POLSKA AKADEMIA NAUK MUZEUM I INSTYTUT ZOOLOGII

ANNALES ZOOLOGICI

Tom 44

Warszawa, 15 II 1993

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Replacement of species in red wood ant colonies (Hymenoptera, Formicidae)

[With 5 tables]

Abstract. There are reported cases of spontaneous changes in species affiliation of colonies within the *Formica rufa* group (*F. rufa* L. \rightarrow *F. polyctena* FOERST.) resulting from the adoption of foreign queens by orphaned workers. Thus it is shown that mixed colonies of these species can function temporarily, and this widens the knowledge about the ways of colony founding by their queens. The data were collected in the Gorce Mts. (the Western Carpathians) from 1985 to 1990.

INTRODUCTION

The original Linnean species *Formica rufa* L., 1761, and now the so called *F.rufa* group (red wood ants) still poses a taxonomic problem (Gösswald, Schmidt 1960b, Pamilo, VEPSÄLÄINEN 1977, PAMILO et al. 1979, ROSENGREN, CHERIX 1981). The situation seems paradoxical because there are no other ants studied for so long, with such intensity and under so many respects (COTTI 1963). The trouble is caused by great intraspecific and even intracolonial mutability, as well as by partly overlapping ranges of individual variability of particular taxa.

The *F. rufa* group includes: *F. lugubris* ZETT., *F. aquilonia* YARR., *F. rufa* L., and *F. polyctena* FOERST. (DLUSSKY 1967, VEPSÄLÄINEN, PISARSKI 1981). It is also extended, though this is groundless, to comprise the entire subgenus *Formica* s. str. (eg., BETREM 1960, KUTTER 1977).

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DESCRIPTION OF THE EXPERIMENTS AND OBSERVATIONS

The material for this paper has been provided by studies connected with the artificial colonization of *F. polyctena* in the Gorce Mts. (the Western Carpathians; southern Poland) (PISARSKI, CZECHOWSKI 1990a, b). They were carried out from 1985 to 1990 in the valley of the stream Jaszcze (Ochotnica Górna). The *F. rufa* group is represented there by *F. polyctena* and *F. rufa*. Their populations differ distinctly from one another in their habitat preference (PISARSKI, CZECHOWSKI 1990b, MABELIS 1988) and in the morphology of individuals (CZECHOWSKI, DOUWES, unpubl.), and also in the structure of societies (indubitable polygyny and potential polycaly of *F. polyctena*; presumed monogyny and exclusive monocaly of *F. rufa*). The distinct character of these taxa should raise no doubts (Table 1). Other ants of the subgenus *Formica* L. in the Jaszcze valley are represented by *F. truncorum* FABR. (in great numbers) and *F. pratensis* RETZ. (rarely) (MABELIS 1988).

Table 1. Morphometric characteristics of the populations of *F. rufa* and *F. polyctena* in the Gorce Mts.: A – relative size of the dark spot on the thorax [after the 6-degree scale of GõSSWALD and SCHMIDT (1960b)]; B – width of the head (mm); C – length of the thorax (mm); D – number of erecthairs on the bottom of the head; E – number of hairs on the occiput; F – number of hairs on the thorax [v – coefficient of variability (SD/ $\overline{x} \times 100\%$)]. [Material analysed: *F. nufa* – 330 workers (30 from each of the 11 colonies); *F. polyctena* – 930 workers (30 from each of the 31 colonies)]

Feature	Characteristic	F. rufa	F. polyctena	Difference
А	x̄ (± 1.96SE) SD υ	3.76 (± 0.15) 1.37 36.41	4.44 (± 0.06) 0.96 21.71	Highly significant $(P < 0.001)$ in each case (after
В	x SD υ	1.56 (± 0.02) 0.22 13.75	1.28 (± 0.02) 0.24 19.08	the Student t-test)
С	π SD υ	2.56 (± 0.03) 0.31 11.92	2.13 (± 0.02) 0.30 14.03	and were called as
D	π SD υ	5.24 (± 0.34)* 3.17 60.59	0.35 (± 0.07)* 1.04 293.82	
E	π SD υ	2.83 (± 0.25)* 2.33 82.39	0.45 (± 0.06)* 0.95 213.71	The original Prifa graup for Vision 1960
F	π SD υ	22.18 (± 1.01) 9.40 42.38	1.38 (± 0.17)* 2.64 191.00	CHERRY 1981)

