

INTERSPECIFIC TROPHALLAXIS IN ANTS,  
ITS ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE

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SUMMARY

Interspecific trophallaxis or ingluvial liquid food exchange between certain species of ants is prevalent at intergeneric and intertribal level in neotropical and nearctic Myrmicinae and palearctic Formicinae. Radiotracer studies on the workers and reproductives of *Formica*, *Lasius* and *Camponotus* species in Central Europe and observations on the confrontation behavior of *Solenopsis invicta*, *S. geminata*, *Pheidole dentata* and *P. morrisi* at the methylene blue-dyed sucrose baits in the fire regenerated habitats in Florida brought out the occurrence of food exchange between their colony members. This behavior may indicate the coadaptation in ants, regardless of their nesting in similar or distinctly different habitats or geographical regions, should certain species confront one another. The evolutionary significance of interspecific trophallaxis in relation to social symbioses is discussed.

ZUSAMMENFASSUNG

**Interspezifische Trophallaxis bei Ameisen, ihre ökologische  
und entwicklungsgeschichtliche Bedeutung**

Interspezifische Trophallaxis oder Austausch von flüssigem Kropfinhalt zwischen bestimmten Arten, Gattungen und Tribus von Ameisen ist weit verbreitet bei gewissen

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neotropischen und nearktischen Myrmicinae sowie palaarktischen Formicinae. Untersuchungen mit radioaktiven Markierungssubstanzen an Arbeiterinnen und Geschlechtstieren von *Formica*, *Lasius* und *Camponotus* Arten Zentraleuropas und Beobachtungen des Konfrontationsverhaltens von *Solenopsis invicta*, *S. geminata*, *Pheidole dentata* und *P. morrisoni* an Methylenblau gefärbten Sucrose-Ködern in feuer-regenerierten Habitaten Floridas ergaben eine interspezifische Trophallaxis zwischen den Mitgliedern ihrer Kolonien. Sollten sich gewisse Arten einander begegnen, so läßt dieses Verhalten auf eine Koadaptation bei Ameisen schließen, ungeachtet ihres Vorkommens in gleichen oder völlig unterschiedlichen Lebensräumen und ihrer geographischen Verbreitung. Die entwicklungsgeschichtliche Bedeutung der interspezifischen Trophallaxis bezüglich sozialer Symbiosen wird diskutiert.

## INTRODUCTION

Ingluvial exchange of food beyond a colony or species level, especially in non-symbiotic species of ants, has not received enough attention. Stray observations by earlier workers neither document the phenomenon per se nor include the behavioral repertory of the species in question. Kutter (1964) noted food exchange between *Lasius fuliginosus* and several species of *Formica* (*exsecta*, *fusca*, *truncorum*, *rufa*, *pratensis*) by interconnecting their colonies to form so called «alliance» colonies in an arena. Gösswald and Kloft (1960) observed the transfer of radioactivity from *L. niger* to *L. flavus* workers when the former carried  $^{32}\text{P}$  mixed honey water. Bhatkar (1973) documented a delay in colony invasion when *Solenopsis invicta* was confronted to the food carrying workers of *Pheidole dentata* or *P. morrisoni*. Near the nest entrance these latter species offered food to *S. invicta*, and the major workers received more food than the minors when any one of these species was a donor (Bhatkar and Kloft, 1977). Among symbiotic species, the dulotic species seem to be dependent on their hosts for feeding, and less so the temporarily parasitic species (Gösswald and Kloft, 1960 ; Beck, 1961). Interspecific food exchange seems to be occasional in xenobiotic species, such as *Formicoxenus nitidulus* and *Formica* spp. (Wheeler, 1910 ; Stumper, 1950), and parabioc species, such as *Camponotus femoratus* and *Crematogaster limata parabiocica* (Wheeler, 1921 ; Swain, 1980). Here, I report the prevalence of interspecific food exchange beyond specific, generic and tribal level in the subfamilies Formicinae and Myrmicinae, with special reference to non-symbiotic species, occurring in ecologically similar and distinct habitats and discuss the evolutionary significance of the phenomenon. Comparative investigations on the members of two major subfamilies of ants in two geographical areas are discussed below.

## MATERIALS AND METHODS

The comparative investigations involved two sites, the Tall Timbers Research Station, Tallahassee, Florida during 1973-75 and the Institute of Applied Zoology, Bonn during 1975-1977. The ants involved contained neotropical and nearctic species in Florida and palearctic species in Central Europe. The direct observations were given more weight over supplementary quantitative data on indirect observations.

### Baiting experiments

Annually burned, regenerated, 0.2 hectare square plots, containing some tall trees and annual vegetation in North Florida, were baited along their diagonals at 5 m distant 10 sites. For this, cotton wicks, about 3 cm in length and 0.5 cm in diam (Dispo, Scientific Products, Illinois), were soaked in 20 % sucrose solution and placed individually at the bottom of the 17 x 7.5 cm wire-rimmed Whirl Pak (Nasco) plastic bags. The aqueous sucrose solution contained 5 % methylene blue as a tracer and it could be seen in the fed ants and in the ants that acquired food secondarily from the fed ants by squashing them on pieces of blotting paper. The bags were laid horizontal with their wired rims separated open and observations were made by periodically walking from each bait site for about 6 h. Three such 150-200 m distant plots were baited at the study site. Once the ants of one species recruited to food, close behavioral observations on the next species recruited continued at the same site. The wick was now separated from the 2nd species in the bag by placing a heavy metal rod beside the wick but over the bag. This seemed not to markedly change their behavior. Usually several cases of food transfer between the species in contest occurred within first 20 min. After this the ants were immediately killed with chloroform, and bags were sealed by pulling the wires close and folding three times. Only the ants in the front one-half of the bag were sampled by squashing.

