POLSKA AKADEMIA NAUK
MUZEUM I INSTYTUT ZOOLOGII

ANNALES ZOOLOGICI

Tom 44 Warszawa, 15 II 1993 Nr 3

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Mixed colonies of red wood ants (*Hymenoptera, Formicidae*)

[With 8 text-figures and 5 tables]

Abstract. Two cases of the existence of permanently mixed colonies of *Formica polyctena* FOERST. + *F. rufa* L. were discovered and biometrically proved. They came into being thanks to secondary allometrosis. The data are from the Gorce Mts. (the Western Carpathians), collected there from 1987 to 1990.

INTRODUCTION

The previous paper presented evidence of the existence of temporarily mixed colonies of red wood ants that are formed as a result of adoption of *Formica polyctena* FOERST. queens by orphaned colonies of *F. rufa* L. (CZECHOWSKI 1991). Further analyses revealed the existence of permanently mixed colonies of *F. polyctena* + *F. rufa* due to the co-occurrence of queens of both species in one nest.

The material for the present paper has been provided by experiments connected with the artificial colonization of red ants in the Gorce Mts. (the Western Carpathians; southern Poland) (PISARSKI, CZECHOWSKI 1990a, b). They were conducted in the valley of the stream Jaszcze (the locality of Ochotnica Górna) from 1987 to 1990. It is beyond any doubt that the Gorce populations of *F. rufa* and *F. polyctena* are morphologically different from each other (Table 1).

Table 1. General morphometric characterization (mean values) of workers of the Gorce populations of *Formica polyctena* and *F. rufa*: A – relative size of the dark spot on the thorax; B – width of the head (mm); C – length of the thorax (mm); D–F – number of erect hairs on the bottom of the head (D), on the occiput (E) and on the thorax (F); in the case of each characteristic the differences between the species are statistically significant (after Czechowski 1991)

Species	A	B	C	D	E	F
F. polyctena	4.44	1.28	2.13	0.35	0.45	1.38
F. rufa	3.76	1.56	2.56	5.24	2.83	22.18

THE COURSE AND THE RESULTS OF THE EXPERIMENTS

Experiment 1.

In July 1987, two monogynous colonies of *F. polyctena* (E-I and E-II), earlier formed artificially in vitro, were installed in the study area. Each of them contained one fecund queen and several hundred workers from the polycalic colony S (Table 2). On the day they were established the colonies were supplemented with workers (about 10,000 to either) and pupae from another polycalic colony (J) of *F. polyctena*. Such an operation was repeated two days later. Ants of different origin were not aggressive to one another.

Table 2. Morphometric characterization (mean values) of *F. polyctena* workers from the polycalic Colony S and derived from it Colony E-II: A–F – characters as in Table 1.[Material analysed: S – 30 individuals from each of the 13 nests; E-II – 60 (1989) and 47 (1990) individuals]

Colony	Year	A	B	C	D	E	F
S	1985	4.20	1.23	2.11	0.09	0.40	0.91
E–II	1989	3.62	1.46	2.24	0.00	0.00	2.53
	1990	3.90	1.45	2.17	0.34	0.19	10.26

Colony E-I occupied their original nest during the first season and in winter. In June of the following year it moved about 12 m away and remained there as long as it lasted, although there were 3 short-lived, unsuccessful attempts to move away (Fig. 1). In autumn Nest E-I reached its maximum dimensions: Φ = 35 cm, h = 15 cm. The colony survived for 3 years and in spring 1990 it began to die out. The nest was dug out at the end of June 1990 and it contained about 300 workers, the remains of (one) queen and a small number of eggs and young larvae. Some workers had greatly enlarged abdomens. Dissection of 10 such individuals revealed egg production in 7 of them. Apparently, Colony E-I had been monogynous and died out following the death of its queen. It did not adopt any new queen even though young wingless females frequently appro-

ached the nest during the period of nuptial flights in 1988 and 1989. However, they faced aggression exhibited by the workers.

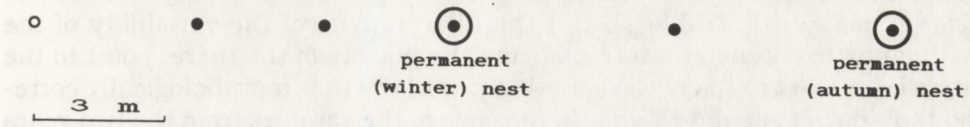

Fig. 1. Removals of Colony E-I (o - place of the nest foundation; • – trial nest).

Colony E-II was more mobile than E-I. It was situated on the edge of a gorge and during the first season of its existence it founded several linearly distributed nests. During the first two years they were alternately inhabited and deserted several times. The colony became relatively stable in summer 1988. Then two of its hitherto temporarily used nests attained to the status of permanent ones: E-II' (Φ = 40 cm, h = 20 cm) and E-II" (Φ = 30 cm, h = 15 cm) (Fig. 2). During 1988 and 1989 the former was basically used as the winter nest, although it was partly inhabited also in the summer of the following years. The latter, where the majority of the colony spent its vegetative season, was deserted for winter. In July 1990, the ants abandoned their separate summer nest (E-II") and moved to E-II', where they joined the rest of the swarm. During the whole period the observations were made the colony developed successfully and each year it produced numerous new workers.

