FORMICA INTEGRA 2. FEEDING, TROPHALLAXIS, AND INTERSPECIFIC CONFRONTATION BEHAVIOR[1,2]

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ABSTRACT

In laboratory screening tests, *Formica integra* Nylander attended honeydew-producing insects such as the aphid, *Neosymydobius albasiphus* Davis, on swamp chestnut oak and a soft scale, *Toumeyella parvicornis* (Cockerell), on slash pine seedlings. Forest insect pest species consumed by *F. integra* included *Neodiprion excitans* Rohwer and *N. lecontei* (Fitch), *Ips calligraphus* (Germar) and *I. grandicollis* (Eichh.), *Reticulitermes flavipes* (Kollar), *Rhyacionia frustrana* (Comstock), and *Tetralopha robustella* Zeller. Trophallaxis between *F. integra* workers taken from the same or widely-separated nests in the field was demonstrated by use of a radioisotope. When 3 potentially competitive ant species were paired with *F. integra* in laboratory confrontation tests and their mortality was compared with that of *F. integra* by a calculated confrontation index, mortality was twice as much for *Crematogaster atkinsoni* Wheeler, one-half as much for *Solenopsis invicta* Buren, and only one-fifth as much for *Camponotus abdominalis floridanus* (Buckley).

Habitat, nest construction, polygyny and biometry of a red wood ant, *Formica integra* Nylander 1856, from west-central Georgia were described in a preceding paper by Kloft et al. (1973). We conducted further studies during 1972-74 on ants from the same area to estimate the potential usefulness of *F. integra* as a predator of pest species such as pine sawflies.

FEEDING BEHAVIOR

Feeding habits of certain species of red wood ants (especially *Formica polyctena* Foerster in Germany) have been reported in detail in the European literature. English abstracts of papers between 1930 and 1961 were given by Cotti (1963); Way (1963) reviewed mutualism between ants and honeydew-producing Homoptera. Adlung (1966) and Finnegan (1971) discussed ant feeding habits in regard to effective use of these predators as biological control agents. Red wood ants attend certain species of psyllids, coccids, and aphids (Kloft et al. 1965) to obtain honeydew, which is reported to contain carbohydrates and proteins in amounts sufficient to maintain colonies during periods when insect prey is scarce. Red wood ants are reported to prey most effectively on hairless caterpillars and sawfly larvae which defoliate hardwood or coniferous trees, but many other kinds of arthropods are also carried to ant nests for consumption. Feeding and foraging activities of *F. polyctena* are mostly diurnal; however, Horstmann

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(1970) found that such activities were primarily temperature-dependent, and 29% of total honeydew collected plus 14% of total prey were collected at night.

In Manitoba, Canada, Bradley and Hinks (1968) found that *Formica* spp. (especially *Formica obscuripes* Forel) attended *Cinara* spp. aphids [especially *Cinara gracilis* (Wilson)] infesting jack pine, *Pinus banksiana* Lamb. In the study area, *F. obscuripes* was seen carrying geometrid, tortricid, and noctuid larvae, adult psyllids and beetles, and parts of grasshoppers, flies, and spiders along the trails to their nests. Many of the larvae were defoliators of jack pine and most were still alive while being carried. Two successful attempts have been made by Finnegan (1975, 1977b) to introduce *Formica lugubris* Zetterstedt 1840 from Italy and *F. obscuripes* from Manitoba into Quebec, Canada. There he found these ants readily preyed on larvae of diprionid sawflies such as *Neodiprion lecontei* (Fitch) and *N. swainei* Middleton (Finnegan, personal communication), and on the spruce budworm, *Choristoneura fumiferana* (Clemens) (Finnegan 1977a).

We made observations in Georgia and Florida to determine whether *F. integra* would attend sucking insects and prey on different species of insects offered to it. Special attention was paid to predation of the sawflies, *Neodiprion excitans* Rohwer and *N. lecontei*, 2 important defoliators of pines in Florida (Hetrick 1959, Wilkinson 1969).