### Colony confrontation experiments

A vertical, centrally partitioned, 40 cm wide, 30 cm high double plastic sheet-nest was used for these studies. It provided 17 x 29 x 0.4 cm nesting space for each of the two species. The top of the nest was sprayed with Fluon (ICI America) to prevent ant escape. The bottom was perforated and held under water up to 4 mm so that the soil within the nest absorbed moisture. Two partitions of the nest could be connected to the ant colonies, reared in 20 cm diam, 3 cm high (18 cm diam, 1 cm high, inner dimensions) Wilson cells (Wilson, 1962) in soil-free conditions. *S. geminata*, *S. invicta*, *P. dentata* and *P. morrisi* thus raised excavated the soil in preference to soil-free condition and moved in. An apical 4 cm piece of the partition was then removed and the confrontation behavior between *S. invicta* and other species observed. Also, the colonies in the Wilson cells

themselves could be connected through a 40 cm long, 0.5 cm diam glass tubing, centrally provided with a two-way stopcock, and the colony confrontations observed under completely soil-free conditions. The details of collecting colonies under soil-free conditions are discussed in Bhatkar and Whitcomb (1982).

The boreomontane species, such as *F. lugubris*, *F. aquilonia*, and *F. exsecta* were obtained from the Austrian Alpine National Park, Königssee. Other formicine species were collected from various areas in Germany : *F. polycтена*, *F. pratensis*, *F. fusca* and *F. sanguinea* from Steinerberg, Eifel ; *F. rufa* (monogynous form) from Krebssee, Kitzingen ; *F. rufa* (polygynous form) from Reupelsdorf in Franconia ; *Camponotus ligniperda* from Landesacker near Würzburg, and *L. niger* from Kottenforst near Bonn. All these species were reared in 30 cm square plastic boxes, 10 cm wide, in their own nesting material and fed on artificial diet, supplemented with some insect and fruit tissue (Bhatkar and Whitcomb, 1970). The nests were connected to two 10 cm diam, 5 cm high plastic dishes, which could be interconnected through a 30 cm long, 1 cm diam glass tubing with a two-way stopcock. The bottoms of the dishes were provided with a fine screen and they could be mounted on similar such dishes containing certain saturated salt solutions (Winston and Bates, 1960), to hold 60 % RH at  $25 \pm 2^\circ$  C. Any two species of ants were allowed to collect in the upper dishes and the passage between them was opened.

### Radioisotope experiments

A procedure similar to that for myrmicine species (Bhatkar and Kloft, 1977 ; Bhatkar, 1979) was used for the formicine species, except that larger confrontation cages were constructed using 2.5 cm diam, 2.5 cm wide plastic ring, hinged together to a similar 1 cm wide piece with sealing tape. The top ring was provided with a fine screen (material of lady's single-knit stockings, Fig. 1) to prevent ant escape and to avoid accumulation of formic acid that is otherwise autocidal to the secreting ants. About 50 foraging ants were fed to satiation with 20 % aqueous sucrose and  $\text{H}_3^{32}\text{PO}_4$  (sp. act.  $7.4 \text{ MBq ml}^{-1}$ ) mixture in 10 cm diam, 5 cm wide glass dishes. They were surface decontaminated by passing through plain water, 3 %  $\text{NaH}_2\text{PO}_4$  solution and plain water by holding them in the middle with fine watch spring forceps and blotting on a tissue paper. As a test of decontamination externally decontaminated dead ants were used in control. The efficiency of a similar procedure is discussed in Kloft et al. (1976). Individual ants were held in uniformly horizontal position in 0.7 cm pieces of clear plastic tubing, slightly larger in diam than the ant's length, and placed on 1 cm aluminum discs. The tops of the enclosures had a fine screen mentioned above. The radioactivity of live ants was measured with GM-end-window (thickness  $1.2\text{-}1.4 \text{ mg cm}^{-2}$ ) counting tube in conjunction with Philips Scaler Timer, Printer and Automatic Sample Changer. First, a satiated (with high radioactivity) worker or reproductive of one species and then 4 unfed workers or reproductives of another species were inserted in the confrontation cage by slightly tilting its top ring. Behavior of the contestants was observed under a stereoscope and they could be simultaneously