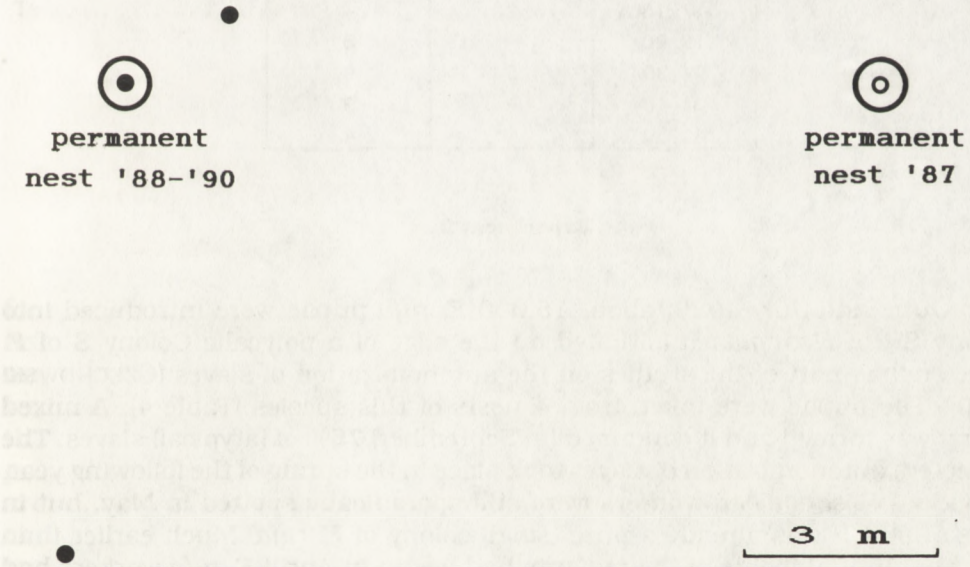

Fig. 2. Removals of Colony E-II (symbols as in Fig. 1).

In June 1989 and September 1990, samples of workers were taken from Colony E-II and a morphometric analysis of these was made. In each case the mean values of the characters analysed: colouration class, width of the head, length of the thorax, number of erect hairs on the bottom of the head, on the occiput, and on the thorax (Table 2) generally place this colony between *F. polyctena* and *F. rufa* (Table 1). But the distributions of the variability of the basic diagnostic character, and this being the pilosity of the there, point to the occurrence of two groups of workers there: workers that morphologically correspond to *F. polyctena* and *F. rufa*. In the case of the samples from the two years the distributions are asymmetric, more (1990) or less (1989) distinctly two-peaked (Table 3).

Table 3. Proportions (%) of workers with various degrees of the pilosity of the thoraxin Colony E-II during two years

No. of hairs	1989	1990
0	77	42
1, 2	3	13
3, 4	3	
5, 6	2	9
7, 8	3	2
9, 10	–	–
11, 12	5	2
13, 14	–	4
15, 16	–	–
17, 18	2	–
19, 20	–	6
21–30	5	9
31–40	–	9
41–50	–	4

Experiment 2.

In June and July 1989, about 15,000 *F. rufa* pupae were introduced into Colony SR of *F.sanguinea* (situated on the edge of a polycalic Colony S of *F. polyctena*) as part of the studies on the autonomization of slaves (Czechowski 1990). The pupae were taken from 4 nests of this species (Table 4). A mixed colony was formed and it contained (in September) 75% of (atypical) slaves. The (expected) autonomization of slaves took place in the spring of the following year. Individual *F. sanguinea* workers were still sporadically spotted in May, but in June 1990 SR was already a pure, small colony of *F. rufa*. Much earlier than that (the nuptial flights of the red ants had begun in April) *F. rufa* workers had started to adopt numerous young queens.

Table 4. Morphometric characterization of *F. rufa* workers from the nests that provided pupae (and the number of these pupae) introduced into Colony SR of *F. sanguinea*: A–F – characters as in Table 1. (Material analysed: UB – 60, the other colonies – 100 individuals from each)

Colony (no. of pupae)	A	B	C	D	E	F
UB (7,000)	4.88	1.50	2.33	1.53	2.12	21.08
U-VII (4,000)	2.48	1.54	2.75	5.78	2.64	18.61
T-II (2,000)	2.65	1.43	2.47	6.01	1.78	21.52
T-IV (2,000)	2.45	1.52	2.62	5.68	3.25	22.14

Nest SR was situated under a stone. One inspection on 12 June revealed over 30 queens of the *F. rufa* group and batches of eggs and larvae. In July there was mass emergence of pupae. The number of workers decreased considerably at that time, but this was due to the dying out of previous year's slaves. In August they were gradually replaced by emerging new workers – much smaller (the usual case in a young colony) and thus easy to recognize. The queens kept laying eggs all the time and even in September the nest contained huge numbers of young larvae.

Table 5. Morphometric characterization of workers from Colony SR: A–F – characters as in Table 1. (Material analysed: 100 individuals)

A	B	C	D	E	F
3.68	1.41	2.19	3.14	1.22	22.18

The mean values of the morphological characters (except the size) recorded for workers of a new brood (a sample taken on 19 September 1990) (Table 5) do not differ from those typical of the entire Gorce population of *F. rufa* (Table 1) and the colonies the slaves came from (Table 4). However, the distributions of variability of the analysed characters (pilosity in particular) show very clearly that the nest contained individuals with features of two species: *F. rufa* and *F. polyctena* (Figs 3,4). The high mean values recorded for Colony SR as a whole are due to the exceptionally abundant pilosity of workers belonging to the group corresponding to *F. rufa*, though essentially within the mutability range of this species (Figs 5,6). The pilosity of workers of the group corresponding to *F. polyctena* is typical of the Gorce population of the species (Figs 7, 8).

