POLISH ACADEMY OF SCIENCES • MUSEUM AND INSTITUTE OF ZOOLOGY
MEMORABILIA ZOOLOGICA

MEMORABILIA ZOOL.	48	181–186	1994

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Ways to reproductive success of wood ant queens[1]

Abstract. The notion of "reproductive success" in queens of the *Formica rufa* group is discussed in the context of the life strategy and evolutionary success of these species. A queen is successful whenever she manages to produce her own family, regardless of the fact whether this occurs in a nest of *Serviformica* ants, in an orphaned colony of her own or related species of wood ants or within a conspecific polygynous society.

Ecological evolution of species is best expressed by their tendency to more and more complete control of the environment (ALLEE et al. 1949). Wood ants of the *Formica rufa* group are an example of animals whose success in this field has been spectacular. New societies of these ants are founded through temporary social parasitism of queens in other colonies. Most myrmecologists share the opinion that the effectiveness of this particular way is very low. Young (mixed) colonies established in this way are recorded extremely seldom. At the same time, however, wood ants are very common and their abundance and biotic pressure exerted on the habitat ensure their position as dominants not only within multispecific competitive communities (SAVOLAINEN, VEPSÄLÄINEN 1988, PISARSKI, VEPSÄLÄINEN 1989) but in entire forest zoocoenoses as well. In order to explain this (apparent) contradiction it is essential to consider an analysis of the biological features which characterize the species under discussion together with an analysis of their geographical and habitat distribution.

Ants of the *F. rufa* group inhabit forests, mainly coniferous ones, in the northern Palaearctic. Thus, they have evolved in permanent, stable and trophically rich habitats. (The food basis of these ants consists of aphid honeydew – a constant and inexhaustible source of the so-called energetistic food). Wood ants owe their position in the competitive hierarchy to the high abundance of their societies (millions of individuals), to the high level of social organization (efficient exchange of information, division of labour), to the type of nest construction which guarantees not only safety

[1] An extended version of a lecture presented at the First European Congres of IUSSI "Biology and Evolution of Social Insects", Leuven, 1991.

but also the best conditions for the development of their offspring, and to their territoriality and a system of routes that make foraging more effective. The above are direct prerequisites for the evolutionary success of wood ants. At the basis of this success, however, lies the ability of these species to adapt their life strategy to the conditions prevailing in stable forest habitats.

Most eusocial insects form "closed" monogynous societies, i.e. they do not accept additional mated queens, either alien ones or those from their own nest. Their existence is limited by the longevity of the queen whose life-span varies from a few to over a dozen years (WILSON 1971). The developmental course of such societies is divided into the following stages:

1) Nuptial flight of a young queen and her search for a place to establish a nest;
2) "Claustral" period connected with rearing the first workers;
3) Young colony with a small number of workers inhabiting a small, primitive nest;
4) Mature colony abundant in workers and inhabiting a large, complex nest.

Losses suffered by a new generation are the highest during the first stage of development and later, at each subsequent stage, they decrease gradually. Moreover, the energetistic expenditure of a colony on nest building and foraging is considerably higher in young societies (proportionally to the colony size) than in mature ones. The relatively short life-span of monogynous closed societies makes them produce a lot of sexuals and establish a great deal of new colonies. In accordance with this strategy (*r* type) the abundance of a population maintained at a constant level is paid for by high energetistic costs in colony reproduction.

An alternative strategy (*K* type) is meant to prolong the life of a society to the maximum to allow for a reduction in the energetistic expenditure on the production of sexual forms and on building new colonies. The energy saved is used for producing workers, for building durable, safe nests quaranteeing the optimum development of the brood, for defending the territory and managing the trophic area to make foraging more efficient.

Wood ants have carried this strategy into effect by "opening up" their societies. Orphaned (queenless) colonies are capable of adopting a new queen (queens) and this makes their further existence possible. Simultaneous adoption of several queens paves the way for polygyny in a given colony (at least that is the case in *Formica exsecta* NYL.; SKIBIŃSKA 1982). Adoption of additional queens gives already polygynous colonies a possibility to develop dynamically, and when mature colonies supplement their pool of queens, their potential is sure to be maintained at a constant level. (Particular societies can live for tens or even hundreds of years provided there is no drastic change in the habitat conditions). Polygyny, together with its derivative – polycaly, combines the adventages afforded by Strategy *K* (size and stability of a society) with the adventages of Strategy *r* (unceasing reneval of the reproductive caste). A monogynous colony of wood ants, e.g. of *F. rufa* L., is a typical "organism" following Strategy *K*. A polygynous colony, on the other hand, while retaining *K* character is composed of many families[1] of *r* type.

[1] The term "family" as used here refers to a given queen with her brood (workers and, at times, sexuals); this is the basic unit of a society. A monogynous colony consists of one family while a pologynous one of many families (they are, as a rule more less related to one another).