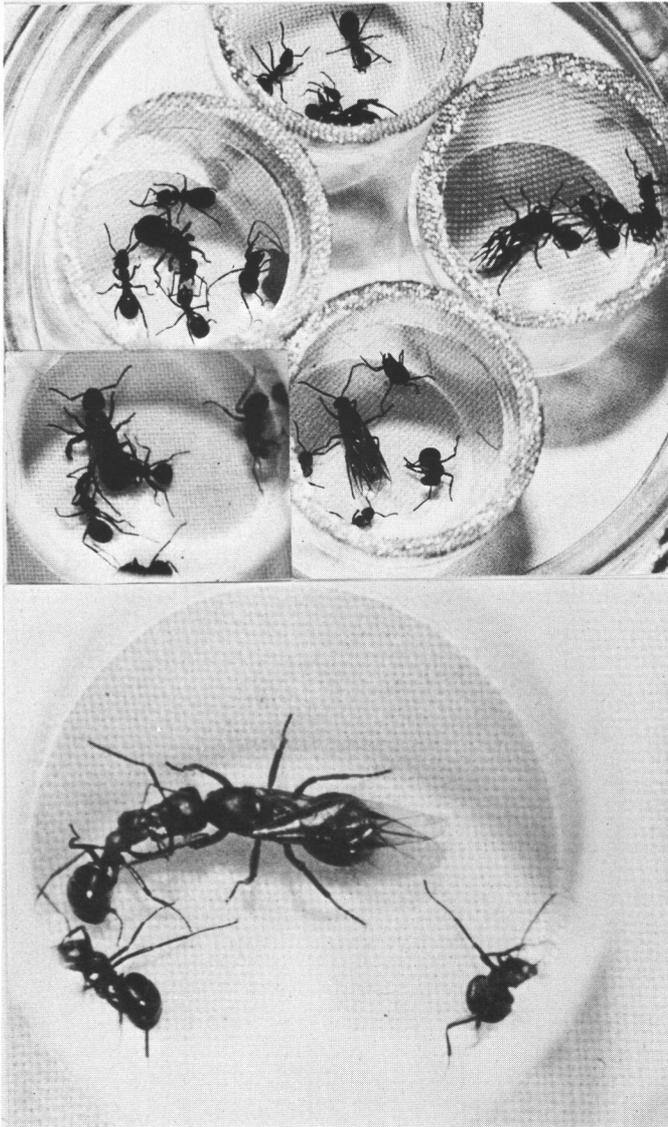


Fig. 1 — Interspecific food exchange between the alate queens of *Formica pratensis* and workers of *F. polycтена*. The queens offered food in response to aggression from workers (queen with malformed wings) and grooming followed such food offering.

Abb. 1 — Interspezifischer Futteraustausch zwischen geflügelten Königinnen von *Formica pratensis* und Arbeiterinnen von *F. polycтена*. Die Königinnen erwiderten das aggressive Verhalten der artfremden Arbeiterinnen mit Futterabgabe, der eine Säuberung folgte (Königin mit Mißbildungen der Flügel).

photographed. The ants were killed after a 20-60 min exposure, surface decontaminated and measured for acquisition of radioactivity through food exchange. The merits and general details of using radioisotopes in food exchange studies can be found elsewhere (Gösswald and Kloft, 1958 ; IAEA, 1977).

## RESULTS

### Baiting experiments

The experimental plots W1A, W1B and W1C have been burned during February-March annually since 1959 for a long duration floral and faunal succession study. Records indicate that the burns were carried out at 10-24° C and 30-72 % RH with a thorough back fire (fire backing into the wind direction) at 1400 h. The resultant vegetation included such regenerated trees as *Pinus echinata* (W1A, B), *P. taeda* (W1A, B, C), *Quercus virginiana*, *Q. nigra*, *Q. falcata* (W1B), *Q. velutina* (W1C), *Carya* spp. (W1A), *Liquidambar styraciflua* (W1A, C), *Nyssa silvatica* (W1B) and such annuals as *Cassia fasciculata*, *C. nictitans*, *Eupatorium* spp., *Solidago* spp., *Richardia scabra*, *Digitaria* spp. and *Paspalum* spp. Honeydew producing Homoptera, floral and extra-floral nectaries and insects provided a major diet for over 30 species of ants year-round. Only 13 species nesting in bare clay-loam spots predominantly exploited the baits. According to the degree of finding the baits and the persistence at feeding on them against the contestants, the species were divided into 1st degree, 2nd degree and 3rd degree recruiters.

Rapidly moving dolichoderine *Conomyrma flavopecta*, *Iridomyrmex pruinosum* and formicine *Camponotus floridanus*, *Paratrechina* spp., reached to the baits first, within 1/2 h of their placement. *P. dentata*, *P. morrisoni* (nesting in the cultivated fire breaks around the plots), *S. geminata* and *S. invicta* first scouted the baits and recruited their workers within 2-4 h. They displayed alarm responses (rapid movement on antennal contact with the alien, opening mandibles, raising gaster and secreting venom droplets at the sting) towards the 1st degree recruiters already present. On attack by seizing appendages of the stingless dolichoderine and formicine species, the 2nd degree recruiters quickly dominated while the former disappeared and moved to yet undiscovered baits. A third group of tiny, 2-2.5 mm long ants, *Diplorhoptrum* (*S.*) *texana*, *D. pergandei*, *P. metallescens*, *Brachymyrmex* spp., recruited to the baits the last and fed simultaneously with the 2nd degree recruiters, keeping a 2-5 mm distance from them. They moved among them and slipped through their mandibles on attack. The 3rd and 1st degree recruiters never offered food to the aggressive 2nd degree recruiters, what the

