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Further Studies on Mixed Colonies in Ants

R. L. KING[1] AND R. M. SALLEE[2]

Abstract. Mixed colonies of ants (*Formica fossaceps* Buren and *Formica obscuriventris clivia* Creighton) offer unique opportunities to determine the extent to which two species living together share a single communal life. The proportion of workers of the two species present in a single colony differs from colony to colony but is relatively constant over periods lasting up to 16 years. Worker ants from four pure and from four mixed colonies have been measured with the scape as an index of size. The same size series of workers is found in pure and in mixed colonies, but the relative proportion of workers of different sizes in mixed colonies is similar within a given colony from year to year. In certain colonies the mean size of the two species is alike, but in others it is different. Whether these differences are trophogenic or blastogenic has not been determined.

In a series of papers the authors have published in these proceedings the results of studies on two closely related members of the fossaceps group of the genus Formica: *Formica fossaceps* Buren and *Formica obscuriventris clivia* Creighton. (1, 2, 3, 4, 5, 6). Although each of these usually lives in pure colonies, both species are occasionally found in a single colony. The mixed colonies, contrary to expectations, have remained mixed for periods up to 16 years. The workers of the two species are present in relatively constant proportions in a given colony, but the proportions differ from colony to colony. The figures for the eight mixed colonies surviving from those already reported (5), and for the six new ones found since 1956 are presented in the second part of this paper. In our second paper on mixed colonies (2) the following statement was made: "the same size series of workers of both species is present, but the proportion of workers

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of various sizes probably is different." Since that time many workers have been measured, from both mixed and pure colonies. The results are reported in the first part of this paper.

I. Size Distribution in Mixed Colonies

In our papers on winged workers (3, 4) we used the length of the scape of the antenna as an indication of the size of a worker. The right scape of each ant was removed, mounted under a cover glass, and measured with an ocular micrometer in a binocular microscope. One division was equal to 30 microns. The measurement was made from the funiculus to the neck of the bulb. More than twelve-thousand scape lengths are reported here; about one-fifth from pure colonies and four-fifths from mixed colonies. There are two sets of data from each of the mixed colonies; one set was made in 1954, the second set in 1959.

Percentages of ants were plotted against scape length to produce the graphs shown in the figures, where *F. fossaceps*, hereafter called "hairless," is represented by a broken line, and *F. o. clivia*, hereafter called "*hairy*", by an unbroken line. Workers were measured from two pure colonies of hairless, and from two pure colonies of hairy.

The results from the pure hairless colonies, G3 and 49F, are shown in Figs. 1 and 2, respectively. The mean scape length of workers from G3 is 52.3 divisions; that of 49F is 56.1 divisions. The means are significantly different far beyond the 0.001 level (t is 11.9 for 1546 d. f.). Figures 3 and 4 show the graphs from pure hairy colonies G2 and XW respectively. The mean scape length for G2 is 56.2 divisions; that for XW is 55.8. These might very well be samples of the same population (t is 0.2 for 705 d. f.). The graphs of both species are very similar to those reported for *Formica obscuripes* by King and Walters (7), in that they show a marked skewness to the right, as do samples we have collected from other species of the genus *Formica*.

Scapes of workers from four mixed colonies were measured, and the size distributions are shown in Figs. 5 to 12 inclusive. Colony G1 has been under observation for 12 years; during this time about 74% of its workers were hairless and 26% hairy. It has produced both hairless and hairy females, but only hairy males. Workers collected from this colony in 1959 are shown in Fig. 5. The mean scape length for hairless (broken line) is 55.1 divisions; for hairy (unbroken line) the corresponding mean is 50.6. The difference is significant beyond the 0.001 level ($t = 8.5$, for 672 d.f.). Figure 6 shows the ants collected from 1950 to 1953: the mean scape length for hairless is 57.2, that for hairy is 51.9 divisions. The difference between the means is also significant beyond the 0.001 level ($t = 18.0$ for 1681 d. f.). The

Figure Legends

In all figures the percentage of ants is plotted against scape length. The distribution of *Formica fossaceps* (hairless) is represented by broken lines, that of *Formica obscuriventris clivia* by continuous lines.