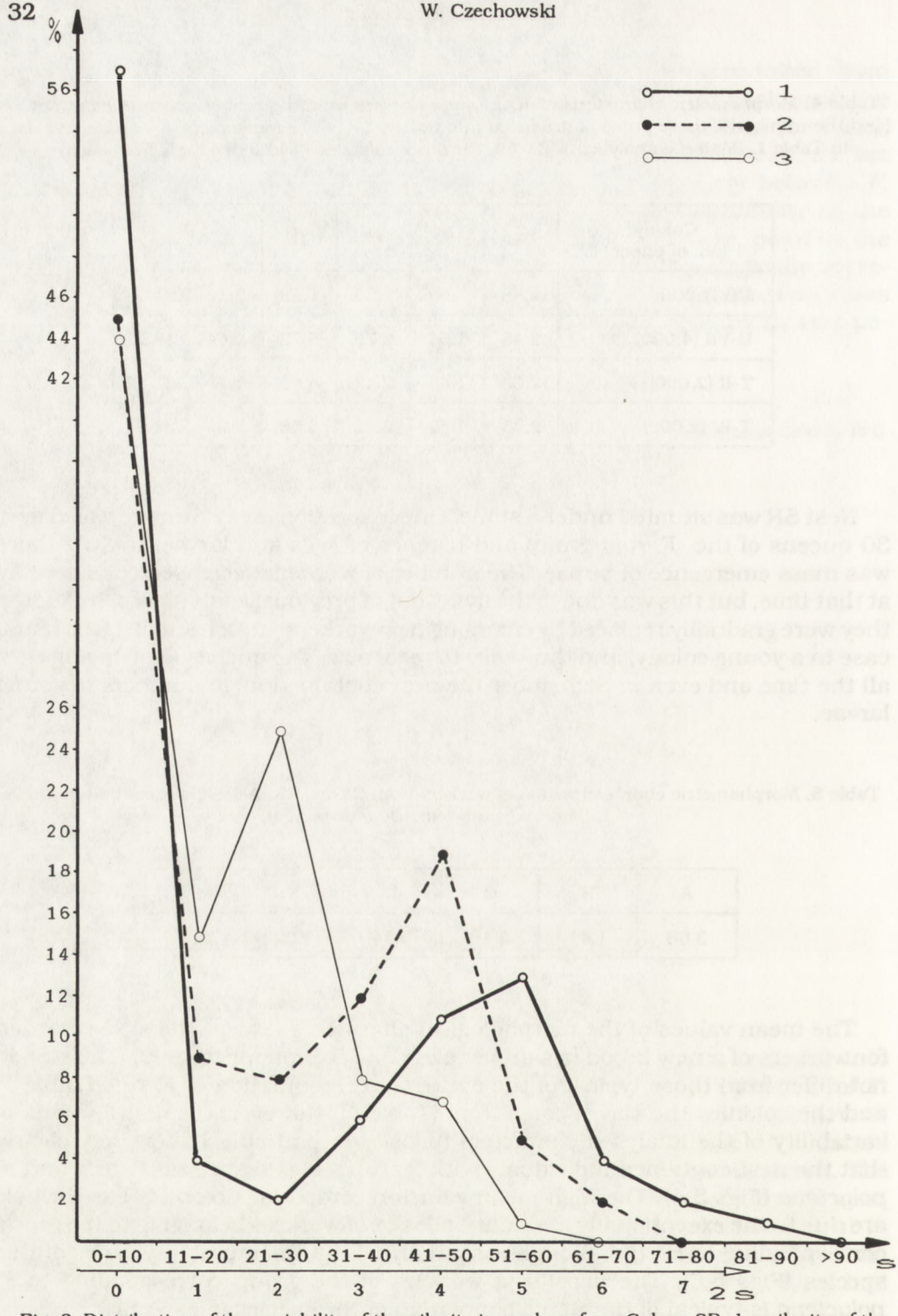

Fig. 3. Distribution of the variability of the pilosity in workers from Colony SR: 1 – pilosity of the thorex (scale s); 2 – pilosity of the bottom of the head; 3 – pilosity of the occiput (scale 2s) [% – proportion of individuals; s – number of hairs (ranges); 2s – number of pairs of hairs (odd values have been made up to even ones)].