METHODS.—Field observations were made at the site in Georgia described by Kloft et al. (1973). *F. integra* worker ants from Georgia were transferred to a laboratory at Gainesville, Florida and established in a 1-m diam by 20-cm deep plastic "nest arena" containing nest material from Georgia on moistened sand. The nest arena was connected by 2 large plexiglass tubes to a similar "feeding arena" in which artificial ant diet (Bhatkar and Whitcomb 1970), 10% honey-water, and water were offered daily. The laboratory room was maintained at 27 ± 2°C, 50-80% RH, and light:dark cycle of 14:10 h. Worker activity during dark periods was observed by use of a red light. Live insect prey, or plants or branches infested with insects, were placed in the feeding arena to observe feeding-foraging activities of *F. integra*. At least 10 specimens of each species were offered as prey in each trial.

RESULTS.—*F. integra* workers attended and obtained honeydew from *Neosymydobius* spp. aphids feeding on 2 closely-related species of chestnut oaks growing in Georgia and Florida (Table 1.). Honeydew was also obtained from a soft scale, *Toumeyella parvicornis* (Cockerell), which is commonly found on young pines in Florida. Naked, unprotected insects (including many pest species) were preyed upon in most cases, but webbing readily protected larvae of the pine webworm, *Tetralopha robustella* Zeller. *F. integra* workers did not open sawfly cocoons, but carried off live sawflies and sawfly parasites. Both *N. excitans* and *N. lecontei* sawfly larvae were constantly harassed by *F. integra* workers, were unable to feed, and eventually fell to the soil in the feeding arena. Fallen larvae were immediately seized and carried into the nest arena. Ant feeding-foraging activity was noticeably greater during light periods, but attendance of the soft pine scale and oak aphids as well as harassment and predation of feeding sawfly larvae continued at a reduced rate during dark periods.

DISCUSSION.—Foraging and predation activities of *F. integra* under laboratory conditions were very similar to those reported for European and

Canadian species of red wood ants under laboratory and field conditions. Attendance of *Neosymydobius* sp. aphids by *F. integra* in the field in Georgia (southern edge of *F. integra* range) and the readiness of *F. integra* to utilize a related *Neosymydobius* sp. farther south in Florida are desirable traits in relation to potential use of *F. integra* as a biological control agent (cf. Finnegan 1971, 1975). This relationship might be exploited in Florida by introducing *F. integra* into loblolly pine, *Pinus taeda* L., sawtimber stands where swamp chestnut oak, *Quercus michauxii* Nutt., is often present and is commonly infested with *Neosymydobius* spp. aphids. Outbreaks of *N. excitans* sawflies commonly occur in such sawtimber stands in Florida (Wilkinson, unpubl.).

Trophallaxis

A typical behavior of red wood ants is the distribution of liquid food from 1 individual to another by regurgitation (trophallaxis), so that all individuals in a nest share food gathered by foraging workers. This could be an important factor in successful establishment and maintenance of colonies in new areas (Finnegan 1971). Food distribution in certain European species has been studied with radioactive tracers (Goesswald and Kloft 1956, 1958, 1960, 1963; Kneitz 1963; Lange 1958, 1960). Similar experiments were conducted to determine whether trophallaxis occurs in *F. integra*.

Method.—In all 3 experiments, radioactive sugar-water (20%, labelled as ^{32}P orthophosphate, specific activity 0.3 mCi/ml, was offered to 1 worker which fed to the point of satiation. After careful external decontamination by washing in buffered phosphate "chaser" solution (Kloft 1977), the satiated ant (donor) was placed with a group of 54-58 workers which had been removed from a laboratory nest and starved for 4 h (acceptors). Three single experiments involved (1) a donor from nest "A" and 58 acceptors from nest "A"; test ended after 4.5 h, (2) a donor from nest "A" and 58 acceptors from nest "A"; test ended after 20 h, and (3) a donor from nest "A" and 54 acceptors from nest "B"; test ended after 4.5 h (Fig. 1). Experiments were terminated after 4.5 or 20 h by killing all ants with chloroform. The dead workers were individually checked for radioactivity measured in counts per minute (cpm), which was considered to be proportional to an individual's participation in the chain transfer of liquid food initiated by a single donor. Workers from laboratory nests "A" and "B" were originally obtained in Georgia from nests located about 200 m apart in the field.

Results.—The cpm values for individual workers are grouped in logarithmic classes in Fig. 1. Both donors and acceptors in experiments 1 and 2 came from laboratory nest "A" and only the observation times differed. A fairly normal distribution was obtained in experiment 1 after 4.5 h, even though 8 out of the 58 acceptors had still received practically no food (0-10 cpm). The peak of radioactivity in experiment 2 shifted to higher values after 20 h indicating that all individuals had participated in trophallaxis. Transfer of radioactivity in experiment 3 from a donor in nest "A" to nearly all of the 54 potential receptors from nest "B" corresponded with the results of experiment 1.