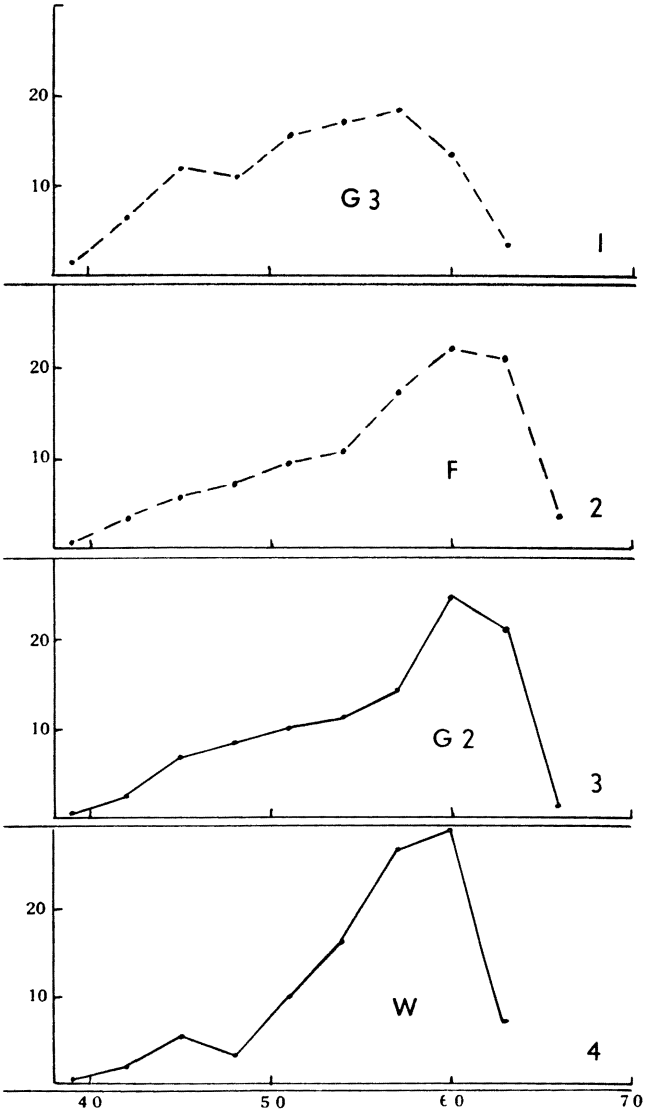


Figure 1. Distribution of 743 workers from pure hairless colony G3.
Figure 2. Distribution of 805 workers from pure hairless colony 49F.
Figure 3. Distribution of 430 workers from pure hairy colony G2.
Figure 4. Distribution of 277 workers from pure hairy colony XW.