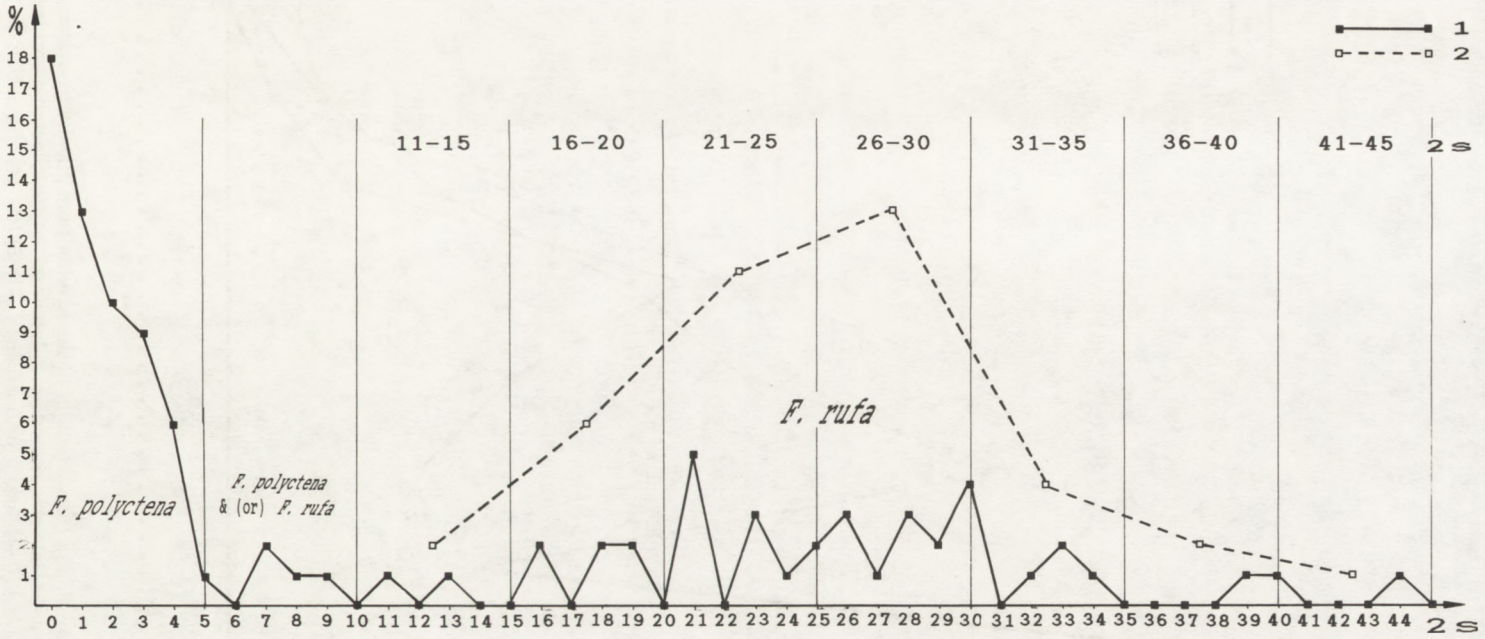

Fig. 4. Distribution of the variability of the thorax pilosity in workers from Colony SR: 1 – detailed diagram (lower scale); 2 – general diagram for the part corresponding to *F. rufa* (upper scale) [% – proportion of individuals; 2s – number of pairs of hairs (odd values have been made up to even ones)].

