model system that appears to be especially suited for the purpose. My conclusion from these investigations is that while *Ropalidia marginata* has little or no genetic predisposition, it has significant extents of ecological, physiological and demographic pre-dispositions to the evolution of eusociality.

In addition, two general conclusion emerge from these investigations. The first has to do with the role of developmental plasticity in social evolution. I argue that not only will demographic factors like time taken to attain reproductive maturity make it worthwhile for some individuals to assume queen-like roles and for others to assume worker-like roles, but also that such demographic factors will coevolve with eusociality (Gadagkar, **1991).** For example, late reproducers in a eusocial species will have a smaller selective disadvantage compared to those in a solitary species because of the possibility of gaining indirect, social fitness in the former. What this means is that one can also envisage the evolution of highly eusocial species starting from solitary ancestors through selection for developmental plasticity. In a solitary species, any character such as time taken to attain reproductive maturity , ovary size, mandible size etc., will have limited developmental plasticity because both queen and worker functions will have to be optimized under a single developmental programme.

As the worker-like individuals begin to rely increasingly on the social component of inclusive fitness and the queen-like individuals continue to rely on the direct, individual component, I speculate that there would begin quite a different regime of selection. There would be a relaxation of stabilizing

selection on genes that regulate the making, in workers, of structures and behaviours needed only in queens. Conversely, there would be a relaxation of stabilizing selection in queens, on genes that regulate the making of structures and behaviour needed only in workers. This should make possible, previously impossible levels of directional selection in workers, on genes that regulate the making of structures needed for workers and in queens on genes that regulate the making of structures needed in queens. In a process analogous to evolution by gene duplication, genes needed in workers and in queens can evolve to new and extreme levels because worker and queen developmental programmes need no longer be optimized in the same individual.

The second general conclusion concerns the direction of social evolution. The inclusive fitness models I have developed to test the role of demographic factors in the evolution of eusociality are completely symmetrical with respect to whether the worker is fitter or whether the solitary foundress is fitter. Only the values of the parameters in the models will decide which is fitter. What this means is that evolution should be able to move both from the solitary to the eusocial as well as from the eusocial to the solitary. The evolution of solitary life or selfishness from the eusocial condition or the process of reverse social evolution as it may be called, has seldom been considered and never been adequately documented and it may truly be rare. It is significant however that the cape honey bee has evolved thelytoky, permitting workers to produce female offspring. Perhaps even more significant is the fact that in many ponerine ants, workers mate and reproduce and may rear no queens at all. These examples, however limited, I argue, can be used as model systems in the study of reverse social evolution.

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