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Insular ecology of the red wood ant *Formica truncorum* FABR.
II. Distribution, reproductive strategy and competition.

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Nest density and distribution of *Formica truncorum* and related *Formica* species was studied on islets in the Gulf of Finland. Competitive exclusion between the species appeared unlikely at the level of whole islands but case studies as well as experimental transfer of nests suggested interference competition between some of the species. Both distributional and experimental data suggested that *F. truncorum* and *F. sanguinea* especially may be strong contest competitors. Introduction of a nest population of *F. truncorum* to an islet previously free from this and related species was found to reduce the nest number of *Lasius niger* dramatically.
The distribution pattern of *F. truncorum* in the archipelago habitat is discussed with reference to reproductive strategy, sex ratio and dispersal mechanisms and related to an observed low level of intraspecific aggression negatively correlated with the distance between the sources of tested batches of workers. The clustering together of islets harbouring polydomous colonies of the species is discussed. Some tentative explanations for this "beach head effect" are offered.

Island biogeographers using distributional data for conclusions on interspecific competition have recently been criticized (e.g. SIMBERLOFF, 1982; CONNOR & SIMBERLOFF, 1983). This type of scepticism has in fact been directed against most of the theoretical framework developed from the "competition paradigm" (see SCHOENER, 1982; CONNELL, 1980, 1983; ROUGHGARDEN, 1983 and SIMBERLOFF, 1983 for different opinions in this debate). A lesson to be drawn from this discussion is that theoretical models and the new hypothetico-deductive thinking needs a complement in autecological data on single species and in ecological field experiments (CONNELL, 1980; SCHOENER, 1983; VEPSÄLÄINEN &PISARSKI 1982), and that an analysis of distributional data with respect to single pairs of potential competitors provide a usable alternative to a more generalized approach when analyzing the effect of competition on patterns of species occurrence in an archipelago (WRIGHT & BIEHL, 1982).

The autecological approach is difficult because many methodologically different aspects of the biology of a given species have to be interrelated and we usually lack sufficient knowledge for this. "Red wood ants" are known to be top predators and competitively dominant within the boreal ant assembly (VEPSÄLÄINEN & PISARSKI, 1982) but we still lack relevant data on many species within that group although some species have been studied for decades.

We here continue our outline of the autecology of *Formica truncorum* FABR. (see also ROSENGREN *et al.* 1985) with the ultimate aim of understanding the causes of its success on Baltic offshore islets. We provide some preliminary data on the distribution of other mound-building *Formica* species too, as a background to our autecological work, but do not aim at a formal biogeographic description. We do not avoid presenting preliminary observations, as our aim is to find alternative clues to a problem rather than test a predetermined hypothesis. Our excuse for using an extensive instead of an intensive approach is that neither the scale (in time and space) nor the causal context of all the studied phenomena can be known beforehand.

STUDY AREA, MATERIAL AND METHODS

Study area

The archipelago of the Gulf of Finland consists of granite islands, islets and skerries bordering the south coast of Finland (see HAILA *et al.* 1982 for general characteristics). Our main study area within this region is situated between the Porkala peninsula and Orslandet (area 2, fig. 1) but we included for comparison 14 islets from the Biskopsön-Bergön area north of Hitis (area 1, fig. 1) and 16 islets from the stretch Simsalö to Emsalö (area 3, in fig. 1, a map of the latter area published in a biogeographic study by MARTIN, 1983). Excluding islands on which we happened to know the ant fauna beforehand we selected sparsely pine-forested rocky islets within the size-class 3 ha to 6 ha. The islets corresponded to "typical" *F. truncorum* habitats (see ROSENGREN *et al.* 1985 for vegetational characteristics). Rock patches representing the same type of vegetation were selected from the mainland of area 2 (Ingå and Sjundeå rural district 40–50 km west of Helsinki). Replicas of similar vegetation on granite rock was easy to find in all areas but the degree of isolation of offshore islets was difficult to determine because the coast line is broken by long mainland peninsulas (fig. 2) or large islands far off from the coast may function as source areas especially when the prevailing wind blows against the mainland (the exceptionally "ant-rich" Sibbo Fagerö situated in area 3, 10 km from the coast, is e.g. a case in point here). The selected islets were all situated 2–6 km from a potential source area (not always identical with the mainland). Differences in height of the islets selected for survey constituted another source of uncertainty. This often neglected parameter may, as shown in a mathematical model for flying propagules, influence colonization probability (BARONI URBANI, 1971).