Such "opening up" of a colony is not unlimited, of course. In fact, quite the opposite is true; it is restricted by many factors and evidence of this is provided by massacres of young queens which, after their nuptial flights, descend to the territories of polycalic colonies of their own species (YAMAUCHI et al. 1994). There surely is a time limit to such "opening up" (FORTELIUS et al. 1990, CHERIX et al. 1991). It may also be assumed that the degree to which young queens are related to the adopting colony constitutes one of the criteria by which workers are guided in their queen selection (YAMAUCHI et al. 1994). However, a possibility that kin-recognition is involved in this case raises some doubts (FORTELIUS et al. 1993), such relationship is often, but not always, shown by affinity analyses of queen nestmates (PAMILO 1982). Adoption of new conspecific queens into polygynous colonies of wood ants is a fact, though. "Opening up" of orphaned colonies is even wider. Such colonies may go as far as adoption of queens of other related species (CZECHOWSKI 1993a).

What is connected with polygyny and "opening up" of societies is their ability to reproduce through colony splitting. Filial nests, built by big groups of workers, are established on the edges of the territory of the maternal colony. Queens are then transported from the maternal nest to the branch. For the initial 3–4 years, the branches are greatly reinforced by their maternal colonies (adult transport or spontaneous immigration of workers, transfer of pupae). Thanks to this, filial colonies of wood ants may, within such a short period, reach maturity and an abundance equal to that of the maternal colony (PISARSKI, unpubl. data). It is, therefore, an extremely effective way of founding new colonies, virtually with no losses among the queens involved in the process.

The change in social behaviour leading to "opening up" of colonies and to adoption of alien queens is bilateral; it cannot be restricted to workers only but must involve queens as well. In species that adopt their queens the latter must have developed such types of behaviour which allow them to assimilate into foreign nests. Ones even speak about intraspecific "parasitism" of queens (ROSENGREN, PAMILO 1983, WOYCIECHOWSKI, pers. comm.). It is, however, parasitism without quotation marks to use other species for founding a colony. *Formica fusca* L. is a classical example of a host to queens of wood ants.

F. fusca is a successive species of open areas and, just as any pioneer species, a typical *r*-strategist. It founds small colonies that produce plenty of sexuals and thanks to this the species can settle over a large area within a short time, for instance areas such as a clearing, fire-ravaged ground or a "dead forest" after an outbreak of pests. Such a population of *F. fusca*, with a high density of nests and at an appropriate stage of forest succession, makes it easier or simply possible for ants of the *F. rufa* group to invade a given area. The more so because a gradual change in habitat conditions (as forest succession progresses) is generally unfavourable for *F. fusca*. Its colonies grow weaker, many of them presumably lose their queens, and this makes it undoubtedly easier or, in the case of *F. polyctena* FOERST., probably even entirely possible (GÖSSWALD 1953) for queens of wood ants to infest their nests. (A strong, usually polygynous colony of *F. fusca* is able to deal with an invasion by foreign queens, even by numerous groups of them. In June 1985, in the Gorce Mts there was recorded a nest of this species that was literally besieged by young dealated queens,

most probably *F. rufa* ones. Dozens of them were killed by *F. fusca* workers and the colony retained its specific status; CZECHOWSKI, unpubl. data).

There is no doubt that only an insignificant number of young queens of the *F. rufa* group achieves reproductive success through parasitism in nests of *F. fusca* (or, for that matter, of other ants of the subgenus *Serviformica* FOR.). Even a myrmecologists who does a lot of field work generally records only a few initial mixed colonies throughout his life. However, reproductive success of a queen is achieved when she establishes her own family, irrespective of the circumstances. Queens are therefore successful even when, after mating, they get into some already existing nests of their own species. (Or, due to intranidal mating, they never leave them at all; MARIKOVSKY 1961, HIGASHI 1983, FORTELIUS et al. 1990, CHERIX et al. 1991). The number of queens achieving success in this way is incomparably higher. Let's assume that a colony of highly polygynous wood ants comprises 1,000 queens. (This number is not exaggerated in view of the fact that in spring, when the queens gather near the mound surface, 100–200 queens of *F. polyctena* can be found in 10 l of nest material; CZECHOWSKI, unpubl. data). With the mean longevity of a queen being 10 years, a given colony must adopt 100 new queens a year only in order to maintain its potential unchanged. This means that, with the assumed mean annual production of 10,000 queens, only in this way, 1% of females achieve reproductive success. This is fairly lots, and the estimate has been made very carefully indeed. This percentage is even higher in the scale of a polycalic society because the sexual castes are not produced in all the nests, these nests are all potential hosts to them.

Some unmated queens enter already existing colonies. Even these individuals achieve reproductive success, by producing males, they have a possibility to transmit their own genes (SCHMIDT 1971, FORTELIUS et al. 1993).