* Due to the skew distribution of the variability of this character the value of the standard deviation (SD) and the calculations based on it (standard error, confidence interval, variability coefficient, level of the significance of the difference) are only approximate.

Replacement of species in red wood ant colonies

In laboratory experiments small groups of *F. polyctena* workers (up to several hundred individuals) readily accepted or at least tolerated queens of related species: *F. rufa, F. aquilonia, F. pratensis, F. truncorum.*¹ (Queens of *F. sanguinea* LATR. were, under identical conditions, attacked fiercely at once). That was the reason why some attempts (unsuccessful ones) were made to artificially create temporarily mixed colonies. In order to do this *F. polyctena* workers were in vitro brought together with queens of foreign species, the abundance of workers was gradually increased to about 1000 individuals (pupae were added, too) and then the entire colony was settled in the field.

In June 1986, two such colonies were produced: A-III – with 8 *F. rufa* queens and A-IV – with 1 *F. pratensis* queen. These colonies when transferred into their natural habitat changed their place of nesting several times. During removals, at least in the case of Colony A-IV, *F. polyctena* workers carried specifically foreign queens. At the end of July, both (mini)colonies escaped control and vanished. They must have died out soon afterwards. Maybe the queens, accepted under artificial conditions, had not been inseminated. They were young queens caught in the field after their nuptial flight. Most of such (already wingless) queens of red ants remain uninseminated (YAMAUCHI, CZECHOWSKI, unpubl.).

A colony that lived the longest was the experimental F-I formed when *F. polyctena* workers were provided with *F. aquilonia* queens brought from Finland (the species is a rarity in Poland). These were old (and therefore fertilized) queens obtained from a nest near Espoo on 1 July 1987. The initial group consisting of 8 queens and about 100 accompanying workers of *F. aquilonia* was supplemented with workers and pupae of *F. polyctena* during ten days from 5 to 16 July. There were no conflicts between the ants of the different species. On 17 July the colony was installed in the field; 5 *F. aquilonia* queens were living in the mixed swarm at that time. Colony F-I existed for one year, moving from one place to another, splitting and uniting. It died out in August of 1988.

The fact that the colonies described moved so often in the habitat imposed on them (it was *Calluno-Nardetum* overgrowing with spruces) indicated that the environment was not favourable for them. Moreover, not abundant "artificial" colonies have limited adaptable abilities. Therefore, the cause of the failure of the experiments was not univocal.

It soon became evident that the phenomenon which had failed when brought about experimentally occurred spontaneously in nature. This was proved thanks to constant supervision over the development of colonies founded (for various purposes) artificially, and to long-term observations of natural colonies in the study area.

In May 1987, under the same habitat conditions (on the edge of a pasture surrounded with a spruce-larch-beech forest) there were installed 5 colonies representing all the species and forms of the *F. rufa* group occurring in the Gorce Mts.: *F. rufa* (Colonies M-I and M-IV), mono- and polycalic *F. polyctena* (Colonies M-II and M-V, respectively), and also polygynous (!) *F. pratensis* (Colony M-III).

Interspecific adoptions within the F. rufa group have been shown experimentally by Gösswald (1953, 1957, 1960).

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They were founded according to the methods of artificial colonization used in the Gorce Mts. (PISARSKI, CZECHOWSKI 1990b). Both the habitat selected and the sites for particular nests proved to be suitable (only Colony M-III moved 10 m away from its nesting place to an open site). All the "artificial" nests have survived up till now (1991) in excellent condition, even producing sexual castes. However, no *F. rufa* can be found there. During the 1988 season (one year after the initial establishment) both colonies representing this species were converted spontaneously into colonies of *F. polyctena*. The natural colonies of *F. rufa*, maternal to Colonies M-I and M-IV (UB and T-IV, respectively) are still alive as typical representatives of the species (Tabs 2, 3).