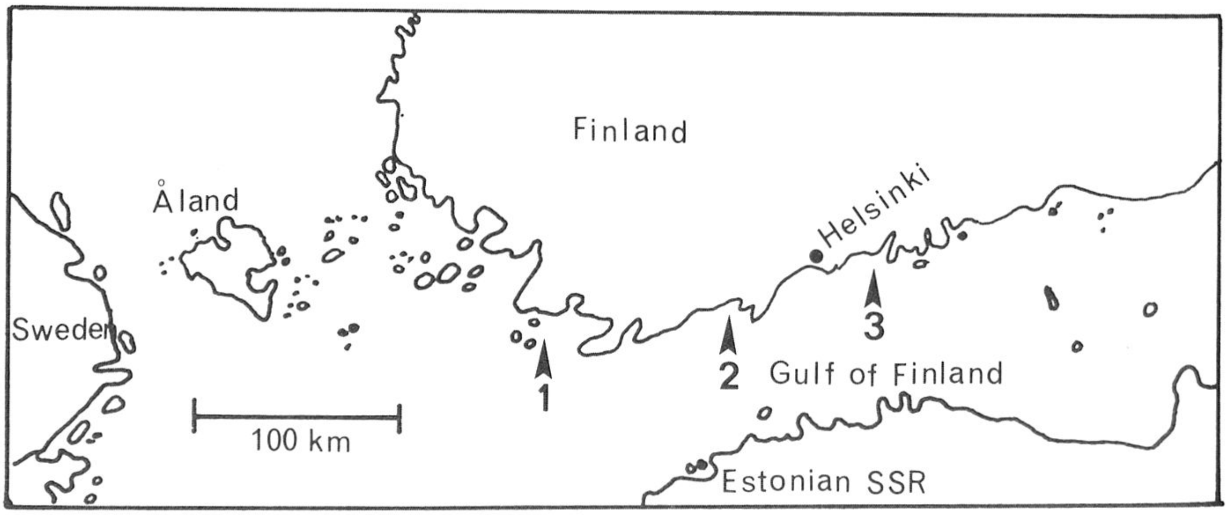

Fig. 1. Situation of the study areas 1, 2 and 3 in the archipelago of the Gulf of Finland. Rock patches examined on the mainland corresponded to area 2 (Ingå and Sjundeå rural district 40–50 km west of Helsinki).