species of 2nd degree recruiters appeared to do, should *S. invicta* or *geminata* reach the bait and gradually replace them in contest. Whenever *P. dentata*, *P. morrisoni* or *S. geminata* recruited to the baits prior to *S. invicta* by laying trails, the latter species elicited aggression by raising gaster, secreting a venom droplet at the sting, vibrating (stridulating) the gaster, opening mandibles and gradually moving towards the bait. They attacked (seized, severed, stung) the aliens still approaching the bait. The alien food carrying workers moved slowly, oriented their heads to the aggressive *S. invicta* or *S. geminata* as the case may be, opened mandibles and regurgitated a droplet of fluid, pointing it to the attacker. The number of the two species of workers varied between 200-500 during the 20 min observation period and of these 50-80 % contained methylene blue (were potential donors) in the case of *P. dentata*, *P. morrisoni* or *S. geminata*. The proportion of aggressive food recipients (*S. invicta* or *S. geminata*) was 8-10 times lesser than that of the donors (Table I). The food receiving workers elicited a diminished aggression by holding their mandibles open or seizing the legs of the food carrying aliens, groomed themselves or exchanged food with the sister workers. To observe the extent of this repertory, both the species in contest were separated from the food bait per se (see Materials and Methods). *P. morrisoni* usually recruited to the bait sites towards the periphery of the plots and was not observed feeding together with *P. dentata*. Although *C. floridanus* and *Conomyrma flavopecta* nested close to the *S. invicta* and *geminata* mounds and fed on their dead workers, they never exchanged food. Whenever *S. invicta* recruited to the baits, it persisted the longest, displacing any other species that was its predecessor. However, the mortality of ants at the bait sites was less than 5 % of the total number recruited of any single species. Such contests were also observed at aphid-ant associations.

Table I – Proportion (%) of food donors and recipients containing methylene blue during the first 20 min of their confrontation. Summed data of 24 observations at 10 bait sites during September - November 1973-74 in 3 replicated plots.

Tabelle I – Verhältnis (%) von Futtergeber und Futterempfänger während der ersten 20 Minuten ihrer Konfrontation (als Nachweis dient Methylenblau). Zusammengefaßte Ergebnisse von 24 Beobachtungen an 10 Köderstellen in 3 Versuchsfeldern während September bis November 1973-74.

Donors	Recipients	Proportion of donors % ± SD	Proportion of recipients % ± SD
<i>P. dentata</i>	<i>S. invicta</i>	61.5 ± 15.4	5.6 ± 3.4
<i>P. morrisoni</i>	<i>S. invicta</i>	72.3 ± 21.5	7.2 ± 3.2
<i>P. dentata</i>	<i>S. geminata</i>	59.3 ± 5.9	7.4 ± 3.2
<i>P. morrisoni</i>	<i>S. geminata</i>	60.3 ± 15.9	6.8 ± 3.8
<i>S. geminata</i>	<i>S. invicta</i>	52.3 ± 14.3	4.2 ± 2.3
<i>C. floridanus</i>	<i>S. geminata</i>	80.7 ± 8.3	none

### Colony confrontation experiments

An overt form of aggression was usually observed when the colonies of *P. dentata*, *P. morrisi*, *S. geminata* were confronted to those of *S. invicta*, or those of *S. geminata* were exposed to the attack of *Pheidole* spp. (Bhatkar, 1973 ; Wilson, 1976). The minor or major workers confronting first regressed to their own colonies and recruited a large number of major workers to the site near the entrance of *Pheidole* or *S. geminata* nests, as the case may be. The majors of *P. dentata* and *morrisi* were more aggressive than minors in these dimorphic species (attack responses by 100 majors of *P. dentata*,  $61.2 \pm 19.23$  ; *P. morrisi*,  $43.2 \pm 7.63$ ,  $P < 0.05$  ; their minors,  $14.2 \pm 3.27$  and  $17.2 \pm 9.12$ , respectively : replications 5), when exposed to equal numbers of *S. invicta* or *geminata* in Wilson cells. The attacks involved mandibular clasps, severing of legs, stinging by the species involved. When equal-sized colonies (1000 workers and a queen) of *P. dentata*, *P. morrisi* or *S. geminata* were confronted, *S. invicta* killed about 4 times its number of *Pheidole* spp. and twice its number of *S. geminata*, as a simple comparison. During 3-5 out of 10 confrontation studies, however, the food carrying workers of *P. dentata*, *P. morrisi* or *S. geminata* first opened their mandibles and alarmed the sister workers to the site of confrontation, and were also seen to regurgitate a droplet of fluid between their mandibles, orienting it towards an attacking alien. Initially, when the number of invading species was small, many workers accepted the regurgitate, redistributed it to the closest sister and groomed themselves, a repertoire that ceased colony invasions for 20-30 min. This behavior was also observed when an exodus of *S. invicta* workers entered the tunnels of these species and reached the queen and brood chambers. The chambers are usually inhabited by several major and few minor replete (with distended gasters) workers. These workers were still holding their antennae in repose, and upon encounters with an aggressive *S. invicta*, antennated it and offered food. The queen also took part in such a food exchange but the callow workers did not. The next response was swarming away from the site of attack by the queen, callows and rest of the workers, carrying the brood to deeper parts of the nest. Under laboratory conditions, the brood and the queen were stung and carried by *S. invicta* to its nest. In nature, the escape swarms by the attacked species may be successful. In fact, invasion by *S. invicta* of the colonies of *Pheidole* spp. and *S. geminata* was observed in the field in many instances and actual escape swarms occurred.

*Formica rufa* complex (*rufa*, *pratensis*, *polycytena*, *lugubris*, *aquilonia*) elicited aggression not beyond vigorous antennation, retreat, opening mandibles, alarming nestmates to the site of attack and pulling appendages of the alien workers when any two species were allowed to confront one another.

