

MIXED COLONY OF *FORMICA PRATENSIS* RETZ. + *FORMICA CINEREA* MAYR + *FORMICA SANGUINEA* LATR. (HYMENOPTERA: FORMICIDAE) AND ITS PRESUMED ORIGIN

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Abstract.— A case of a queenright colony of *Formica pratensis* Retz. mixed with the workers of *F. cinerea* Mayr and some workers of *F. sanguinea* Latr. is described. The colony characterized by this composition has evolved from a pure *F. cinerea* colony that had been raided by *F. sanguinea* two years earlier. Another conflict with the same *F. sanguinea* revealed the composition of this colony. The presumed circumstances of the origin of the specific mixed colony are discussed in this paper.



Key words.— Ants, *Formica pratensis*, *Formica cinerea*, *Formica sanguinea*, mixed colonies, social parasitism, slavery, colony founding.

INTRODUCTION

Until recently, there have been no direct observations of the circumstances of the taking over nests of slave species by young queens of *Formica sanguinea* Latr. under natural conditions. Previous accounts are based mainly on laboratory experiments (e.g. Wheeler 1906, Wasmann 1908, Vieh Meyer 1908, Gösswald 1951). Finally, field observations by Mori and Le Moli (1998) have shown that the newly mated *F. sanguinea* queens (aside from other ways to start new colonies) take part in slave raids organized by their nestmates which enables them to invade a host nest. Adoption of a parasite queen in a foreign nest is facilitated by the panic engendered in the raided host colony (see also Mori et al. in press). The disorganization of a *Serviformica* colony raided by *F. sanguinea* workers not only facilitates the invasion of the foundatrices of *F. sanguinea* but also the foundatrices of wood ants (e.g. of *Formica truncorum* F.; Czechowski 1998). The example described here shows that one host colony raided by *F. sanguinea* may be invaded by queens of both species.

TIME AND STUDY AREA

The observations were carried out in a complex of sandy dunes, overgrown with pine forest, near Tvärminne in southern Finland (Fig. 3). Different aspects of the interspecific social parasitic relations in ants including *F. sanguinea* (Czechowski and Rotkiewicz 1997, Czechowski 1999, 2000, Czechowski

and Vepsäläinen, in press) have been observed annually from 1996 to 2000 (each time during a period of two weeks beginning in the end of June). The structure and succession of ant communities in a dune habitat were investigated earlier in the same site (Gallé 1991). The major host species for *F. sanguinea* colonies living in the dunes, was *Formica cinerea* Mayr (subsp. *cinerea*) which was very numerous at this site.

OBSERVATIONS

On July 8th 1998 a polydomous complex of *F. cinerea*, composed of four nest subcomplexes, was raided by *F. sanguinea* nesting 30 meters further (Fig. 1). Within a few hours the *F. sanguinea* ants had occupied superficially three nest subcomplexes (A, B and C; see Fig 6 in Czechowski 1999); however the interior of the nests had not been penetrated. The following evening *F. sanguinea* withdrew completely from the invaded area mainly due to the interference of a nearby colony of *Lasius fuliginosus* (Latr.) (see Czechowski 1997).

A year later (in July 1999) it has been observed, that *F. cinerea* still survived without harm only in nest subcomplex D – the most distant from the other three and the only one which had not been raided by *F. sanguinea* during the previous year's observations. There was no trace of subcomplexes B and C, and the main nest of subcomplex A was occupied (at least superficially) by a small number and relatively inactive group of *F. sanguinea* ants. These ants made occasional contact with the colony that had raided *F. cinerea* in the previous

year. The workers were large, which is typical for mature colonies. Therefore, it almost certainly was not an incipient colony, which is important for interpreting future events. *F. cinerea* ants, even if were present in the nest, they never revealed themselves. Two meters away from this nest was a second (and last) remainder of subcomplex A – a small nest of pure *F. cinerea* (Fig. 1).

During the next season (in the end of June 2000), this old main nest of subcomplex A of *F. cinerea* was inhabited by a mixed colony of *Formica pratensis* Retz. + *F. cinerea* + *F. sanguinea*. The nest was located under a patch of dry moss partially covered by sand at a ground elevation partly surrounded by granite boulders (Fig. 2). In spite of the presence of wood ants, the overall appearance of the nest was not changed; there was not even sign of an incipient organic mound. The mixed colony was minimally active. At one time no more than twenty ants could be observed in the surface area of the nest. Depending on the time of day almost only *F. pratensis* or *F. cinerea* or both in equal numbers were present; *F. sanguinea* individuals appeared sporadically. All the *F. pratensis* workers were very small and very dark, which is typical of the first progeny of a young queen. The workers of *F. sanguinea*, which were occasionally observed, were also very small. The *F. cinerea* workers from this mixed colony and conspecific workers from a nearby pure *F. cinerea* colony proved to be aggressive against each other, when experimentally confronted.