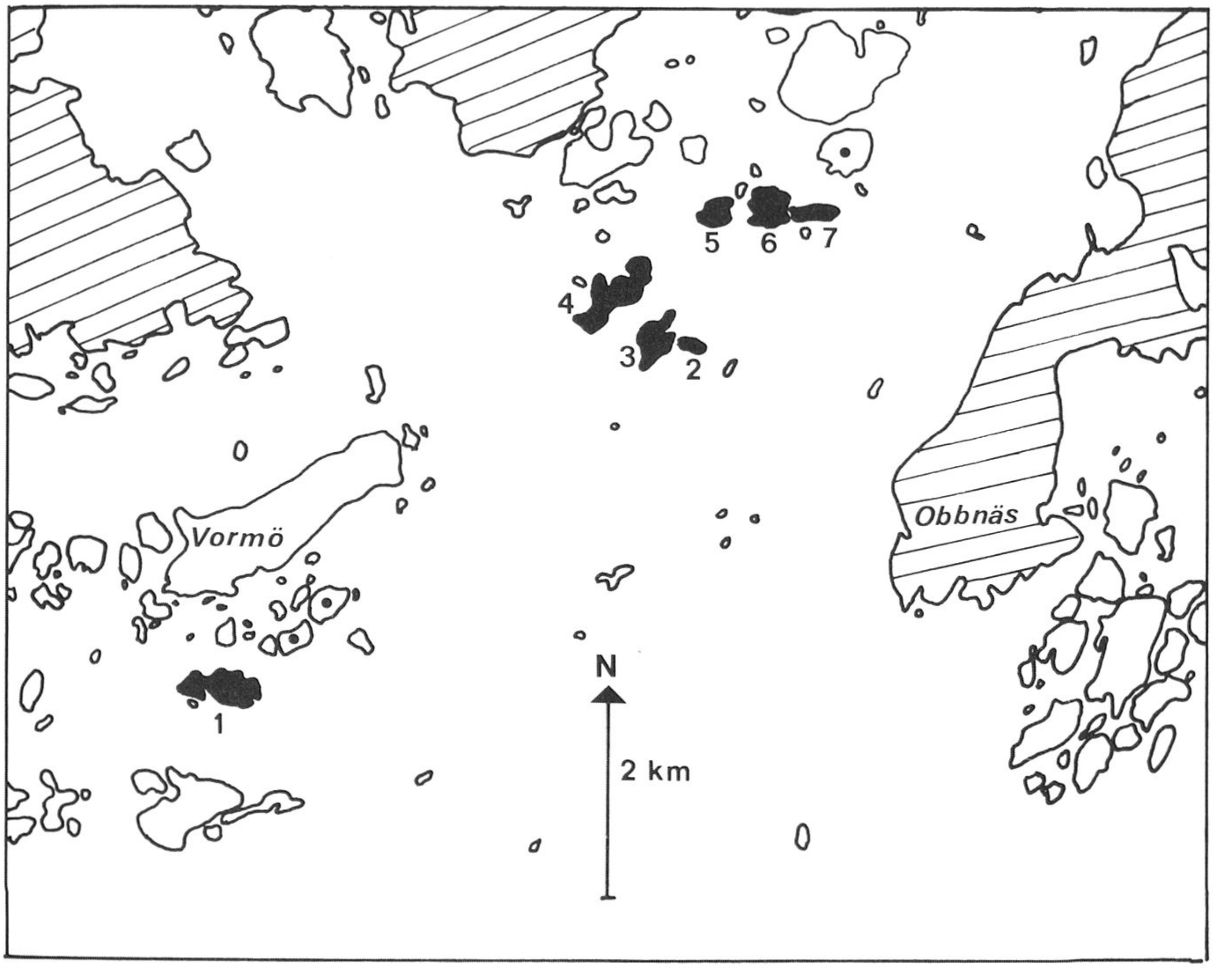

Fig. 2. Part of area 2. Mainland peninsulas are streched, islands harbouring polydomous colonies of *F. truncorum* marked black, and island harbouring 1–5 isolated nests of the species marked with black dots. Island 1 is identical with Halstö in fig. 7 while islands 2–7 correspond to islands mapped in fig. 3.

5 nonforested or semiforested skerries (only a few pines and *Juniperus* sp.) of a special, not especially common type, were selected for an ecological field experiment. The skerries which were 1–3 ha (area 2 and 3) were densely covered by stones situated on fine sand mixed with humus. The rather flat islets had in some cases shallow bays on the leeward with steeper shores on the windy side, thus acting as "traps" for organic deposits from the sea. Although situated up to 14 km from the coast they consequently supported a rather rich flora of herbs and a high density of ant nests, practically all occurring under stones. Species which, like *Lasius flavus,* build humus hillocks in mainland habitats "switch" to stones in exposed archipelago habitats (cf. the switch from mound-nesting to nesting under stones observed in the Alps by Steiner, 1929). Such exposed stony fields were found on some of the forested islets too.