Table 2. Morphometric characteristics (mean values) of the natural colony UB of *F. rufa* and derived from it "artificial" colony M-I after its transformation into *F. polyctena* (A-F – features as in Table 1). (Material analysed: 60 workers from either colony; data from 1989)

Colony	А	В	С	D	E	F
UB	4.88	1.50	2.33	1.53	2.12	21.08
M-I	4.13	1.43	2.14	0.00	0.05	0.00

Table 3. Morphometric characteristics (mean values) of the natural colony T-IV of *F. rufa* and derived from it "artificial" colony M-IV after its transformation into *F. polyctena* (A-F – features as in Table 1). (Material analysed: Colony T-IV₁₉₈₅ – 100, Colonies T-IV₁₉₈₉ and M-IV – 60 workers from each)

Colony	Year	А	В	С	D	E	F
T-IV	1985	2.45	1.52	2.62	5.68	3.25	22.14
	1989	2.38	1.67	2.57	4.00	2.22	22.95
M-IV	1989	4.97	1.46	2.10	0.00	0.03	0.00

In June 1989, Nests M-I and M-IV (both *F. polyctena* by then) were dug out. Their dimensions were: $M-I - \Phi = 1.1 \text{ m}$, h = 40 cm, $M-IV - \Phi = 60 \text{ cm}$, h = 30 cm. The former contained about 160 fertile queens and a huge amount of offspring. The latter had no queen, but since it contained (relatively few) larvae and pupae of workers it may be assumed that Colony M-IV was monogynic (one queen can easily be overlooked). Both colonies survived the total destruction of their nests and quickly rebuilt them near the old sites.

The above described cases of specific transformations of *F. rufa* colonies were initiated by the interference of man. But colonies may undergo changes of this kind even under entirely natural conditions. Such was the situation of Colony U-VI. In 1985-1987 it was a small colony of *F. rufa* occupying a nest whose diameter was 40–50 cm and height: 15–20 cm. In the autumn of 1988 this was spontaneously transformed into a colony of *F. polyctena* (Table 4). During the 1989 season the colony changed its nesting place and moved out of the open

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site, then settled under cover of dense shrubs. The dimensions of the nest built there were: $\Phi = 70$ cm, h = 30 cm (recorded in 1990). Colony U-VI was one of the 10 *F. rufa* colonies in the Gorce Mts. that were regularly inspected during the six-year studies.

Table 4. Morphometric characteristic (mean values) of the natural colony U-VI after its transformation into *F. polyctena* (A–F – features as in Table 1). [Material analysed: 60 workers; data from 1989. (No morphometric data for the period with *F. rufa*)]

A	В	С	D	E	F
5.20	1.08	1.79	0.25	0.68	0.67

A transformation into *F. polyctena* is one of the three possible ways in the development of artificially established (orphaned) colonies of *F. rufa*. Two other ways (biologically more natural) were revealed by the following experiment.

In mid-May 1989, the natural colony of *F. rufa* U-I was artificially divided into 3 parts. The underground part of the nest remained untouched but the entire mound with the dimensions: $\Phi = 80$ cm, h = 30 cm was removed and used as the foundation of two "artificial" nests: Y-I and Y-II. These were built about 1.5 km away from the maternal nest and at a distance of 200 m from each other in a habitat with no red ants. The ants left in Nest U-I managed to reconstruct the mound almost to its original size by the end of the same season.