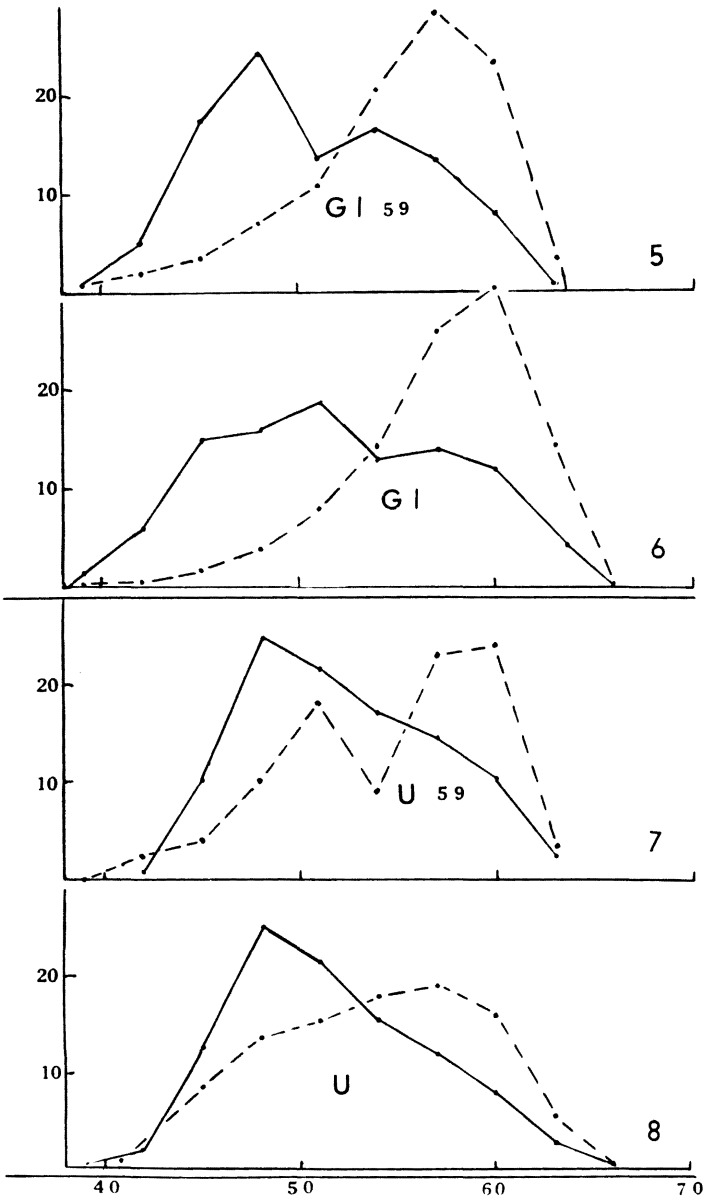
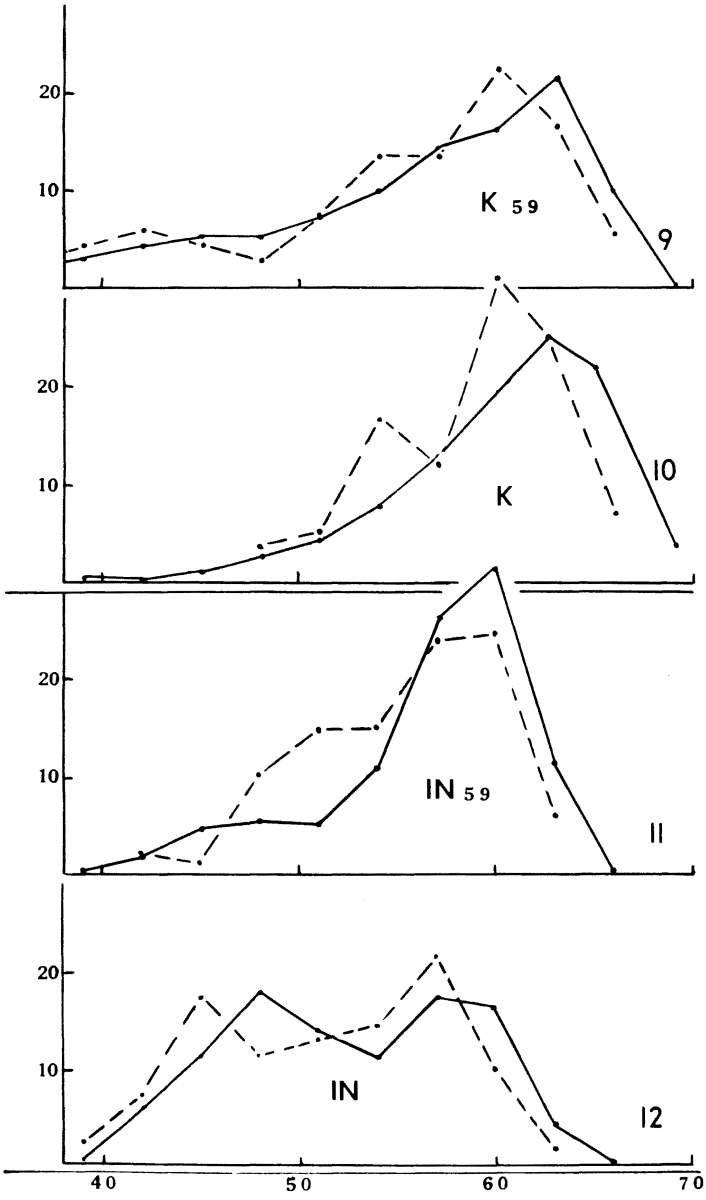


Figure 5. Distribution of 674 workers (498 hairless, 176 hairy) from mixed colony G1, collected in 1959.

Figure 6. Distribution of 1683 workers (1317 hairless, 366 hairy) from mixed colony G1, collected in 1950 to 1953.

Figure 7. Distribution of 644 workers (170 hairless, 474 hairy) from mixed colony XU, collected in 1959.

Figure 8. Distribution of 4925 workers (1437 hairless, 3488 hairy) from mixed



colony XU, collected in 1948 to 1952.

Figure 9. Distribution of 727 workers (67 hairless, 660 hairy) from mixed colony 48K, collected in 1959.

Figure 10. Distribution of 669 workers (84 hairless, 585 hairy) from mixed colony 48K, collected in 1948 to 1952.

Figure 11. Distribution of 363 workers (133 hairless, 230 hairy) from mixed colony IN, collected in 1959.

Figure 12. Distribution of 468 workers (220 hairless, 248 hairy) from mixed colony IN, collected in 1949 to 1951.

graphs in Figs. 5 and 6 show a remarkable similarity in that the hairless ants are larger than the hairy ones raised in the same colony. The distribution of hairless is like that shown for pure colonies of that species shown in Figs. 1 and 2; while the graphs for hairy are skewed to the left.