The species

The taxonomically and ecologically unique status of *F. truncorum* and its close relatives in East Asia and North America has previously been pointed out (Rosengren *et al.*, 1985). *F. truncorum,* which prefers the same type of xerothermic, open habitats as *F. sanguinea,* is considered a rare species in most of central Europe (Buschinger, 1975, 1979) and is here usually characterized as monogynous and

Tab. 1. Comparison of 3 archipelago areas and one mainland area with respect to nest number per ha (mean and standard deviation for each area and species). The parenthesis in the row "no. nests" refers to the percentage of a given species of total nest number within the sampled area. The column "*rufa*-group" refers to *Formica s. str.* excluding *F. truncorum.*

ARCHIPEL.	area	no.sites	exsect.	sang.	trunc.	prat.	lugubr.	rufa	aq.-pol.	rufa-group
area 1	61 ha	14								
no. nests			3 (5)	0. (0)	15(27)	1 (2)	11(20)	17(30)	9 (16)	38(68)
nests/ha			0.071	0.000	0.259	0.018	0.175	0.286	0.143	0.597
SD			0.156	0.000	0.437	0.067	0.243	0.516	0.284	0.594
area 2	81 ha	19								
no. nests			13(13)	6 (6)	24(24)	0 (0)	1 (1)	50(49)	8 (8)	59(58)
nests/ha			0.132	0.053	0.333	0.000	0.021	0.615	0.082	0.718
SD			0.226	0.137	0.854	0.000	0.092	0.781	0.229	0.888
area 3	70 ha	16								
no. nests			7 (12)	2 (3)	25(44)	0 (0)	16(28)	3 (5)	4 (7)	23(40)
nests/ha			0.070	0.021	0.303	0.000	0.227	0.042	0.042	0.311
SD			0.199	0.083	0.576	0.000	0.339	0.098	0.167	0.403
SUM :	212 ha	49								
no. nests			23(7)	8 (2)	64(19)	1 (0)	28(8)	70(21)	21(6)	120(36)
nests/ha			0.091	0.025	0.298	0.006	0.141	0.314	0.089	0.542
SD			0.246	0.073	0.622	0.022	0.225	0.466	0.227	0.628
MAINLAND										
area 2	66 ha	15								
no. nests			7 (7)	54(52)	6 (6)	2 (2)	1 (1)	6 (6)	28(27)	37(36)
nests/ha			0.094	0.798	0.078	0.028	0.011	0.073	0.344	0.468
SD			0.261	0.694	0.259	0.075	0.043	0.173	0.582	0.669

monodomous (LANGE, 1958; BETREM, 1960; but see observations by PREUSS, 1979, and KUTTER, 1963). The species which probably shows a tendency to boreoalpine distribution (BETREM, 1960) approaches the Arctic sea in Fennoscandia (BARONI URBANI & COLLINGWOOD, 1977). It occurs on dry clearing patches and pine-growing rock throughout the mainland of Finland but appears to be especially common in the archipelago. Of 68 different colonies or populations of the species visited by us in the archipelago of the Gulf of Finland 16 (23%) were found to be polydomous (arbitrarily defined as 5 or more nests situated close to each other). *F. truncorum* is as a rule restricted to islands or islets supporting a stand of pine (*Pinus sylvestris*) but was once found on an islet lacking other conifers than *Juniperus.*

Sampling procedures

The *Formica* nests on some islands (fig. 3 and 7) were indicated on aerial photographes (1 : 1000 or 1: 2000) but in most cases (table 1) the nests were counted without mapping. Each islet or patch was examined for 1–3 h. Searching time appeared sufficient due to the open terrain but all nests of *F. sanguinea,* a very poor mound-builder, cannot be found by visual inspection. Our nest numbers for the latter species thus only has a relative meaning in comparing mainland and archipelago patches.

