

Evidence of intercolonial food exchange in fire ants and other Myrmicinae, using radioactive phosphorus

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**Summary.** Food exchange occurred as an appeasement response in distant ant colonies of *Solenopsis invicta*, *S. geminata*, and *Pheidole dentata*. More regurgitated radioactive fluid was given to major workers than to minors by the donors from the alien colonies of these species.

Colony of a supervigorous<sup>2</sup>, territorial<sup>3</sup> and primarily monogynous<sup>4</sup> species, such as, the red imported fire ant, *Solenopsis invicta*, is not ordinarily expected to exchange food with its other colonies<sup>3,5</sup>. Yet this phenomenon of intercolonial food exchange seems to occur also in the indigenous fire ant, *S. geminata* and its ecological competitor, *Pheidole dentata*<sup>4</sup> when the donor of one colony is made to encounter the aggressors from the other more distant colony. These species otherwise fight<sup>4,6</sup>, and elicit interspecific food exchange to suppress initial aggression and to escape<sup>7</sup>. The ant colonies were collected from 100 to 325 km apart areas in Florida, thus providing enough isolation. The major and minor caste donors of a colony of one species were fed on radioactive sucrose solution and made to confront the aggressive solicitors of the other (1 donor: 4 solicitors) in 1.5 cm diameter glass cells, using the technique described earlier<sup>7</sup>. The solicitors oriented towards the donor ant, contacted its antennal flagella with theirs and opened mandibles to seize and bite its body parts in aggression. The donor regurgitated a droplet of fluid between its mandibles and held it towards the aggressive workers from the alien colony in offering fashion, a response that suppressed aggression and provoked feeding and solicitation in them. The donor offered the regurgitate for 15–60 min on even a slight antennal contact at its antennal scapes by any approaching solicitor. The fed workers groomed themselves, a pause that would make the donor's escape possible in nature. When no food was offered on solicitation, the aggressive frenzy (seizing, pulling, stinging, and so on) in the alien workers intensified and the donor was dismembered or killed, especially in *P. dentata*. The donor's food-offering behaviour was different

towards the solicitors of its own colony. The solicitors followed the donor and groomed its thorax, femurs of legs, lateral and ventral portions of head, antennated its head vigorously and were then fed for 5–25 sec, singly or in groups of 2–3. They were warded off by the donor with vigorous antennation (distress signal), turning away from them during subsequent food solicitation. Evidently, the food-offering behaviour towards the alien colony workers in suppressing their aggression by masking the colony odour with ingluvial food odour, was at par with the appeasement behaviour in higher animals. Intercolonial food transfer is apparent in nature during accidental territorial confrontations<sup>3,8</sup>, and in more compatibly nesting ants<sup>9–11</sup>. Immediately following feeding, the minors reduced their food reserve by offering the regurgitate to sister majors, or expelled it in droplets on the substratum, a phenomenon that indicated the nonstoring function of their crops. The majors acquired food from the minors and also themselves fed in several intervals (each ranging from 3 to 8 min) without vomiting, indicating the first evidence of repletion which is characteristic of the majors in *Solenopsis*<sup>12</sup> and *Pheidole* species. The minor donors transferred food readily, regardless of the solicitor's caste (or species<sup>7</sup>), while the majors transferred it more to the majors than to the minors of the alien colonies (table). Few aggressive solicitors received food repeatedly, while the others showed diminished aggression by keeping their mandibles merely open; later they seemed to accept food in small amounts. The minors of *S. invicta*, *S. geminata* and *P. dentata* are similar in size (3.2 mm) and the majors in the former 2 species are larger (7.5–7.7 mm) than those of *P. dentata* (3.5–5.5 mm). The largest major workers in the polymorphic *Solenopsis* species were thus readily sorted by letting

Food exchange in ants from distant colonies expressed in terms of transfer of radioactivity from the donor of one colony to the recipient of other colony

Donor species and caste Colony 1	Recipient species and caste Colony 2	Radioactive ants per ants exposed in all replicates	Mean c.p.m. in donors	c.p.m. radioactivity per recipient Mean	SD
<i>Solenopsis invicta</i>					
minor	minor	16/16	6974.50	773.27	823.24
minor	major	15/16	7688.00	632.69	702.43
major	minor	16/16	24910.50	814.06	528.32
major	major	14/16	19063.50	1877.43	2160.93
<i>Solenopsis geminata</i>					
minor	minor	16/16	6518.00	205.19	255.59
minor	major	16/16	7422.50	93.75	62.51
major	minor	15/16	11346.50	112.27	22.47
major	major	16/16	12973.50	269.94	207.12
<i>Pheidole dentata</i>					
minor	minor	12/12	3888.00	106.58	90.06
minor	major	12/12	1102.00	289.17	189.27
major	minor	12/12	5768.00	37.75	27.49
major	major	12/12	1559.50	267.17	166.94

Colony 1 and 2 were from Tallahassee and Tampa in the case of *S. invicta*, from Tallahassee and Jacksonville in the case of *S. geminata*, and from Tallahassee and Gainesville in the case of *P. dentata*, respectively. Food distribution from donor to recipients, and secondarily among recipients, was not normal. High SD was due to some workers receiving food repeatedly while others received only small amount. Experiments were conducted at 28°C, repeated 3 or 4 times, and the exposure of one donor to 4 aggressive solicitors in each replicate was 1–5 h.

all the intermediate and small-sized workers pass through a glass tube, slightly smaller than the major's thorax (2.5 mm in diameter). The caste specific difference in appeasement food transfer seems to be due to differential aggressive element present in the largely defensive majors over minors<sup>4</sup>.