Discussion.—Trophallaxis between *F. integra* workers taken from the same or widely separated nests in the field was demonstrated under laboratory conditions; results were similar to those obtained by laboratory and field

TABLE 1. FEEDING AND PREDATION ACTIVITIES OF *Formica integra* WORKERS.

Insect species observed		Condition of observation	Response to insect by *F. integra*
		(Field study in Georgia)	
(H:A)*	*Neosymydobius* sp., possibly *quercihabitus* Miller	on *Quercus prinus* L.	Attended
		(Laboratory studies in Florida)	
(H:A)	*Neosymydobius albasiphus* Davis	on *Quercus michauxii* Nutt.	Attended**
(H:D)	*Phenacaspis*, prob. *pinifoliae* (Fitch)	on *Pinus elliottii* Engelm.	None
(H:A)	*Unilachnus parvus* Wilson	on *Pinus taeda* L.	None
(H:A)	*Myzus persicae* (Sulzer)	on *Datura* sp.	None
(H:A)	*Acyrthosiphon pisum* (Harris)	on *Vicia faba* L.	Carried to nest
(H:C)	*Toumeyella parvicornis* (Cockerell)	on *Pinus elliottii* Engelm.	Attended**
(Hy:D)	*Neodiprion excitans* Rohwer	larvae, pupae, adults, parasitoids within cocoons	None
(Hy:D)	*N. excitans*	dead forms dissected from cocoons	None
(Hy:D)	*N. excitans*	female in partially-opened cocoons	Removed to nest
(Hy:D)	*N. excitans*	females emerged from cocoons	Carried to nest
(Hy:D)	*N. excitans*	live forms dissected from cocoons	Carried to nest
(Hy:D)	*N. excitans*	stage 1-5 larvae on *P. taeda*	Carried to nest
(Hy:D)	*Neodiprion lecontei* (Fitch)	stage 4-6 larvae on *Pinus palustris*	Carried to nest
(C:S)	*Ips calligraphus* (Germar)	adults	Carried to nest
(C:T)	*Ips grandicollis* (Eichoff)	adults	Carried to nest
(C:T)	*Tribolium castaneum* (Herbst)	adults	Carried to nest

(I:R)	*Reticulitermes flavipes* (Kollar)	workers	Carried to nest
(L:G)	*Phthorimaea opercullella* (Zeller)	10-day-old larvae	Carried to nest
(L:G)	*P. opercullella*	larvae in tubers	None
(L:N)	*Trichoplusa ni* (Hubner)	stage 4 larvae	Carried to nest
(L:O)	*Rhyacionia frustrana* (Comstock)	stage 5 larvae	Carried to nest
(L:P)	*Tetralopha robustella* Zeller	stage 3-5 larvae and pupae (naked)	Carried to nest
(L:P)	*T. robustella*	larvae in webbing on *P. elliottii*	None

* (H:A) = Homoptera:Aphidae, (H:C) = Homoptera:Coccidae, (H:D) = Homoptera:Diaspididae, (Hy:D) = Hymenoptera:Diprionidae, (C:S) = Coleoptera: Scolytidae, (C:T) = Coleoptera:Tenebrionidae, (I:R) = Isoptera:Rhinotermitidae, (L:G) = Lepidoptera:Gelechiidae, (L:N) = Lepidoptera:Noctuidae, (L:O) = Lepidoptera:Olethreutidae, (L:P) = Lepidoptera:Pyralidae.

** *N. albasiphus* was attended by the ant, *Crematogaster atkinsoni* Wheeler, in nature and *T. parvicornis* was attended by the red imported fire ant, *Solenopsis invicta* Buren, in nature. The Florida carpenter ant, *Camponotus abdominalis floridanus* (Buckley), also commonly attends *T. parvicornis* scales on young pines in Florida (Wilkinson, unpubl.).