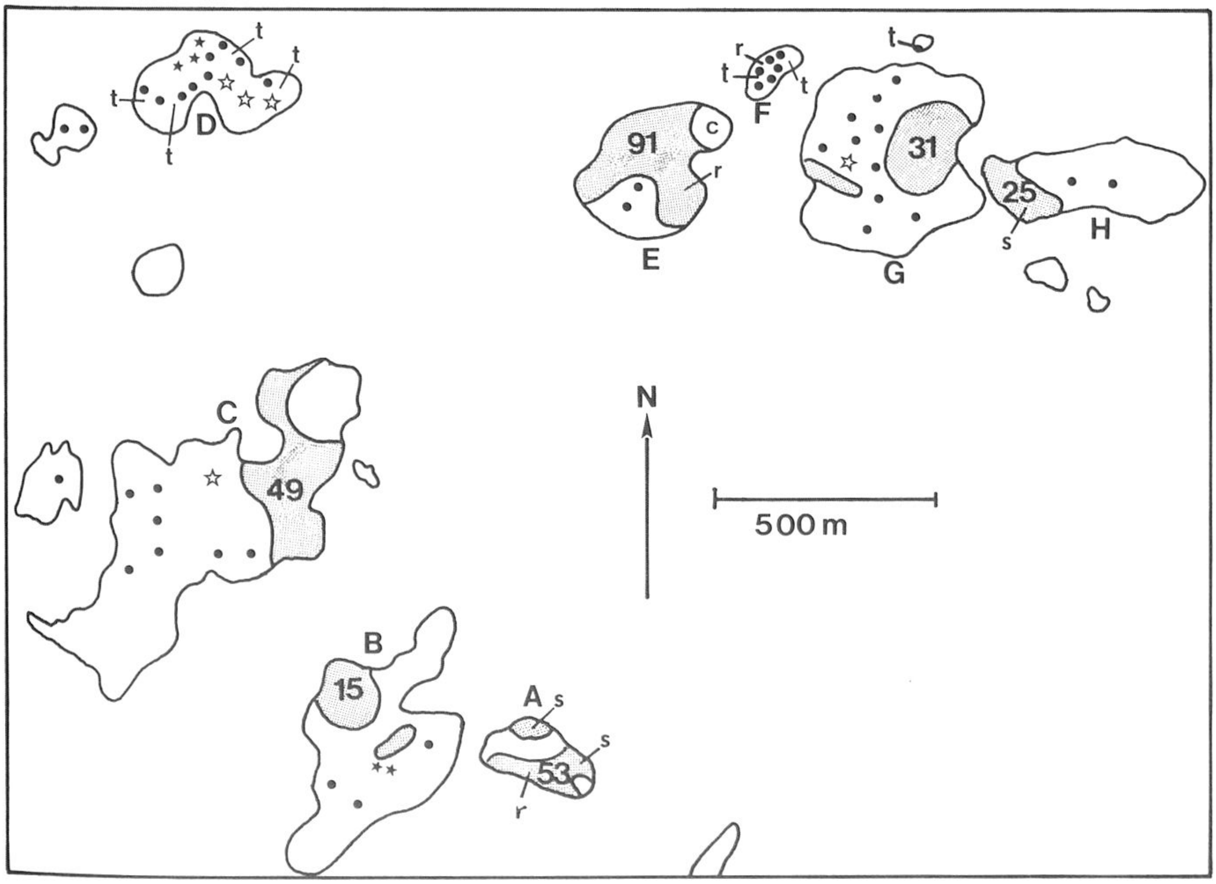

Fig. 3. Nests of *Formica s. str.* and *Coptoformica* mapped on islands of area 2 (fig. 1) and corresponding to islands 2–7 in fig. 2. Grey areas: polydomous colonies of *F. truncorum* (number = sum of all *F. truncorum* nests on the island). ● = nest of *F. rufa* ☆ = nest of *F. polyctena* ★ = nest of *Formica (Coptoformica) exsecta.* t = transplanted nest of *F. truncorum* (see text and table 3). r = transplanted nest of *F. rufa.* s = transplanted nest of *F. sanguinea.* c (on island E) = group of nests of *Camponotus ligniperda.*