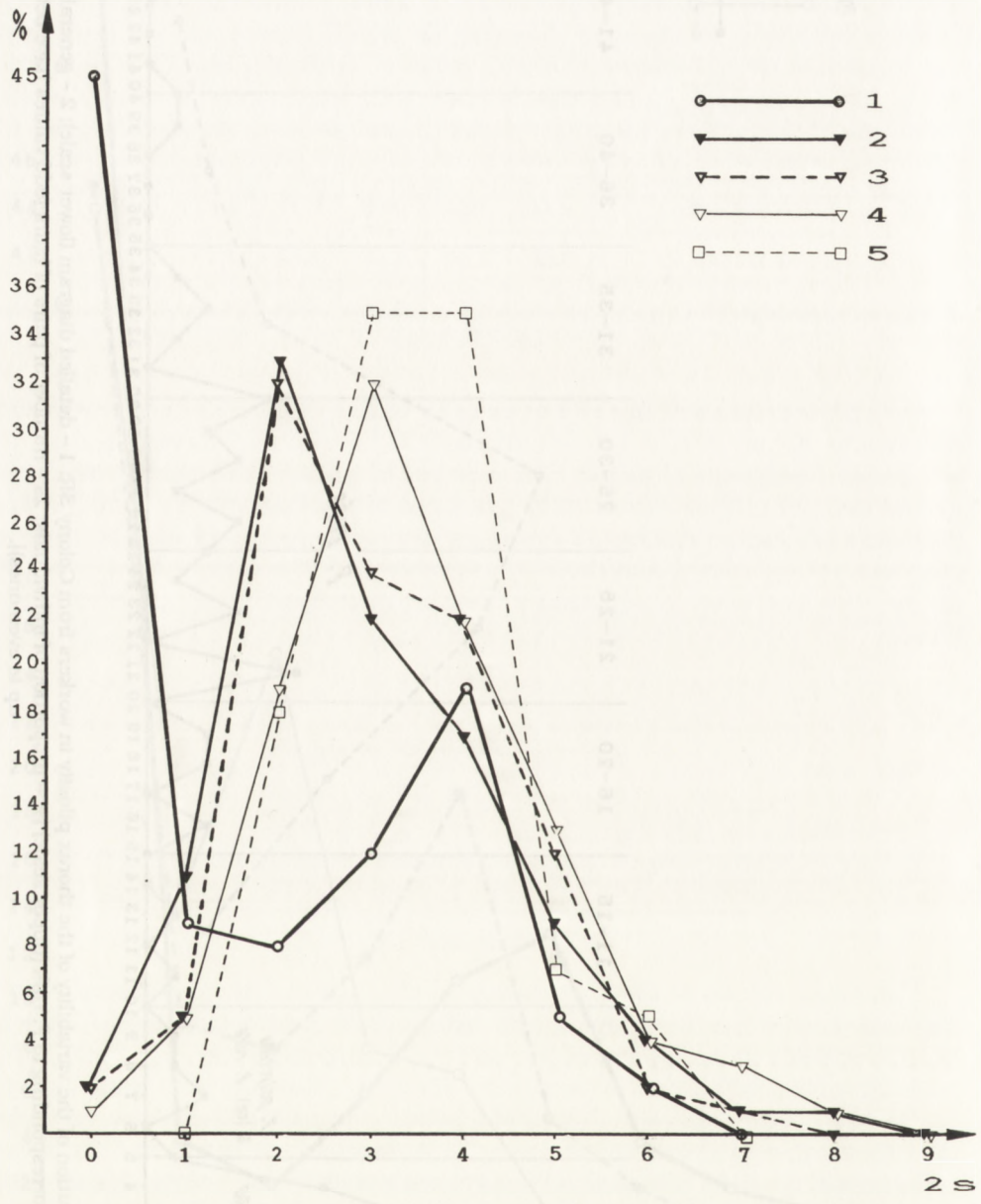

Fig. 5. Distribution of the variability of the head bottom pilosity in workers from Colony SR (1) in comparison with the same in mature colonies of *F. rufa* selected as an instance: Nk (2), T-II (3), U-VIII (4), and a young colony Y-II (5) (the other symbols as in Fig. 3).

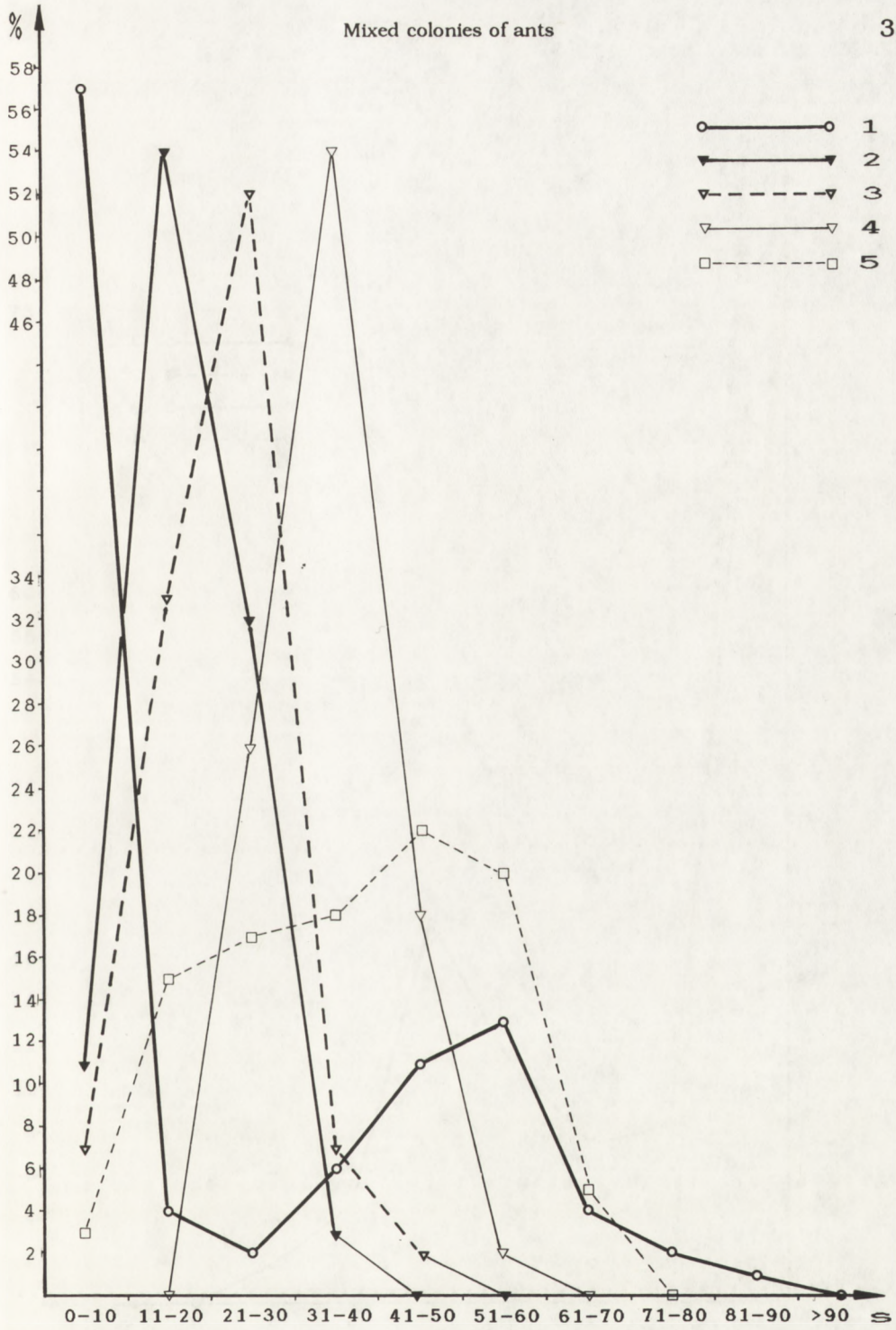

Fig. 6. Distribution of the variability of the alitrunk pilosity in workers from Colony SR (1) in comparison with the same in *F. rufa* colonies (2–5 – see Fig. 5) (the other symbols as in Fig. 3).