On July 10th, at 3 p.m., *F. sanguinea* (the same as before) raided the pure *F. cinerea* colony next to the mixed colony nest, and very quickly (but only superficially) occupied it. Simultaneously, the blood-red ants started to approach the mixed colony nest, and at 3:45 p.m. attacked it massively. The defenders (of all three species), which got out on the surface of the nest in great numbers, were able to repulse the first attack in no more than 15 minutes. This situation revealed, that in the group of *F. sanguinea* ants which were a part of the mixed colony, besides the very small workers, were workers of normal size (a few have been observed, all of them killed in the battle with conspecifics).

A second attack, made at 4:10 p.m., was a success. After outflanking the mixed nest, the attackers laid a siege to other entrances, while the defenders hid in the nest. The entire nest area measuring about 1,5 m², was superficially invaded around 4:30 p.m. The blood-red ants revealed the presence of 13 holes (or small-hole clusters) in the mixed nest; before the attack the mixed colony has used only a few entrances, the others were permanently closed. Around 5 p.m. the attackers finally reached the inside of the nest, from which they started to carry out larvae and worker cocoons. A few minutes later the workers of the mixed colony together with the brood begun to escape in panic from the raided nest. The *F. pratensis* queen also escaped. All of the nearly 20 collected and identified pupae belonged to *F. pratensis*. The *F. sanguinea* workers carried out the spoils from the nest for nearly 1,5 hours. During that time most of the

refugees, at first scattered on the area of 10 m², began to assemble under a patch of lichens at a distance of 4 meters from their raided nest, where they have remained together with the *F. pratensis* queen and rescued young till the end of observations on July 12th. This group was composed of about 200 workers, out of which 70% were *F. pratensis* and about 30% *F. cinerea*. There were no more than 5 individuals of *F. sanguinea*. The actual original share of *F. sanguinea* in the mixed colony was probably higher (it has already been noted that their losses in the conflict were proportionally highest). It is also possible that a part of the mixed colony, especially the *F. cinerea* ants (see Dobrzańska and Dobrzański 1962, Czechowski and Rotkiewicz 1997) was sealed in nooks and corners of the nest. From the area of the mixed colony refugees 19 dead ants were collected, probably deadly wounded in the battle: 13 (68%) *F. pratensis*, 5 (26%) *F. sanguinea* and 1 (5%) *F. cinerea*. The difference in the proportions of living and dead ants is a good indicator of the engagement of different species in the defense of their common nest.

On July 11th and 12th the interest of blood-red ants in both attacked objects – the unsuccessfully raided nest of pure *F. cinerea* and successfully invaded nest of the mixed colony of *F. pratensis* + *F. cinerea* + *F. sanguinea* was clearly decreasing.

One episodic observation concerning an adoption of nonspecific queens by *F. cinerea* colonies disorganized by an attack of *F. sanguinea* is worthy of mention. On July 6th 1999 *F. sanguinea* (the same colony as before) attacked a nearby (distance of 8 meters), annually unsuccessfully raided, nest complex of *F. cinerea* FcI (Fig. 3). The conflict in its main phase – from fight in the foregrounds to a siege of the nest entrances by *F. sanguinea* – was typical (see Czechowski 1977). During two days all the nests of the complex were superficially occupied by *F. sanguinea* ants, but the attackers, as it is often when the defenders are *F. cinerea*, were not able to reach the pupae hidden deep in the nest (see Fig. 4). Before that, some of *F. cinerea* workers from endangered nests moved to a different, 12 meters distant, conspecific nest complex FcII (Fig. 3).

On July 8th the activity of the *F. sanguinea* ants in the area of complex FcI distinctly dropped and they gradually withdrew from the invaded region. At the same time some *F. cinerea* workers began to appear on the surface. They moved around the *F. sanguinea* ants, sometimes even coming into contact with them, almost without any signs of aggression from either side. The number of these ants increased, and finally the ants, which escaped to nest complex FcII began returning to FcI. At a certain moment, in the area of the nest complex FcI appeared a dealate *F. sanguinea* queen. For several minutes the queen moved around trying to approach the nest entrances, from which it was driven away by *F. sanguinea* workers. Finally, the queen encountered a *F. cinerea* worker, which, after a few seconds of antennal contact, grasped the queen with palps and without any



Figure 1. Location of the nest of the mixed colony of *F. pratensis* + *F. cinerea* + *F. sanguinea* (old position of the main nest of subcomplex A of *F. cinerea*; Fpcs, the nest of the pure *F. cinerea* colony (Fc) and the nest of *F. sanguinea* (Fs) (photo W. Czechowski).



Figure 2. The nest of the mixed colony of *F. pratensis* + *F. cinerea* + *F. sanguinea* after the attack of *F. sanguinea* (the sticks mark the location of entrances, mostly revealed by the attackers) (photo W. Czechowski).



Figure 3. Dune habitat at Tvärminne: the location of the nest of *F. sanguinea* (Fs) and nest complexes of *F. cinerea* attacked and not attacked (Fc and Fc' respectively) by *F. sanguinea* (photo W. Czechowski).



Figure 4. A nest of *F. cinerea* superficially dug up by *F. sanguinea* (photo W. Czechowski).