Colony Y-I remained where it had been established and Y-II moved a few metres away after a month. This removal revealed an interesting detail in the biology of *F. rufa*. Both "artificial" nests contained young worker larvae and numerous pupae of sexual offspring. Alate queens emerged from the pupae in June (their flight took place in July). When Swarm Y-II moved to its new place about 20 June, almost all young queens (hundreds of them) remained in the old deserted nest. They spent there a week waiting to be transported – until the new nest was ready. During the first season the mounds of both new colonies reached the diameter of 70 cm, but there was a difference in their height: Y-I – 60 cm, Y-II – 20 cm. This was connected with the specific character of their habitat conditions. The former was situated in a shady and wet place, the latter in a sun-lit and dry one.

Both "artificial" colonies of *F. rufa* functioned very well in the spring of the following season. The first larvae emerged in both of them in May. In July, however, a difference was noticed. At that time the abundance of Colony Y-I decreased rapidly (most workers from the brood of the previous year had died out) and the larvae turned out to be males. They pupated in August and imagines emerged in September (in an almost dead nest). No new batch of workers reinforced the nest.

No noticeable change in abundance was manifested in Colony Y-II. New *F. rufa* workers emerged in July. Their emergence was accompanied by enlargement of the nest and a change in its shape. At the turn of July and August the flat mound was raised by 15 cm thus gaining a distinct top.

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Although belonging to the same species the workers from the new brood in Colony Y-II were morphologically different from their predecessors – they were darker, smaller and more hairy (Table 5). Colony U-I (a control one) retained its species affiliation and produced new broods – both workers and females – in 1989 and 1990.

Table 5. Morphometric characteristics (mean values) of the natural colony U-I of *F. rufa* and derived from it "artificial" colony Y-II after the adoption of a new queen(s) (A-F – features as in Table 1). (Material analysed: 60 workers from either colony)

Colony	Period	А	В	С	D	E	F
U-I	May, 1989	3.05	1.58	2.39	6.55	2.75	25.03
Y-II	July, 1990	4.82	1.39	2.26	6.98	2.45	49.00
	August, 1990	4.88	1.30	2.07	7.30	1.75	38.90
	September, 1990	5.22	1.24	1.99	6.30	1.95	37.50

The reason is obvious. Both "artificial" colonies lacked queens at the moment they were established. Colony Y-I was not able to adopt any queen and therefore died out. Prior to that, the queenless workers had started to lay haploid eggs – hence males. Colony Y-II on the other hand, adopted a young queen (or queens) during the following season and she (they) happened to belong to its own species. Due this the colony provided itself (?) a further existence.

DISCUSSION

Orphaned colonies of the *F. rufa* group are able to adopt young queens – belonging not only to their own but also to related species – that after their nuptial flight try to enter already existing nests. This, at any rate, can be done by *F. rufa* workers with *F. polyctena* queens. The phenomenon should be expressed in a different way though: it is *F. polyctena* queens who can easily invade orphaned colonies of *F. rufa*. WOYCIECHOWSKI (pers. comm.) is right when saying that during the so called adoption queens, and not workers, are the active party (with "generally" as the only reservation [W. Cz.]). Workers' orphanhood is a factor that lessens their natural hostility towards foreign queens, and apparently to a degree, which makes social parasitism even of a different species possible.

During the operation of artificial colonization of ants in the Gorce Mts. (PISARSKI, CZECHOWSKI 1990a, b) and the accompanying experimental work there were established dozens of *F. polyctena* colonies, 3 colonies of *F. pratensis* (a polygynic form) and 4 *F. rufa* colonies (described here). Two of the last colonies underwent species replacement. This poses three questions: 1) why did only *F. rufa* colonies undergo transformation?; 2) why did queens of an alien species more frequently win the competition for orphaned colonies (a target that was undoubtedly attractive to foundatrices)?; 3)how was it possible that numerous

F. polyctena queens were accepted by the orphaned swarm of F. rufa (M-I) descended from a colony that must have been permanently monogynous?The first point is clear. F. polyctena colonies in the Gorce Mts. are highly