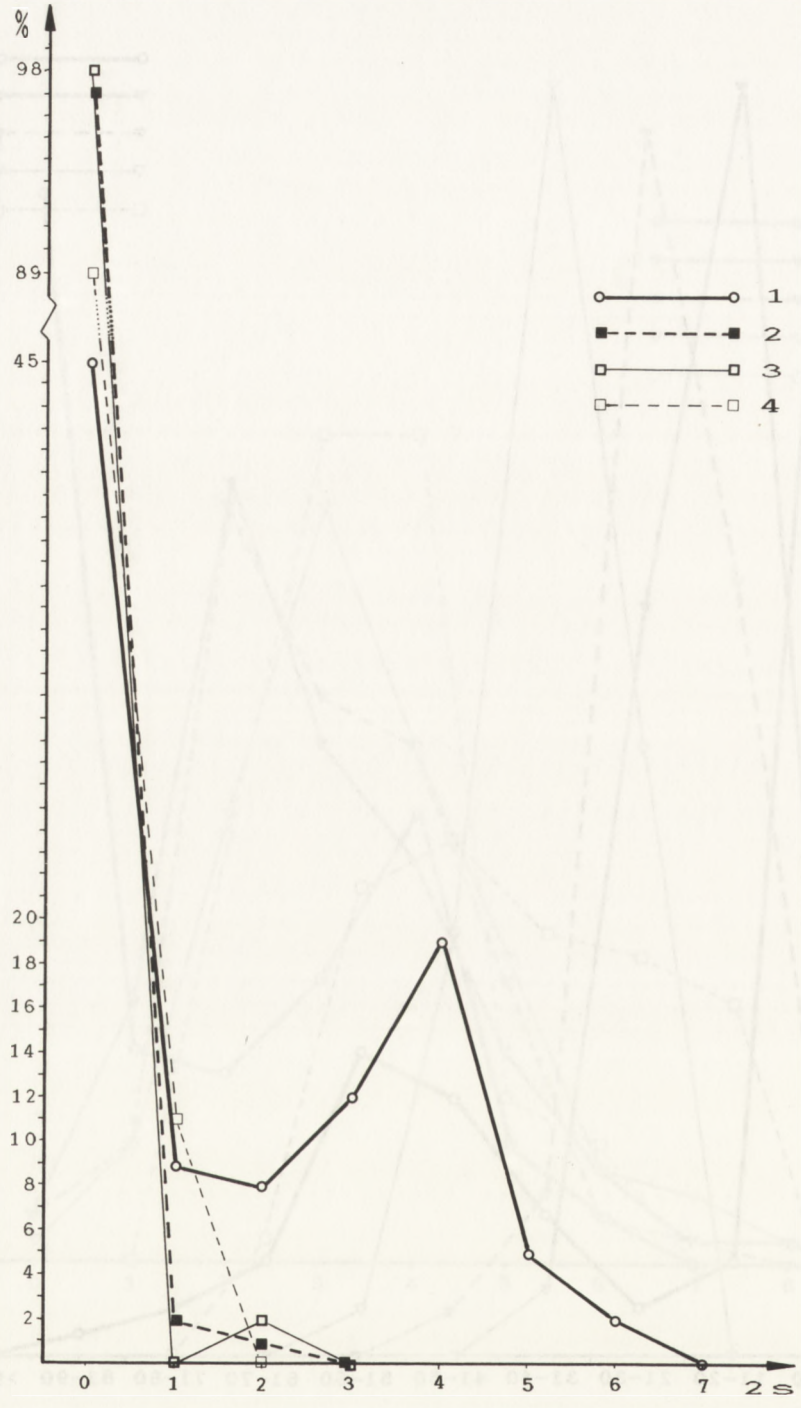

Fig. 7. Distribution of the variability of the head bottom pilosity in workers from Colony SR (1) in comparison with the same in *F. polyctena* colonies selected as an instance: S-VIII (2), S-X (3) and J-VIII (4) (the other symbols as in Fig. 3).