Colony XU has been under observation for 16 years; during that time about 25% of its workers were hairless and 75% hairy. The only sexual forms produced were hairy males. Workers collected from this colony in 1959 are shown in Fig. 7. The mean scape length for hairless is 54.7 divisions, for hairy 52.2. The difference between the means is significant beyond the 0.001 level ($t = 11.5$ for 642 d. f.). Figure 8 represents the ants collected from this colony in 1948 to 1952 inclusive: the mean scape length for hairless is 53.8, that for hairy is 52.6 divisions. The difference between the means is significant beyond the 0.001 level ($t = 5.6$ for 4923 d. f.). Here as in Figs. 5 and 6, the distribution for hairless ants in the mixed colony is similar to that in the pure colonies.

Colony 48K has been under observation for 14 years; during that time about 6% of its workers were hairless and 94% hairy. The only sexual forms produced have been hairy males. Workers collected in 1959 are shown in Fig. 9: the mean scape length for hairless is 55.2 divisions, for hairy 56.2. The t-number for the difference, in favor of hairy, is 1.0 for 725 d. f.; there is no difference. Figure 10 represents the ants collected from this colony in 1948 to 1952 inclusive: the mean scape length for hairless is 59.0, that for hairy is 60.4 divisions. The t-number for their difference, in favor of hairy is 2.3. This may be significant ($t\ 0.05 = 1.96$; $t\ 0.01 = 2.57$). The distribution of both species is similar to that in pure colonies.

Colony IN has been under observation for 16 years; during that time about 46% of its workers were hairless and 54% hairy. This colony produced both males and females of the two species. Workers collected in 1959 are shown in Fig. 11: the mean scape length for hairless is 55.4, for hairy 56.6 divisions. The t-number for the difference, in favor of hairy, is 2.06 for 361 d. f. The difference may be a valid one. Figure 12 shows the workers collected from this colony in 1949 to 1951 inclusive: the mean scape length of hairless is 51.5, that for hairy is 52.6 divisions. The t-number for the difference, in favor of hairy, is 2.00 for 466 d. f.; they may be different ($t, 0.05 = 1.96$, $t, 0.01 = 2.57$). The distribution of hairless and hairy is different in the new and old samples: for hairless the t-number is 5.89 for 476 d.f. in favor of the 1959 data also.

The dulotic habit (slave-making) is the usual explanation for

permanently mixed colonies in ants: the raiding columns of the slave-makers return to their own nest with larvae and pupae of the slave species. The mixed colonies studied here, however, are probably caused by the indiscriminant adoption of fertilized females belonging to a closely related species. The resulting colonies offer a unique opportunity to determine the extent to which two species living together share a single communal life. *Formica fossaceps* (hairless) seems to be at a disadvantage in these colonies as far as the production of sexual forms is concerned. *Formica obscuriventris clivia* (hairy) may sometimes be at a disadvantage as to the size development of the worker caste, at least in certain colonies.

In an ant community the differences among individuals may be under blastogenic or trophogenic control. Thus, the difference between females (queens and workers) and males are usually referred to genetic differences: the females hatch from fertilized eggs, the males from unfertilized. The differences among the females are thought to originate from nutritional causes. The metabolic environment of a mixed colony might be such as to affect the development of workers, or even be detrimental to the development of sexual forms. Males of hairy are found in all mixed colonies, and sometimes in colonies which seem to be pure hairless; males of hairless are found only in a few mixed colonies. Gosswald and Bier (8) have shown that the summer eggs of the small red forest ant normally develop into workers when raised by their own kind, but; if raised by the meadow ant (a different sub-species of *Formica rufa*), may result in queens and intercastes. It is quite possible that trophogenic factors might be more influential than blastogenic factors in one species than in another.

II. The Mixed Colonies.

The data for the eight old nests surviving from the 15 reported in 1957 (5) are listed in Table 1, together with those for the six new nests found since 1956. The table includes 22,402 workers (12,380 hairy and 10,022 hairless), 2,484 males (1,829 hairy and 655 hairless), and 1,067 females (373 hairy and 694 hairless). Together with those given in (5), we have identified 55,398 ants from the mixed colonies. The following summary of the total figures for the eight old colonies may be compared with the more recent data given here.

In nest M (found in 1947), all the workers and females have been hairless; all males hairy.

In NRW (found in 1955), 99.7% of the workers and all females have been hairless; 95.4% of the males hairless.