Other species of ants, including *Serviformica,* were sampled only on a few islands (table 4) characterized by fields of stones usable as nesting sites. We define such "suitable stones" as flat, not too heavy stones situated on humus and/or fine sand in sun-exposed places not regularly flooded by water. A "nest" was defined as a brood-containing unit situated 0.5 m or more from the nearest site inhabited by the same species. Even the latter precautionary measure appeared insufficient as stones inhabited by the same species formed extensive mosaic patterns. Our method thus probably overestimates true nest number but we here use it only as a relative measure of population size. Stones inhabited by *F. truncorum* or situated in the immediate vicinity of nests of that species were not included in the recording.

Methodological problems in sampling and estimating sex ratios in *Formica* ants is discussed by PAMILO & ROSENGREN (1983) and by ROSENGREN & PAMILO (1986). The problems are, due to the small size of each nest unit, probable less severe in *F. truncorum* than in some other *Formica* s. str. species. The sex ratio of examined nests was in the present case usually determined from pupae only (at least 20 sexed pupae of reproductives in each sample from a nest). Mating of queens was determined by dissection and examination of squashed spermatheca by dark field microscopy.

Transfer experiments

Nests of *Formica* were transferred to new sites in order to study contest competition with other ant species. The transferred material included in the case of *F. truncorum* usually 50 to 100 l of leaf litter and approximately 25000 to 50000 ants (based on the mean of a large number of 1 dl samples taken from such leaf litter after anaesthetizing the ants with CO_2–gas, see ROSENGREN *et al.,* 1985). The material transferred to the nonforested islet (table 4) was, however, larger, about 600 l of nest material distributed in 3 different heaps on an 1,5 ha islet.

Acceptance in conspecific nests was tested with the aid of "graft tests" (ROSENGREN & PAMILO, 1983) in which a large number of ants from one nest were spray-marked and transferred to another nest where a batch of workers had been marked with another colour (the size of the "graft" was adjusted to the size of the recipient colony but was usually approximately 1000 to 2000 workers). The proportional frequencies of the two colour groups in the host nest was determined immediately after the transfer (considering the bias that transferred ants have a stronger tendency to hide within the nest material) and after a given time span of days.

RESULTS

The distribution pattern

The following *Formica* species (excluding *Serviformica*) has been observed by us in the archipelago of the Gulf of Finland: *F. polyctena* FÖRST., *F. aquilonia* YARR., *F. rufa* L., *F. lugubris* ZETT., *F. pratensis* RETZ., *F. truncorum* Fabr. (all of subgenus *Formica* s. str.), *F. exsecta* NYL., *F. pressilabris* NYL., *F. foreli* EMERY, *F. suecica* ADLERZ (all of subgenus *Coptoformica)* and *F. (Raptiformica) sanguinea.* Most of those species may be found in the xerothermic habitat of sparcely pine grown rock studied here but *F. polyctena* and *F. aquilonia* usually prefer richer forest. *F. exsecta* (like other *Coptoformica)* usually occur in meadow patches on the mainland but is fairly common in rocky sites of the archipelago.

Tab. 2. Sex ratios given as population means for numerical frequencies of males (male pupae to all sexual pupae) in different localities and years (A and E in fig. 3, I = Fårholm and II = Halstö in fig. 7). Observe that both the population mean for the sex ratio and the proportion of nests producing sexuals are different in polydomous and monodomous populations of *F. truncorum.*