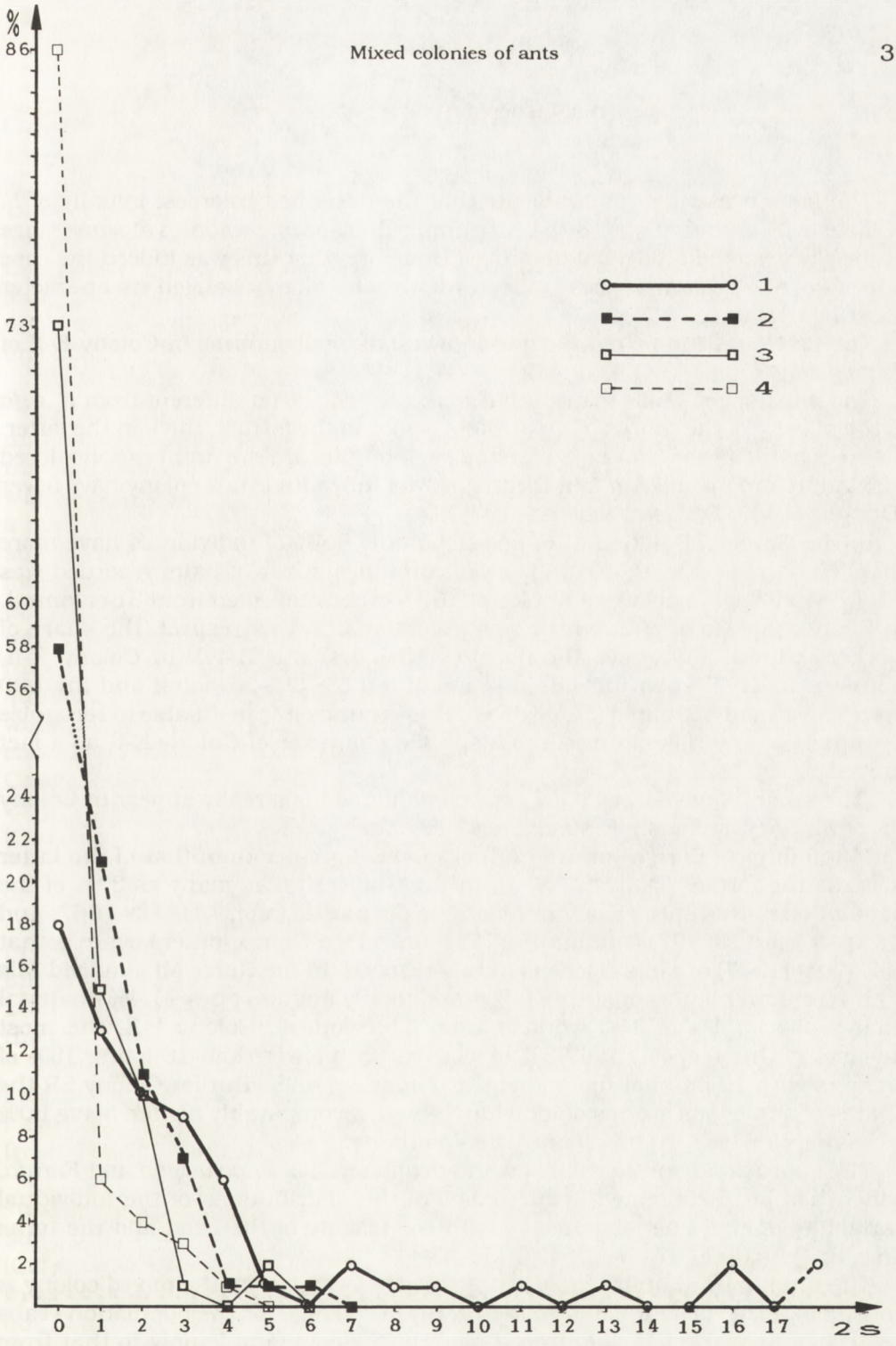

Fig. 8. Distribution of the variability of the thorax pilosity in workers from Colony SR (1; the initial part of the diagram) in comparison with the same in *F. polyctena* colonies (2–4 – see Fig. 7) (the other symbols as in Fig. 3).

DISCUSSION OF THE RESULTS

The facts presented here indicate that the described colonies, initially of *F. polyctena* (E-II) and *F. rufa* (SR), became mixed, bispecific colonies at some stage of their development. It must be proved therefore, that this was indeed the case and if so, the circumstances under which each colony changed its character must be explained.

The first question is: did *F. rufa* individuals really appear in Colony E-II of *F. polyctena*?

The most spectacular feature that makes *F. polyctena* different from *F. rufa* is the pilosity of the thorax of its workers – poor in the former, thick in the latter. 18 erect hairs on the thorax (3 pairs on each tergite) are the number considered maximum for *F. polyctena*, but the majority of individuals in a colony have fewer (DLUSSKY 1967, DLUSSKY, PISARSKI 1971).

In the Gorce population of *F. polyctena* only 0.4% of individuals have more than 18 hairs (> 20 – 0.1%, and the maximum number of hairs recorded was 22) (the material analysed: samples of 100 workers collected from 31 colonies). In (monocalic) Colony Kł, which was exceptional in this respect, the share of workers with hairy above the norm (> 18 hairs) was 3.4%. In Colony E-II, however, in 1989 such individuals constituted 5% (23–25 hairs) and in 1990 even 28% (up to 45 hairs!) (Table 3). On this grounds it is justifiable to recognize (with hardly any risk of error) the bispecific character of Colony E-II as a fact proved.

The second question is: did *F. polyctena* individuals really appear in Colony SR of *F. rufa* (previously *F. sanguinea* + *F. rufa*)?

Mutability of *F. rufa* towards *F. polyctena* is greater than that of the latter towards the former (DOUWES 1981). In the Gorce Mts. as many as 32% of the population of this species do not reach the diagnostic (after DLUSSKY 1967, and DLUSSKY, PISARSKI 1971) minimum of 18 hairs on the thorax [other keys, e.g. that of KUTTER (1977) are less rigorous in this respect]. In the Gorce Mts. individuals with 10 or fewer hairs constitute 8.5%, and totally hairless ones – 1.4% (material analysed: samples of 100 workers from 11 colonies). Colony P-II, the most atypical in this respect, had 38% of workers with fewer than 18 hairs, 16% of workers with 10 hairs at most, and 7% of hairless ones. But for Colony SR the shares of analogous groups of individuals were incomparably higher, being 60% (< 18 hairs), 57%(≤ 10 hairs) and 18% (no hairs).