In GI (found in 1950), 74.1% of the workers and 64.4% of the

females have been hairless; 0.5% of the males (a single one) hairless.

Table 1. Mixed Colonies of ants observed at Iowa Lakeside Laboratory, 1957-1961.

	Workers			Males			Females		
	Hairy	Hairless	percent Hairless	Hairy	Hairless	percent Hairless	Hairy	Hairless	percent Hairless
Old Nests									
M (57-58)	0	118	100.0	..	..	..	0	9	100.0
NRW (57-60)	11	4015	99.7	6	279	97.9	0	193	100.0
GI (57-61)	819	1755	68.2	175	0	0.0	176	361	67.2
IN (57-61)	849	615	42.0	264	293	52.6	126	129	50.6
XU (57-61)	2044	568	21.7	591	0	0.0	..	..	..
MW (57-61)	1262	291	18.7	1	0	0.0	67	0	0.0
TB (57-61)	1856	288	13.4	96	0	0.0	4	2	33.3
48K (57-61)	2773	235	7.8	202	0	0.0	..	..	..
New Nests									
Mx (57-58)	448	373	45.4	396	83	16.9	..	..	..
LC (58-61)	636	102	13.8	..	..	..	..	..	..
MC (58-59)	342	201	37.0	..	..	..	..	..	..
SL (59-61)	1265	293	18.8	98	0	0.0	..	..	..
CRS (61)	22	1009	97.9	..	..	..	..	..	..
INa (61)	53	159	75.0	..	..	..	..	..	..

In IN (found in 1945, when it was pure hairless), 45.8% of the workers, 49.5% of the females and 52.9% of the males have been hairless.

In XU (found in 1945), 25.4% of the workers have been hairless and all the males hairy. No females present.

In MW (found in 1955), 20.2% of the workers have been hairless; all the females and males have been hairy.

In TB (found in 1955), 12.7% of the workers and 33.3% of the females have been hairless; all males hairy.

In 48K (found in 1948), 6.4% of the workers have been hairless; all the males hairy. No females present.

Data from nests IN and XU may exemplify the relatively constant proportions of hairless workers present over their entire history: in 1945 IN had only hairless workers; in 1946, 56.4% hairless workers; in 1948, 57.7%; 1949, 48.2%; 1950, 44.6%; 1951, 46.2%; 1953, 49.6%; 1954, 47.8%; 1955, 49.0%; 1956, 46.0%; 1957, 40.5%; 1958, 45.6%; 1959, 36.9%; 1960, 41.2%; 1961, 43.6%. XU was mixed when found in 1945, but no figures are available. In 1946, 38.2% of the workers were hairless; in 1947 28.5%; 1948, 41.3%; 1949, 27.9%; 1950, 23.4%; 1951, 27.6%; 1952, 22.2%; 1953, 22.3%; 1954, 20.8%; 1955, 26.2%; 1956, 21.6%; 1957, 24.2%; 1958, 18.3%; 1959, 29.7%; 1960, 18.4%; 1961, 13.2%.

Perhaps we should expect greater variation if the population of egg-laying females changes from year to year due to the death of old or the adoption of new females of one or the other species. For a consideration of the possible explanations of the mixed colonies see (5).

INa is a nest which probably originated by swarming from IN, but note that the percentage of hairless workers (75%) is quite different from that in the parent colony IN (42%). The mixed colonies are undoubtedly polygynous, with females of both species present but this explanation is hardly adequate.

Trials have shown that alate *Formica fossaceps* females are not rejected by small aggregations of *Formica obscuriventris clivia* workers, and vice versa. Small groups of workers of the two species from different colonies will also work out a peaceful *modus vivendi*.

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Spiders of Dubuque County

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Abstract. A collection of spiders, taken from Dubuque County and neighboring counties in 1961, consisted of representatives of 13 families and 54 species.

Between the years 1938 and 1944 a systematic collection of Iowa spiders was inaugurated by Karl Stiles and students at Coe College. In the interval between 1944 and the present, no published reports have been given on the distribution or taxonomy of Iowa spiders. Since the work of Stiles and his students was obviously incomplete, the author thought it worthwhile to add to this beginning in the classification and distribution of Iowa spiders.

METHODS AND MATERIALS

The spiders were caught during the spring, summer, and fall of 1961 in Dubuque and its neighboring counties. Most were caught by hand, since this afforded an opportunity for observation of the type of web, which was an aid in the classification of the spider. A sweep net was used to cover wide areas or inaccessible habitats as nettles or thistles. This usually obtained a

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