The workers mixed and exchanged food among themselves and with the aliens whenever the latter were aggressive. Over a 24 h period, more than 60 % of the mixed colonies again separated and they completely separated over a 3-5 days period. Concurrently, the interspecific food exchange was occasional. *F. exsecta*, *C. ligniperda* and *L. niger* colonies were the most aggressive towards *F. rufa* complex, and mandibular attacks, spraying of formic acid via acidopore, severing of appendages and heads were observed between the workers in contest. After 2-4 h initial aggression, the food carrying workers of *F. exsecta* and *C. ligniperda* appeared to offer the regurgitate to any alien worker in a fashion similar to the myrmicine species discussed above. However, *L. niger* workers apparently never offered food to any of these species. Trophallaxis also occurred between *C. ligniperda*, *F. pratensis*, *F. sanguinea*, and *F. fusca*. The members of *F. pratensis*, *F. fusca* and *F. sanguinea* mixed readily, albeit with initial aggression, when akinesis and food transfer were the means of suppressing aggression in the attacker. The recipients groomed themselves and the donors, contrary to the more aggressive myrmicine species. The queens of *fusca* and *pratensis* were invariably dead after a period of 20 days.

### Radioisotope experiments

A certain degree of precision and quantification of the amount of regurgitate received as a proportion of the trophallactic uptake of the ingluvial fluids by the receiving species was possible through the use of  $^{32}\text{P}$ . Since P is a part of the insect metabolism, it and low degree of radioactivity may not alter the behavior of ants (Gösswald and Kloft, 1960). The results of similar experiments on Myrmicinae using  $^{32}\text{P}$  are documented earlier (Bhatkar and Kloft, 1977 ; Bhatkar, 1979a, b) ; those on Formicinae are summarized in Tables II and III and Fig. 2. In all the experiments, adults over 4 days of age were used. The donors usually contained 10-100 times more food (cpm) than they lost to the aggressive recipients. The background radioactivity (10-12cpm) was subtracted from all the readings and the means (rounded to nearest zero) of 10-12 replications are shown in the tables. Only those experiments where all the recipients had radioactivity within the first 1 h exposure are considered.

*F. (Formica) polyctena* worker received regurgitate from *F. pratensis*, *F. aquilonia*, *F. lugubris* and *F. rufa*, and *rufa* and *pratensis* offered almost twice the amount as *aquilonia* and *lugubris* (Table II). *C. ligniperda* gave more food to *F. polyctena* workers than *F. (Coptoformica) exsecta*. *F. (Raptiformica) sanguinea* received more regurgitate from *C. ligniperda* than the species

Table II – Interspecific worker-to-worker and queen-to-worker food exchange in Formicinae

Tabelle II – Interspezifischer Futterraustausch zwischen Arbeiterinnen und Königinnen-Arbeiterinnen bei Formicinae

Donor/caste	Recipient/caste	cpm transfer $\bar{X} \times 10^2$
<i>Formica rufa</i> ♀	<i>Formica polyctena</i> +♂	38.8
<i>Formica pratensis</i> +♂	<i>Formica polyctena</i> +♂	37.5
<i>Formica lugubris</i> +♂	<i>Formica polyctena</i> +♂	13.9
<i>Formica aquilonia</i> +♂	<i>Formica polyctena</i> +♂	15.5
<i>Formica exsecta</i> +♂	<i>Formica polyctena</i> +♂	1.9
<i>Camponotus ligniperda</i> ♀	<i>Formica polyctena</i> +♂	4.9
<i>Camponotus ligniperda</i> ♀	<i>Formica rufa</i> ♀ (monogynous)	1.5
<i>Camponotus ligniperda</i> ♀	<i>Formica lugubris</i> +♂	3.4
<i>Camponotus ligniperda</i> ♀	<i>Formica aquilonia</i> +♂	1.9
<i>Camponotus ligniperda</i> ♀	<i>Formica exsecta</i> ♀	3.0
<i>Camponotus ligniperda</i> ♀	<i>Formica sanguinea</i> +♂	7.4
<i>Formica pratensis</i> ♀	<i>Formica rufa</i> ♀	6.2
<i>Formica pratensis</i> ♀	<i>Formica polyctena</i> +♂	10.1
<i>Formica pratensis</i> ♀	<i>Formica lugubris</i> +♂	44.3
<i>Formica pratensis</i> ♀	<i>Formica aquilonia</i> +♂	61.7
<i>Formica pratensis</i> ♀	<i>Formica sanguinea</i> +♂	2.5
<i>Formica pratensis</i> ♀	<i>Formica rufibarbis</i> +♂	5.9
<i>Formica lugubris</i> ♀	<i>Formica rufa</i> ♀ (monogynous)	21.7
<i>Formica lugubris</i> ♀	(polygynous) ♀	20.9
<i>Formica lugubris</i> ♀	<i>Formica pratensis</i> +♂	83.1
<i>Formica lugubris</i> ♀	<i>Formica polyctena</i> +♂	18.5
<i>Formica lugubris</i> ♀	<i>Formica exsecta</i> +♂	19.7
<i>Formica lugubris</i> ♀	<i>Formica sanguinea</i> +♂	5.8
<i>Formica lugubris</i> ♀	<i>Camponotus ligniperda</i> ♀	26.4
<i>Lasius niger</i> ♀	<i>Formica polyctena</i> +♂	49.6
<i>Lasius niger</i> ♀	<i>Formica lugubris</i> +♂	6.1