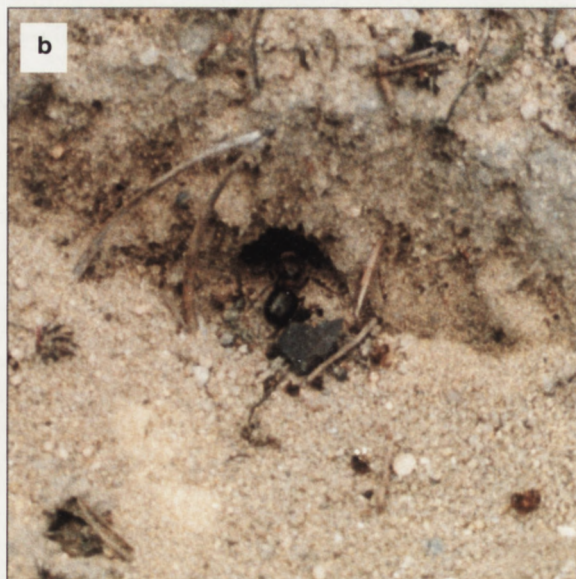


Figure 5. Nest entrance of *F. cinerea* sieged by *F. sanguinea* (a); a queen of *F. truncorum* managing to get inside the *F. cinerea* nest a few days later (b) (photo W. Czechowski); for details see Czechowski (1998).

sign of aggressiveness started to lead her into the nest, what the queen passively accepted. Suddenly, the *F. sanguinea* queen (and not the leading *F. cinerea* worker!) was attacked by a *F. sanguinea* ant. After a few second fight with the conspecific worker, the queen escaped from the raided *F. cinerea* nest complex area.

DISCUSSION

It does happen that *F. sanguinea* enslaves wood ant workers (Czechowski 1989, 1990a, 1994a,c, Czechowski et al. 1995). *F. pratensis* is the most common of such atypical slave species (see Czechowski 1996b). On the other hand, in the early myrmecological literature there are mentions of spontaneous adoptions of *F. pratensis* queens by orphaned *F. sanguinea* colonies (even without wood ants as slaves), leading to nest takeover by the offspring of the new queen (Rüschkamp 1913, Wasmann 1913, Donisthorpe 1915); for nonspecific queen adoption in mixed colonies of *F. sanguinea* see also Czechowski (1996a). Under laboratory conditions the queens of *F. pratensis* (like those of *F. rufa* L.) turned out to be more attractive to *F. polyctena* workers than conspecific queens; *F. polyctena* workers were even ready to kill their own queen and adopt the "odour dominant" queen (Gösswald 1983). Therefore the *F. pratensis* queens are strong usurpers. In the case of *Serviformica* ants, the natural victims of temporary social parasitism of wood ant queens, the actions are additionally facilitated by the disorganization of the host colony caused by the attack of dulotic ants. This was observed when studying the relations between *F. cinerea* (host species), *F. truncorum* (temporary social parasite) and *F. sanguinea* (dulotic species) (Czechowski 1998) (Fig. 5).

Bearing the above in mind, the origin of the mixed colony described in this paper is presumed to be as follows. A colony of *F. cinerea*, disorganized by the *F. sanguinea*, adopted a queen of *F. sanguinea*. This could have been facilitated by the *F. cinerea* workers directly or by *F. sanguinea* workers that were left behind. Leaving behind a group of *F. sanguinea* workers after invading the nest is a common practice, and it was shown that they are able to integrate with the slave species colony (Czechowski and Rotkiewicz 1997).

The possibility of adoption of a nonspecific queen by *F. cinerea* during the conflict with *F. sanguinea* (even without direct actions of the latter) is supported by the described episode with the *F. sanguinea* queen. The probability of adoption is increased by the orphan state of the raided colony. During the attacks of *F. sanguinea* the queens escape from the nests – of *F. cinerea* occasionally and very often in the case of *F. fusca* L. Moreover, some facts prove that the escape of the queen is the agent that disintegrates the colony and makes the *F. cinerea* workers carry out the pupae (Czechowski, unpublished data). Usually, the *F. cinerea* workers facing an invasion of *F. sanguinea*, do not carry out the pupae, but barricade themselves with the brood in the

far parts of the nest (Dobrzańska and Dobrzański 1962, Czechowski and Rotkiewicz 1997).

The *F. sanguinea* queen adopted by the mixed colony of *F. cinerea* + *F. sanguinea* (large workers) has had its offspring (small workers) probably in the same season. (Some *F. sanguinea* queens start egg-laying in their first year; Czechowski 1996a, b). Subsequently, in the next season, the queen, in unknown circumstances, must have been replaced by a *F. pratensis* queen.

It is worth noticing the change of intraspecific social loyalties of individuals caused by "passing over" of some of them from pure colonies to the mixed colony. It concerns both, *F. cinerea* and *F. sanguinea*, which under these circumstances became aggressive towards their old colony mates. This supports ideas related to the exchange and standardization of olfactory discriminators in the interspecific host-social parasite relations in ants (Czechowski 1990b, 1994b, Bonavita-Cougourdan et al. 1996, 1997).

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