The approximate proportion of workers (queens?) of *F. polyctena* and *F. rufa*, which has been estimated on the basis of the distributions of the individual variability of characters connected with the pilosity of the head and the torax (Figs 3, 4), is 60% (57–61%) : 40% (39–43%).

The unusually abundant pilosity of *F. rufa* workers from the mixed colony is conspicuous because it is far greater than the average for the population (Tabs 1, 5). In this respect *F. rufa* from Colony SR is comparable only to that from

Colonies U-VIII and Y-II (Figs 5, 6). At the time when the sample for the biometric analysis was taken, Colony Y-II[1] consisted of workers that were the first offspring of a young queen (queens) recently adopted by the orphaned swarm (CZECHOWSKI 1991). Thus, the case was identical with that of Colony SR. It may therefore be hypothesized that the first brood of young *F. rufa* queens look precisely like this. Certain data indicate that even in mature natural colonies of *F. rufa* in the Gorce Mts. there periodically occurs a replacement of "normal" workers by very hairy ones. This may reflect the situation when the old queen is replaced by a young one in these most probably monogynous colonies.

How did it come about that the mixed colonies described here were formed?

In the case of the initially monogynous colony E-II of *F. polyctena* the origin may be ascribed to a temporary, long-lasting fission of the swarm into two groups that nested separately and only one of these had a queen. The orphaned part was able to adopt its own queen (queens) during the time of nuptial flights. By a mere coincidence, a *F. rufa* queen was the one chosen (or it was among other adopted ones). Later, both parts of the colony merged before the offspring of the foreign queen could dominate its swarm. This fusion was possible because of prior permanent contacts and a presumed exchange of workers between the two nests. The queens of different species were tolerant of one another or the colony functioned as an oligogynous one (with spatial isolation within one nest of queens potentially aggressive to one another). Adoption of queens by groups of workers separated from their maternal swarm is one of the natural ways of colony founding practised by red wood ants (FOREL 1928, CZECHOWSKI 1991). Cases of interspecific adoption (in the nature of temporary social parasitism; [W. Cz.]) are possible here, and this has been recorded both during culture (GÖSSWALD 1953, 1957, 1960) and in nature (CZECHOWSKI 1991).

It may be assumed that the *F. rufa* queen entered Colony E-II in the spring of 1988 (during the season that followed its founding). A sample from June 1989 contained 5% of workers considered to be *F. rufa* and these were the queen's first, not very numerous, brood that had overwintered (it was too early for imagines from the second brood). A sample taken in September 1990 (at least 28% of *F. rufa*-like individuals) represented the third brood of the offspring of the foreign queen.

All these are only suppositions. But no definite solution would have been found even if Nest E-II had been dug out, because no morphological characters have been found that would make it possible to distinguish *F. polyctena* queens from *F. rufa* ones in the Gorce populations.

F. rufa workers from Colony SR remained orphaned for a long time, from the summer of one year to the spring of the following season. [In such cases *F. sanguinea* queens are killed soon after a colony has been dominated by the slaves (CZECHOWSKI 1992)]. In spring the nest was approached very frequently by young inseminated queens of red ants. In such situations workers, while selecting queens, are presumably guided by the principle of kin recognition. It is impos-

[1] Colony Y-II (founded experimentally) was not taken into consideration when the morphometric characteristic of the *F. rufa* population was being made (Table 1).

sible to find out why in this case, although faced with a possibility to choose, they adopted not only conspecific queens, but also some of an alien species. *F. polyctena* females may have appeared first (and surely in greater numbers, due to the proximity of the polycalic Colony S) and some of them must have been already within the nest, when *F. rufa* queens turned out – and these were also adopted.

Anyway, the fact is that queens of two related species settled side by side in one nest, accepted one another (and were accepted by the workers) and they succeeded in reproduction together.

Up till now, permanent mixed colonies within the genus *Formica* L. have been recorded only in North-American species *F. fossaceps* BUREN and *F. oreas comptula* WHEEL. (KING, SALLEE 1951).

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STRESZCZENIE

[Tytuł: Mieszane mrowiska rudych mrówek leśnych (*Hymenoptera, Formicidae*)]

Przy okazji badań nad sztuczną kolonizacją rudych mrówek leśnych w Gorcach (1987-1990) wykazano – na podstawie analiz morfometrycznych – istnienie dwóch mieszanych (dwugatunkowych) mrowisk *Formica polyctena* FOERST. + *F. rufa* L. W obu przypadkach mrowiska (pierwotnie jednogatunkowe) były utworzone eksperymentalnie, lecz dokooptowanie drugiego gatunku dokonało się w nich w sposób naturalny w drodze allometrozy wtórnej.

Mrowisko E-II zostało założone jako monoginiczne społeczeństwo *F. polyctena*. Adopcję obcej samicy umożliwił długotrwały podział roju na 2 części (jedna bez królowej), które następnie połączyły się. Udział robotnic *F. rufa* w tym mrowisku w trzecim roku jego istnienia sięgnął 28%.

Mrowisko SR, pierwotnie *F. sanguinea*, przekształciło się w wyniku autonomizacji (sztucznie wprowadzonych) niewolnic w osierocony rój *F. rufa*. Rój ten spontanicznie zaadoptował liczne samice dwóch gatunków. Ich pierwsze potomstwo było złożone z ok. 60% robotnic *F. polyctena* i 40% robotnic *F. rufa*.

Redaktor pracy – prof. dr hab. B. Pisarski