of *F. rufa* complex, such as *F. polyctena*, *F. lugubris*, *F. aquilonia*, and *F. rufa*, in that order. *F. rufa* occurs in mutually exclusive monogynous and polygynous populations and *F. polyctena* populations are common to both. In *F. rufa*, the monogynous colony members gave less food to polygynous colonies but the reverse was not true. Also, more food was offered to *F. polyctena* workers by polygynous than by monogynous *F. rufa* colony members (Fig. 2). Even the queens (alates and apterous) of *F. pratensis* transferred regurgitate to the workers of *F. aquilonia*, *lugubris*, *polyctena* and *rufo*, in that order. *F. (Serviformica) rufibarbis* of *F. fusca* group received more amount than the enslaving species, *F. (Raptiformica) sanguinea* from the *F. pratensis* queens. *F. pratensis* workers were given more food by *F. lugubris* queens than *F. polyctena* or mono- or polygynous *F. rufa* workers. Also, *C. ligniperda* acquired more regurgitate from *F. lugubris* queens than did *F. polyctena*, *F. rufa* or *F. exsecta*. *L. niger* queens offered food to the workers of *F. lugubris* and *F. polyctena* but *L. niger* workers were never seen to do so and they never received food from any of the above species during

Table III – Interspecific male-to-worker and queen-to-queen food exchange in Formicinae

Tabelle III – Interspezifischer Futteraustausch zwischen Männchen-Arbeiterinnen und Königinnen bei Formicinae

Donor	Recipient	cpm transfer $\bar{x} \times 10^2$
<i>Formica rufa</i> ♂ (polygynous)	<i>Formica polyctena</i> ♀	3.5
<i>Formica rufa</i> ♂ (polygynous)	<i>Formica pratensis</i> ♀	12.1
<i>Formica pratensis</i> ♂	<i>Formica polyctena</i> ♀	1.2
<i>Formica pratensis</i> ♂	<i>Formica rufa</i> ♀ (monogynous)	0.6
<i>Formica pratensis</i> ♀	<i>Formica polyctena</i> ♀	7.7
<i>Formica pratensis</i> ♀	<i>Formica nigricans</i> ♀	16.4
<i>Formica pratensis</i> ♀	<i>Formica fusca</i> ♀	2.0
<i>Formica pratensis</i> ♀	<i>Lasius niger</i> ♀	19.7
<i>Formica lugubris</i> ♀	<i>Lasius niger</i> ♀	2.9

several repeated experiments. The males of *F. rufa* and *F. pratensis* were observed to offer regurgitate differentially to the workers of the alien species (Table III). The males of *F. rufa* (polygynous) offered more regurgitate to the workers of *F. pratensis* than to *F. polyctena*; a small amount of food was received by the males and workers from *F. rufa* (polygynous) (not shown). *F. pratensis* males were less receptive donors to *F. rufa* workers (monogynous colonies) and receptive donors to *F. polyctena* workers or *F. rufa* (polygynous) males. The queens of Formicinae were selective in terms of food exchange (Table III). The queens of *F. nigricans* received more regurgitate from those of *F. pratensis* than did the queens of *F. polyctena*, and *F. fusca* seemed to receive the least amount. *L. niger* queens received more food from *F. pratensis* than from *F. lugubris*.

### INTERSPECIFIC AND INTRASPECIFIC TROPHALLAXIS

#### (FORMICA RUFA AND F. POLYCTENA)

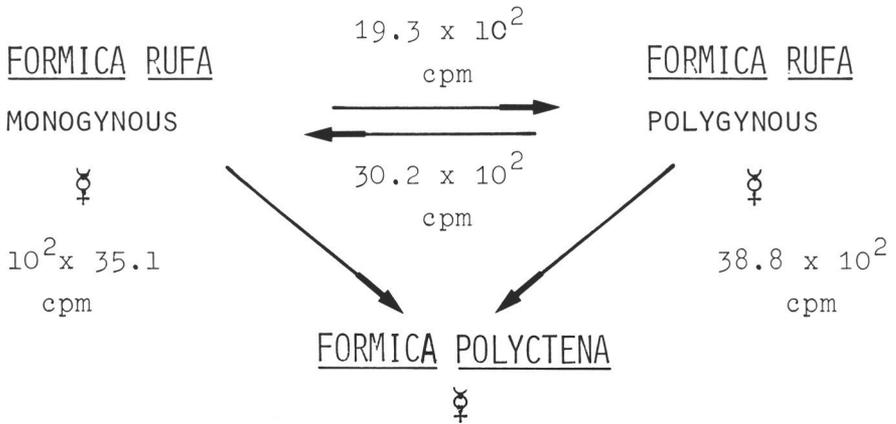


Fig. 2 — Inter- and intra-specific worker-to-worker trophallaxis in *Formica rufa* and *F. polyctena*

Abb. 2 — Inter- und intraspezifischer Futteraustausch zwischen Arbeiterinnen von *Formica rufa* und *F. polyctena*

### Behavior during interspecific trophallaxis

The confronting individuals elicited various degrees of aggression specific to the species in question. The donors and aggressors antennated, contacted one another, regressed, opened mandibles and attacked. *Solenopsis* spp. raised the gasters, pointing them in the direction of the attacker and secreted droplets of venom. Mandibular attacks, holding fast on to the appandages and severing them was common to *Pheidole* spp. *F. exsecta* and *C. ligniperda* held the mandibles and cervices of the donors and severed their appandages under extreme aggression. Similarly, *F. sanguinea* was equally aggressive towards *L. niger* workers and queens. The initial aggression seemed to wane after 2-5 min when the donors exuded a droplet of regurgitate between the mandibles and oriented it in offering fashion to the aggressor/s. The formicines sprayed their donors with the formic acid via the acidopores. Self-grooming was a rule in all the satiated recipients. In exceptional cases, such as when *F. pratensis* queens offered food to *F. sanguinea* workers, the queens groomed the workers. The *Lasius* queens and *C. ligniperda* workers resumed ambulation, as if to show distress, and moved away from the attacker. This was also common to many Myrmicinae. The queens of *F. pratensis* with malformed wings were superior donors to those with normal wings when both were exposed to *F. polycytena* workers, and food transfer occurred much more readily (Fig. 1).