The first point is clear. *F. polyctena* colonies in the Gorce Mts. are highly polygynous. In any case, such were those that provided the material for colonization. Large nests of *F. polyctena* from polycalic colonies may have contained even thousands of queens. Therefore it is highly probable that a certain amount of queens was collected together with the nest material and the "artificial" colonies had their own queens already at the moment of their founding (at least in most of the cases). The situation of *F. rufa* was quite different. Monocaly of the Gorce population and high mutual aggressiveness of colonies point to monogyny (or oligogyny at best) of the species. It was therefore highly improbable to obtain a queen together with some part of a given colony. The presumed monogyny of *F. rufa* in the Gorce Mts. is confirmed by the above described specific transformations of the "artificial" colonies and the natural one, and also by the fact that one colony died out without producing offspring – the phenomena occur when resulting from orphanhood of a swarm.

The second problem is probably connected with a difference in the reproductive potential of the local populations of *F. rufa* and *F. polyctena*. The total production of sexual castes in relatively small monocalic colonies of *F. rufa* is incomparably lower than that in a huge population of *F. polyctena*. Polycalic colonies of this species in the Gorce Mts. produce enormous amounts of queens every year. Thus, statistically, the success of *F. polyctena* is far more probable. Of course, the concept of the stochastic adoption of queens is based on the assumption that orphaned colonies lose their ability to select them.

The last question – the fact that *F. rufa* workers adopting foreign queens did not retain monogyny – is a difficult one. It is well known (taking *F. exsecta* NYL. as an example) that the social structure of colonies is not genetically conditioned and is liable to change when influenced by intracolonial or external conditions. The number of queens (one, several, many) encountered by orphaned workers all at once is a vital factor determining the gynic character of a colony (SKIBIŃSKA 1982). If the principles of adoption are similar to those in *F. exsecta*, then the social structure of a colony thus formed is decided by the number of queens that come into contact with workers simultaneously (i.e., within an appropriately short space of time). The abundance of the swarm adopting queens may also play some role (in the aspect of the worker/queen ratio). In comparison with colonies of ants of the subgenus *Serviformica* FOR. – the typical victims of temporary parasitism practised by queens of the *F. rufa* group – colonies of red ants have far more workers. Therefore (in theory), they are capable of adopting more queens than can be assimilated by *Serviformica* swarms, provided they do not exceed a certain critical value of the worker/queen ratio.

The above described species replacements simply manifest particular cases of colony founding in a dependent way. But maybe there is nothing special about it? Mixed colonies of the type *F. fusca* L./*F. rufa* are extremely rare. Even for experienced myrmecologists such discoveries are occasional cases in their long career (DOBRZAŃSKA, DOBRZAŃSKI, PISARSKI, pers. comm.). No mixed colony of this type was found in the Gorce Mts. during the six-year investigations (including

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myrmecofaunistic quantitative research) – in spite of the fact that red ants were abundant and *Serviformica* ants even more so. One such colony was encountered during intensive zoocoenological studies in moist pine forests (CZECHOWSKI, PISARSKI, unpubl.). Yet problems arising from the inexplicable intracolonial variability (including variability in time) within the *F. rufa* group are common (PAMILO, VEPSÄLÄINEN 1977, PAMILO et al. 1979). Maybe the very mixed colonies themselves are responsible for some of this trouble. [Another reason for hypervariability may be due to hybridization – cross-mating has been recorded in red wood ants (GÖSSWALD, SCHMIDT 1960, PAMILO et al. 1979)].

Orphaned colonies of red ants occur more often than it may seem. The moment the queen dies, each monogynous colony faces the following alternative: to die or to adopt a new queen. Groups of workers that are temporarily or permanently separated from their maternal swarm may also form the basis of a new colony (of the same or different species). That was recorded several times in the Gorce Mts. in the case of the monocalic colony J-I of *F. polyctena*, situated on one bank of a stream. When the water was low the ants foraged on the other bank where they got along branches placed across the stream. But rising water removed the "bridges" and made return impossible. Each time the workers cut off from their nest formed a minicolony and frequently changed their nesting place. As a consequence of this they disappeared from the field of observation (in one case the discovered route of the removal was about 200 m long). Such situations were repeated every year. These groups of workers had every possible chance to adopt queens, as was so often found out in the case of small experimental branches.