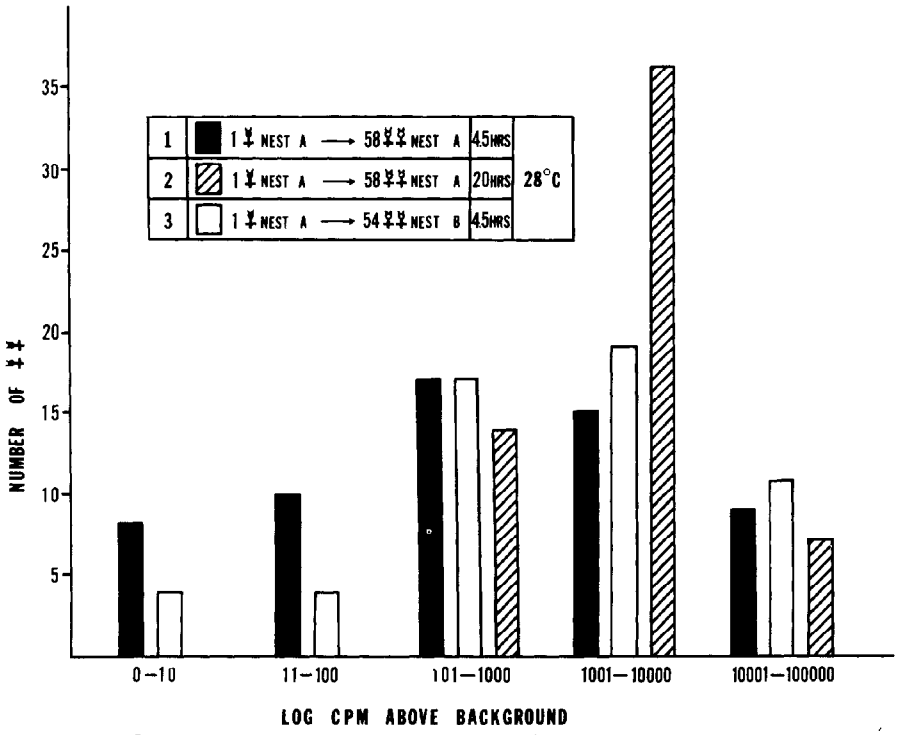

Fig. 1. Transfer of radioactivity among *F. integra* workers from 3 single donor ants fed on ^{32}P sugar-water to 54-58 receptor ants per each of 3 replicates after 4.5 or 20 h. (1) Solid symbol: transfer from donor from nest "A" to acceptors from nest "A" after 4.5 h; (2) Cross-hatch symbol: transfer from donor from nest "A" to acceptors from nest "A" after 20 h; (3) Hollow symbol: transfer from donor from nest "A" to acceptors from nest "B" after 4.5 h.

experiments with *F. polyctena* in Europe (Goesswald and Kloft 1963, Kloft 1967, Lange 1960). Such involvement of large populations in a food chain should increase survival and efficiency of red wood ants as predators. We expect that this situation applies to *F. integra*, but it remains to be proved under field conditions.

Interspecific Confrontation Behavior

Interspecific aggression is a basic drive in ants and may vary from solitary aggression in more primitive forms such as Myrmeciinae, to aggressive recruitment and mass attack in more advanced forms such as Formicinae and Myrmicinae (Robertson 1971). Aggression can be pronounced when species compete for the same nesting sites and forage for the same food at the same time. Our confrontation tests were conducted to determine whether *F. integra* (native to Georgia) might compete successfully if introduced into territory inhabited by 3 species: (1) *Crematogaster atkinsoni* Wheeler (native to Florida), (2) the red imported fire ant, *Solenopsis invicta* Buren (introduced and widely established in Florida), and (3) the Florida carpenter ant, *Camponotus abdominalis floridanus* (Buckley) (native to

Florida). *F. integra* might be expected to compete with these 3 species, since they attend some of the same species of honeydew-producing insects [e.g., *C. atkinsoni* also attends *Neosymydobius albasiphus* Davis aphids on oak, while both *C. atkinsoni* and *C. a. floridanus* attend *T. parvicornis* soft scale on pine (see feeding behavior)]. All 4 species forage during daylight. *F. integra* occurs in terrestrial nests in semi-open woods, while *C. atkinsoni* is found in arboreal nests and *S. invicta* in terrestrial nests in the open. Pronounced aggression might be expected between *F. integra* and *C. a. floridanus*, which both nest in rotting logs and stumps in semi-open woods.