### DISCUSSION

The exchange of alimentary liquids, either unilaterally or mutually, between the members of different species is termed interspecific trophallaxis (Bhatkar and Kloft, 1977) ; the intraspecific, intercolonial or intracolony trophallaxis follow as a corollary (Bhatkar, 1979b). All these forms of food exchange occur in higher Myrmicinae and Formicinae and seem to be vital to the species associations and colony organization. Trophallaxis within the colony members may occur in the most ritualized fashion. The donors may need tactile stimuli through the antennal contacts at the base of scapes, mandibles or palpi or through the grooming of abdomen, legs, thorax, cephalic ventrum, reaching progressively to the labium. A droplet of regurgitate finally oozes between the mandibles of the donor and is available to the solicitor. Wallis (1961) brought out the role of foreleg stroking in addition to vigorous antennation during trophallaxis. Persistent solicitation (as it appears to be) by the same individual may lead to distress antennation in the donor and eventual turning away from the solicitor (Bhatkar, 1979a, b). There may

be a series of such codes by which ants demand, accept or reject trophallactic fluid (Lenoir and Jaisson, 1974).

Under the aggressive stress from an alien, the donor's behavior becomes ritualized. It antennates the alien, regresses, moves away from the site of attack and if attacks or aggressive solicitation persist, regurgitates a droplet of fluid between its mandibles. The droplet is oriented to the attacker's head with vibrant antennation. The overall responses are quick, intense and any delay in food offering may result in an overt form of aggression in the alien recipient. It may involve mandibular attacks, seizing, pulling, grappling or severing appendages, petiole or cervix and may associate with stinging (in Myrmicinae) or spraying (in Formicinae). The donor moves towards the solicitor/aggressor and antennates it, as if invoking a solicitation response and suppressing aggression. The element of aggression in the solicitor seems to be decisive as to whether trophallaxis will occur or not. For example, *F. Pratensis* queens with malformed wings were much more susceptible to the aggression from *F. polycytena* workers and offered food quicker than the alate queens that showed initial aggression by opening mandibles towards the attacker (fig. 1). Among the symbiotic species, such as temporary parasites (*F. rufa*, *F. pratensis*, *F. lugubris*, *F. aquilonia*, *F. exsecta*) and their hosts (*F. fusca*, *F. rufibarbis*, *F. polycytena*, etc.) (Gösswald, 1951 ; Kutter, 1964, 1969), or dulotic species (*F. sanguinea*, *Polyergus rufescens*) (Beck, 1961) and their hosts (*F. fusca*, *F. rufibarbis*, *F. pratensis*, *F. rufa*, *F. polycytena*) (Bernard, 1968), antennation, mandibular widening, seizing and pulling seem to result in regurgitative offering by the hosts. In the species where no symbiosis is established, such as *S. invicta*, *S. geminata*, *P. dentata*, *P. morrissi*, *C. ligniperda* (tribe Camponotini), *L. niger* (Formicini), more intense attacks by the aggressors incited interspecific trophallaxis.

There seems to be a differential aggressiveness among different castes of workers engaged in food exchange. The minors and majors of *S. geminata* are more receptive to similar castes in *S. invicta* than the majors of *S. geminata* to the minors of *S. invicta*. The majors and minors of *P. dentata* offered more food to the dissimilar castes of *S. invicta* (Bhatkar and Kloft, 1977). More the aggressive encounters, better is the receptiveness of the donor. When otherwise aggressive minors of *S. invicta* were exposed to 4 times their number of *S. geminata* minors or *P. dentata* majors, *S. invicta* offered regurgitate to the latter species. The confrontations between polymorphic workers of *S. invicta* and majors and minors of *S. geminata* or *P. dentata* indicated that *S. invicta* workers are 3 times as aggressive as *P. dentata* majors, 3 times as aggressive as majors and minors together and twice as aggressive as *S. geminata* workers (Bhatkar, 1973).

Interspecific food exchange occurred in response to the aggression by a potential recipient against a satiated individual. But not all the species, such as those nesting in the annually burned vegetational habitats in North Florida, show such a behavior. *P. dentata* and *S. geminata* are regarded as the ecological competitors of *S. invicta* (Wilson, 1976 ; Bhatkar and Whitcomb, 1981). *S. geminata*, *P. dentata* and *P. morrisoni* invariably offered food to more aggressive *S. invicta*. Further, laboratory colony invasion studies indicated that satiated donors of these species were able to delay the invasion of the first batch of *S. invicta* entrants by 20-30 min and more workers were recruited to the entrance while the queen and the brood were moved away to a safer place by the nurses underground. The majors of *Solenopsis* and *Pheidole* are replectic (store liquid for a long duration), thus better suited for such an obscure form of defense. The degree of aggressiveness in the contestants which may itself be age dependent (Fielde, 1903 ; Bhatkar, unpublished), satiation of the donors and overall intrinsic potential of the species to exchange food seem to decide the occurrence of interspecific trophallaxis between them.