In the light of the facts presented here the adoption by orphaned swarms of young queens of their own or related species may be considered a natural mechanism that ensures the continuation of a given colony (the former case) and one of the natural ways of establishing new colonies (the latter case) in red wood ants.

APPENDIX

A possibility that colonies are founded by queens of red wood ants individually (independently) cannot be entirely excluded. The following observation points to this.

In 1985, an "artificial" polycalic colony H of *F. polyctena* was installed on Jaworzyna Kamienicka in the Gorce Mts. at 1250 m above see level in a newly made gap in the dense and vast spruce forest there (PISARSKI, CZECHOWSKI 1990b). At the beginning of July 1987, an experimental colony H-VIII of the same species was established in the same area and this nest contained about 100 old queens (obtained from nests of natural polygynic colonies). At the end of August a tiny nest ($\Phi = 6$ cm) of *F. polyctena* was noticed within the territory of Colony H. It was inhabited by few (not more than 10 individuals were seen at any given time) and very small ants – typical first workers of a newly founded colony. They never crossed the boundaries of the nest and the neighbouring ants had no contacts with them. This, and mainly the size of the workers, completely excluded any possibility that the young colony had come from any of the nests in Colony H. It was also impossible that the nest had been built through intervention of *Serviformica* ants – apart from the artificially introduced *F. polyctena* there were no other ants in this habitat. Foundatrices of *Formica lemani* BONDR, began to appear there much later; no colony of this (or any other) species had appeared in that area before 1990.

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The newly founded colony H-VIII changed its site several times, divided and united (queens were often transported), its nest was destroyed by a woodpecker. Under such conditions it was not difficult for a queen to get separated from the swarm by chance. The individual founding of the nest by such a solitary queen is the only possible explanation of the case described. The small colony disappeared after a fortnight – it may have been liquidated by the stronger swarm of it simply joined its neighbours.

It must be added that the queens used in the experiments were in their most fertile period (they laid masses of eggs). This distinguished them from freshly inseminated young queens that attempt to found their own nests just after the nuptial flight. The time when a solitary foundatrix waits for the emergence of the first workers was, in such a situation, much shorter and all the time there was no shortage of food (possibility of oophagy). On the other hand, the environment in which everything happened was far from optimum for red wood ants (PISARSKI, CZECHOWSKI 1990b).

If (!) independent colony founding by queens of red wood ants does indeed take place, then the chances of the foundatrices are undoubtedly enhanced by pleometrosis. Aggregations of queens of the *F. rufa* group after their nuptial flight were recorded by FOREL (1921-1923) and he ascribed to them some role in founding new colonies. However, this was before the knowledge on colony founding in a depended way became deeper. Nevertheless, such aggregations do occur. One consisting of over 100 dealate queens of *F. polyctena* was found under a stone in the Gorce Mts. in 1986. Unfortunately, its further fate is not known.

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> > STRESZCZENIE

[Tytuł: Przekształcenia gatunkowe mrowisk rudych mrówek leśnych (*Hymeno*ptera, Formicidae)]

Przy okazji prac nad sztuczną kolonizacją mrówek z grupy *Formica rufa* w Gorcach (Beskidy Zachodnie; 1985-1990) zarejestrowano 2 przypadki samoistnego przekształcenia się sztucznie założonych (w terenie) mrowisk *F. rufa* L. w mrowiska *F. polyctena* FOERST. oraz jeden przypadek, gdy takiej transformacji uległo mrowisko naturalne. Zmiany gatunku następowały w wyniku adopcji obcych samic przez osierocone roje. Spostrzeżenie to dowodzi istnienia mrowisk (przejściowo) mieszanych w obrębie grupy *F. rufa*, rozszerzając zarazem wiedzę na temat zakresu tymczasowego pasożytnictwa społecznego samic tych mrówek, zakładających nowe mrowiska metodą zależną.

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