After their nuptial flight, young queens fly to nests of wood ants just as to those of *Serviformica*. It is hard to say if they thus manifest species selectivity. One thing is certain, though – this is not returning only to maternal nests or to those related to them. It is fairly common to see numerous queens wandering near mounds and clearly wanting to get into monocalic nests which have produced no sexuals during a particular season (CZECHOWSKI, unpubl. data). It is impossible to find out whether, and to what extent, they succeed in the case of queen-right colonies but there is no doubt that adoption of alien queens is a fact in queenless ones (CZECHOWSKI 1993a).

Parasitism in orphaned colonies of other species in the *F. rufa* group is still a virtually unknown (or, at any rate, clearly underestimated) way leading to the reproductive success of wood ant queens. Under natural conditions there have been recorded cases of a gradual exchange of species in nests of *F. rufa* for *F. polyctena* (HAGEMANN, SCHMIDT 1985, CZECHOWSKI 1993a), of *Formica lugubris* ZETT. for *F. polyctena* (PISARSKI, unpubl. data), and even a successful adoption of an *Formica pratensis* RETZ. queen into an orphaned colony of *Formica sanguinea* LATR. (thus within a different subgenus; DONISTHORPE 1915). And a queen of *Formica truncorum* FABR. (a species outside the *F. rufa* group) "conquered" a colony of *F. polyctena* (KUTTER 1968).

This way of an own family production by queens of wood ants is probably nothing special and should be considered entirely natural, especially for the polygynous forms (e.g. *F. polyctena*). Monogynous forms, that is those prone to being orphaned (e.g. *F.*

rufa), are more predestined to be hosts. The morphological and bionomic similarity of the species makes this phenomenon extremely difficult to record because there apparently are no changes within a given colony. But then it happens quite frequently that in nests of wood ants there are found individuals bearing features of different species, and this is generally attributed to high intraspecific variability along with low interspecific differentiation.

The final way leading to success, so far confirmed only experimentally but potentially possible in nature, is based on adoption of queens of wood ants into colonies of slave-keeping ants *F. sanguinea* and connected with a phenomenon of the so called emancipation of slaves which are conspecific (CZECHOWSKI 1990, 1994) or even nonconspecific (CZECHOWSKI 1993b) to these queens.

All the above mentioned means of securing reproductive success in wood ants are simply different variants of founding colonies in a dependent way. A queen adopted by an already existing society need not look after her brood herself. This is done by the host's workers. Therefore, the queen does not require great energetistic reserves indispensable if she were to survive, without food, the long "claustral" period and were to feed the first workers. This is why queens founding new families in a dependent way may be smaller and may have a poorer fat content than is the case with queens which must rely entirely on themselves (KELLER, PASSERA 1989). It is therefore far less costly for maternal colonies to produce the former. For the ants of the *F. rufa* group which have "bet" on the abundance and longevity of their societies this is yet another (besides the very number of sexual forms produced) source of energetistic economy in sexual reproduction.

The very characteristics which have made it possible for wood ants to achieve their evolutionary success and which have secured them their dominant position in the environment at present pose a threat to the existence of these species in areas managed by man. This, however, is a different question.

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STRESZCZENIE

Drogi do sukcesu rozrodczego królowych rudych mrówek leśnych

Mrówki z grupy *Formica rufa* odniosły sukces ewolucyjny, wyrażający się pełnym opanowaniem właściwych im stabilnych środowisk leśnych. Ich społeczeństwa odznaczają się złożoną organizacją, są długowieczne, a same mrówki stoją na szczycie hierarchicznie uporządkowanych zespołów konkurencyjnych, dominując zarazem w całych zoocenozach. Tę pozycję rude mrówki zawdzięczają "otwarciu" społeczeństw dla nowych królowych, zapewniającemu odnawialność kasty rozrodczej w mrowisku, poliginizm i jego pochodną – polikalizm. Sukcesem rozrodczym młodej królowej jest w tej sytuacji nie tylko założenie nowej kolonii drogą czasowego pasożytnictwa w mrowisku *Serviformica* (co zdarza się stosunkowo bardzo rzadko i służy kolonizowaniu nowych obszarów), ale także wyprowadzenie swojej rodziny w obrębie już istniejącego społczeństwa własnego gatunku – co jest drogą najczęstszą. Możliwe są też adopcje królowych w osieroconych mrowiskach innych gatunków rudych mrówek. Wszystkie drogi do sukcesu rozrodczego królowych to warianty zależnej metody zakładania kolonii. Jej koszty energetyczne są znacznie mniejsze, a efektywność większa niż metody niezależnej. Zaoszczędzona na tym energia może być wykorzystana na rozbudowę i zapewnienie trwałości już istniejących społeczeństw.