METHOD.—Simple confrontation tests (Bhatkar et al. 1972) were conducted in a lighted room at a mean 28°C and 65% RH. Confrontation units consisted of 2 plastic petri dishes 5.5 cm diam × 1.5 cm high, lined with moist filter paper and interconnected with 4 mm diam tubing. *F. integra* was placed in 1 dish and an alien species in the other. Preliminary tests with variable numbers of workers per dish indicated that a conclusive outcome within 24 h could be obtained by pairing workers as follows: 100 *F. integra* vs. 200 *C. atkinsoni*; 100 *F. integra* vs. 100 *S. invicta*; 300 *F. integra* vs. 100 *C. a. floridanus*. Final mortality tests (Table 2) involved 10 replicates each of these 3 pairings and deaths were recorded after 24 h. Confrontation indices for *F. integra* were calculated as follows: average mortality for alien species divided by average mortality for *F. integra*. Auxiliary behavioral tests consisted of observing reactions of *F. integra* workers to introduction of a probe and to manual jarring of dishes. The reactions of 20 workers confronted in dishes by an equal number of alien workers were also observed for 20 min.

TABLE 2. MORTALITY AND CONFRONTATION INDEX FOR *Formica integra* WORKERS AFTER 24-H CONFRONTATIONS WITH *Crematogaster atkinsoni, Solenopsis invicta,* AND *Camponotus abdominalis floridanus* WORKERS.

Paired species	Workers per dish*	Mortality		
		Min.-Max.	Avg.	Index**
C. atkinsoni	200	138-188	167.3	2.01
F. integra	100	75-93	83.4	
S. invicta†	100	27-48	37.5	0.52
F. integra	100	45-97	71.5	
C. floridanus †	100	42-54	49.5	0.20
F. integra	300	247-256	251.2	

*n = 10 pairs of dishes per test. No mortality occurred in 5 control dishes of each species.

**Confrontation index (for *F. integra*) = average mortality of alien species ÷ average mortality of *F. integra*.

†We (W. J. and E. S. Kloft) observed interspecific food transfer from 1 *C. floridanus* worker to 1 attacking *S. invicta* worker during 1977, using the tracer methods of Bhatkar and Kloft (1977). Such "appeasement" behavior might reduce mortality in natural conflicts.

RESULTS.—*F. integra* workers reacted to introduction of a probe and manually-induced vibrations in dishes as follows: (1) opened their jaws, (2) stopped quickly, (3) held their antennae in "U"-shape, parallel to each other and upwards, (4) moved head and forelegs towards source of disturbance, (5) curled abdomen underneath legs and raised forelegs slightly upwards, (6) simultaneously moved head and directed abdomen towards source of disturbance, (7) simultaneously raised forelegs and curled abdomen farther so that the terminal acidopore was directed toward point of disturbance, and (8) sprayed through acidopore.

The principle response of *F. integra* workers confronted by equal numbers of *C. atkinsoni*, *S. invicta*, or *C. a. floridanus* workers also consisted of spraying through the acidopore. *F. integra* workers repeatedly responded as follows: (1) raised their heads and antennae upwards and moved towards alien workers, (2) opened jaws and jerked bodies, and (3) sprayed alien workers either with or without seizure of alien workers' appendages or petiole. Both *C. atkinsoni* and *S. invicta* workers often showed crippled movement and died after 4 or more sprays, but few *C. a. floridanus* workers were killed by spray alone.

The principal responses to confrontation with *F. integra* workers varied according to species: *C. atkinsoni* seized legs and smeared venom from the tip of the abdomen; *S. invicta* seized appendages, smeared venom, stung opponents, and dismembered them; *C. a. floridanus* seized opponents' legs, petioles, or heads and sprayed.

In comparison with mortality inflicted upon *F. integra* workers, about twice as many *C. atkinsoni*, one-half as many *S. invicta*, and only one-fifth as many *C. a. floridanus* workers were killed by *F. integra* (Table 2).

DISCUSSION.—Results suggested that *F. integra* workers could overcome *C. atkinsoni* workers, but not *S. invicta* or especially *C. a. floridanus* workers. In Georgia, *F. integra* had established numerous nests concentrated in an area of about 0.1 ha (Kloft et al. 1973). Large, well-established colonies might ward off *S. invicta* or *C. a. floridanus* attacks in Florida. Finnegan (1975) ensured a more rapid establishment of introduced *F. lugubris* populations in Quebec by treating competing indigenous *Formica* and *Camponotus* species with insecticide.

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