Thus far, interspecific trophallaxis in Myrmicinae and Formicinae was limited to the subfamilies and occurred beyond specific, subgeneric, generic and tribal levels. The evolutionary and adaptive significance of this phenomenon may lay in a rather subtle explanation of the intrinsic potential of the species for «allotrophallaxis». Several closely related forms of *Formica* and *Lasius* occur in palearctic and nearctic regions (Creighton, 1950 ; Betrem, 1960 ; Kutter, 1965 ; Buren, 1968). In *F. rufa* group itself, species are difficult to separate even on the basis of their genitalia (Betrem, 1960). For such instances, if one considers that the parent population fragmented and diverged genetically through geographical and ecological barriers, then the reinvading species thus formed may enter into certain host-parasite relationships. This Emery's rule (Wilson, 1971) can be projected to its further repercussion. First, the genetic divergence of the species in *F. rufa* group prevents them from interbreeding (Betrem, 1960) and disjunct populations of *F. polycтена*, *F. lugubris*, etc. exist (Gösswald et al., 1965). A similar situation seems to be true to *S. saevissima* complex in the Brazilian flood plain region (Buren et al., 1978) wherefrom *S. invicta* and *S. richteri* found their entry to the south-eastern U.S. during 1930s and 1920s respectively. *S. geminata* complex of the Mexican humid tropics poses a parallel problem (Bhatkar, unpublished) and of this red and black forms occur in the southern U.S. *Pheidole* is an expanding genus from Miocene times and *Camponotus* from Oligocene times (Brown, 1973). Under such situations, various forms of parasitisms must occur as a rule. Secondly, one of the intrinsic isolating mechanisms in the speciating forms may be the conceivably less understood colony or species

odors that seem to cause aggression in ants. Such an aggression seems to be subdued in the presence of the regurgitate from the ant to be aggressed upon during intercolonial or interspecific confrontations (Bhatkar, 1979a). The associated behavior of the donor appears to be analogous to appeasement in the higher animals (Bhatkar and Kloft, 1977).

*F. polyctena*, *F. lugubris*, *F. aquilonia*, *F. pratensis* and *F. truncorum* are polygynous and polydomous (Betrem, 1960). Under the competitive pressure from *F. polyctena* and *L. fuliginosus*, *F. rufa* apparently resorts to polygyny (Kutter, 1964) and the same seems to be true in *S. geminata* and *S. invicta* (Bhatkar, 1979b). Social parasitism is realized through facultative polygyny (Buschinger, 1970), and an intermediate state of temporary parasitism is achieved through colony founding by the mated queens in the colonies of specialized nursing hosts. Interspecific trophallaxis should find its adaptive value especially when several oligogynous or polygynous species occur in the same geographical area, find entry in new regions of their establishment or exploit the same habitat. In the present investigation, *F. polyctena* received more regurgitate from *F. rufa*, *F. pratensis*, *C. ligniperda* inhabiting boreal habitats than from *F. lugubris*, *F. aquilonia* or *F. exsecta* inhabiting boreo-Alpine habitats. The queens and males of temporary parasites or dulotic species seem to be selective in their food offering response. The queens of *F. pratensis*, *F. rufa*, *F. lugubris*, and *F. polyctena* are known to found their colonies in those of the species of *F. fusca* group (Gösswald, 1951 ; Kutter, 1964), and can be conjectured to offer less food to their hosts than they would receive. *F. sanguinea* is known to occasionally parasitize *F. pratensis* colonies (Bernard, 1968). Thus, *F. pratensis* queens, usually killed by *F. sanguinea*, offer little food to the hostile *F. sanguinea*. Interspecific trophallaxis seems also to be concurrent with the presence of polygyny. Both workers and males of the polygynous *F. rufa* colonies were more receptive to the workers of *F. polyctena*, *F. pratensis* and *F. rufa* (monogynous) than those of monogynous *F. rufa* colonies. Food exchange is known to occur between the members of *F. polyctena* and *F. rufa* in nature (Chauvin et al. 1961, Gösswald and Kloft, 1963). The founding queens of some species like *L. niger* develop a thoracic dilation of their alimentary tract (Mura, 1973) that seems to facilitate their food offering trait, as against their workers, when confronted with the aggressive queens of *F. pratensis* or workers of *F. polyctena* and *F. lugubris*. It seems that since *F. polyctena* nests in the habitats of mono- and polygynous *rufa*, it obtains regurgitate from both of these forms. The nesting of *F. rufa*, *F. truncorum*, *F. polyctena*, *F. exsecta* and *L. fuliginosus* in proximity prompted Kutter (1964) to conduct his alliance colony experiments. The occurrence of interspecific trophallaxis between the species with no apparent symbiotic relationship, such as *S. invicta*, *S. geminata*,

*P. dentata*, *P. morrissi* in Florida or *C. ligniperda*, *L. niger*, *L. flavus* and *L. fuliginosus* in Central Europe may be a relict trait that was carried over as adaptive, to facilitate the close nesting among aggressive species in their shared habitats. In the light of the present discussion, food exchange between the species of different subfamilies, such as *Formicoxenus nitidulus* cohabiting the nests of *F. pratensis* and *F. rufa* (Wheeler, 1910 ; Stumper, 1950), or between *Crematogaster limata parabiatica* associated parabiatically with *Camponotus femoratus* and *Monacis debilis* (Wheeler, 1921 ; Swain, 1980), or that between *C. floridanus* and *S. invicta* (Wilkinson et al., 1978), may involve a complex semiochemic convergence relative to their behavior and needs a further study.

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