The regurgitate odour seems to mask the hypothetical alien colony odour<sup>4</sup>, which is said to be derived partly from food and nest material<sup>13,14</sup> and partly from genetic make up of the colony<sup>15</sup>. It may itself be regarded as a substance

analogous to surface pheromones, with specificity range slightly above that of colony or even species odour, in space and time. Further specification of such 'trophic pheromones' possibly makes the symbiotic association between phylogenetically and behaviourally related species<sup>4</sup> possible. While territoriality may be important in the survival of a colony, intercolonial trophallaxis seems vital for the survival of species population as a whole. In such species, the use of radiotracers in demarcating the boundaries of their colonies should be cautioned.

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## Comparison of the biological effects of anemia inducing and polycythemia inducing Friend virus complex<sup>1</sup>

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**Summary.** The comparison of the biological effects of FV<sup>P</sup> and FV<sup>A</sup> showed that leukemogenesis appears to be delayed in FV<sup>A</sup> infected mice as compared to FV<sup>P</sup> infected animals after injection of comparable quantities of virus as measured in spleen focus forming units. In addition, no CFU-EI, characteristic for FV<sup>P</sup> induced leukemia, were found in leukemic spleen or bone marrow of FV<sup>A</sup> infected mice. Since it was possible to distinguish both viruses by their different host ranges, which are helper virus determined, it is suggested that the observed differences, especially the lack of CFU-EI in FV<sup>A</sup> infected mice, might be due to differences in the helper virus component of the FV complex.

**Abbreviations:** CFU-E, colony forming unit-erythroid; CFU-EI, colony forming unit-erythroid (erythropoietin independent); Ep, erythropoietin; FFU, focus forming unit(s); FV, Friend virus complex; FV<sup>A</sup>, anemia inducing Friend virus complex; FV<sup>P</sup>, polycythemia inducing Friend virus complex; LLV-F, Friend helper virus; SFFV, spleen focus forming virus.

The Friend virus complex (FV) consists of a replication defective transforming component, the spleen focus forming virus (SFFV) and a helper virus, which is a murine lymphatic leukemia virus (LLV-F)<sup>4-9</sup>. 2 basic strains of FV are known, the original isolate of C. Friend<sup>10</sup>, which causes anemia (FV<sup>A</sup>) and the polycythemia inducing Friend virus (FV<sup>P</sup>), which was isolated by Mirand et al.<sup>6,7</sup>. This virus causes an Ep-independent polycythemia in mice<sup>7</sup>.

Since the development of polycythemia after infection with FV<sup>P</sup> is Ep-independent, that is, non-suppressible by hypertransfusion, the suggestion was made 'that the virus can induce the commitment of erythroid precursor cells independently of erythropoietin'<sup>11</sup>.

More recently this was shown to be the case<sup>12,13</sup>, since Ep-independent erythroid precursors (CFU-EI) were found in FV<sup>P</sup> induced-leukemia. Therefore we asked the question whether CFU-EI are also present in FV<sup>A</sup>-induced leukemia, the anemia being a secondary phenomenon only. Our results show that CFU-EI are absent during FV<sup>A</sup>-induced

leukemogenesis. Therefore the generation of CFU-EI is unique for FV<sup>P</sup>. FV<sup>A</sup> on the other hand seems to be more closely related to Rauscher virus with respect to its biological properties<sup>14,15</sup>.

**Material and methods.** Virus. The N tropic variant of the polycythemia inducing strain of FV (FV<sup>P</sup>) (obtained by courtesy of Dr R.A. Steeves) and the original isolate of C. Friend (obtained by courtesy of Dr W. Ostertag) were grown in DBA/2 mice. FV<sup>P</sup> was a spleen focus forming N tropic virus and FV<sup>A</sup> a spleen focus forming NB tropic virus as determined in the spleen focus test<sup>4</sup> using DBA/2 and BALB/c mice for the comparison of the host range of both viruses.

Mice. DBA/2 and BALB/c mice were either from Gl. Bomholtgaard, Ry, Denmark or Zentralinstitut für Versuchstierzucht, Hannover, Germany. For the purpose of virus infection DBA/2 mice received an i.v. injection of  $1-2 \times 10^4$  FFU of FV<sup>P</sup> or about  $1 \times 10^4$  FFU of FV<sup>A</sup>.

**CFU-E assay.** The method described by Iscove<sup>16</sup> was used. 0.8% methylcellulose, 30% fetal calf serum, EP Step III (Connaught Laboratories), 0.2 units/ml, athioglycerol at an end concentration of  $10^{-4}$  M and bone marrow or spleen cells in the  $\alpha$ -modification of Eagle's medium were mixed. 4 parallel petri dishes with 1 ml of medium and  $3 \times 10^5$  cells were set up and incubated for 48 h at 37 °C in a humidified atmosphere containing 5% CO<sub>2</sub>. CFU-EI were quantified in