POPULATION		FREQUENCY OF MALES (num. populat. mean ± SD)	NESTS SAMPLED	SPECI- MENS	NESTS / HA	SEX NESTS	TOTAL NESTS	% SEX NESTS
Polydomous								
area 2 :								
A	-79	0.71 ± 0.23	11	479	21	16	63	25
A	-80	0.91 ± 0.08	11	728	19	19	58	33
A	-81	0.88 ± 0.19	11	970	16	17	49	35
A	-83	0.76 ± 0.17	11	237	18	14	53	26
A	-84	0.76 ± 0.17	22	446	19	23	58	40
E + II	-83	0.82 ± 0.30	15	438	18	32	161	19
II	-84	0.60 ± 0.20	22	461	23	22	70	31
E	-84	0.66 ± 0.20	24	536	16	47	91	52
area 3 :								
I	-84	0.75 ± 0.17	12	288	16	12	39	31
Betberg	-84	0.75 ± 0.33	13	310	13	17	33	51
I + Betberg	-83	0.89 ± 0.19	12	397	?	?	?	?
Monodomous								
area 1-3,	83	0.40 ± 0.45	17	472	1	17	26	65
area 1-3,	84	0.54 ± 0.35	24	621	1	?	?	?

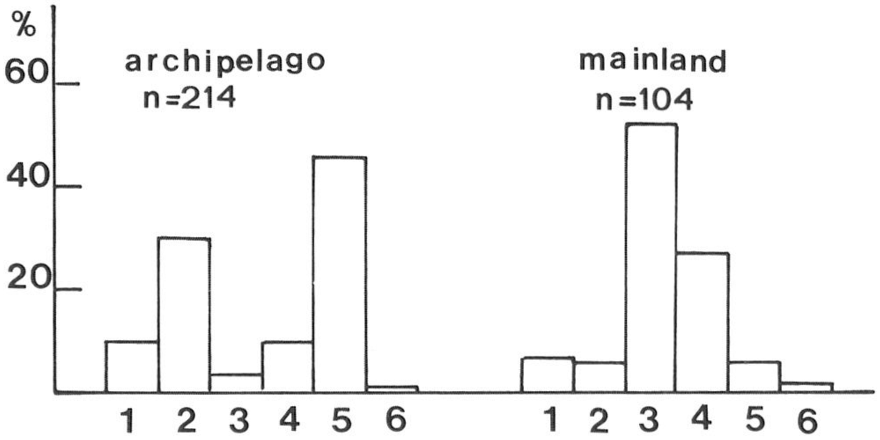

Fig. 4. Frequency of *Formica* nests (excluding *Serviformica)* of different species on archipelago islets (pooled data for areas 1–3; fig. 1) and mainland rock patches respectively. 1 = *F. exsecta,* 2 = *F. truncorum,* 3 = *F. sanguinea,* 4 = *F. aquilonia/polyctena,* 5 = *F. rufa/lugubris,* 6 = *F. pratensis.*

The number of nests/ha was calculated separately for each islet or mainland patch and mean and standard deviation calculated for each species and area. The result of this comparison between mainland and archipelago habitats has been summarized in table 1 and fig. 4. The ratio of nest density of *F. sanguinea* to nest density of *F. truncorum* is significantly higher for mainland patches (χ^2–test, $P<0.0001$). The same is true for the polydomous *rufa*-group species *F. aquilonia* and/or *F. polyctena* to the monodomous or olygodomous species *F. rufa* and/or *F. lugubris. F. aquilonia* and *F. polyctena* are taxonomically very similar in our study area (COLLINGWOOD, 1979, ROSENGREN & CHERIX, 1981) and are often impossible to separate in small samples of workers (we do not therefore keep the species apart in table 1). The species are also ecologically similar, both occurring in vast polydomous colonies, although this "large scale" strategy (ROSENGREN & PAMILO, 1983) is more pronounced in *F. aquilonia* (H. WUORENRINNE personal communication).

What is the reason for those differences in species abundancy between the archipelago and the mainland? *F. truncorum* and *F. sanguinea* occur in the same type of sunny habitats and use the same nesting sites (rock crevices, stumps etc.). This would suggest competitive exclusion but this alone cannot explain our findings. Our observations suggest that *F. sanguinea* is quite common on some large islands like Vormö (fig. 2) or Sibbo Fagerö (the latter is situated 10 km from the coast) while lacking or rare on islets of the size class studied here (see PAMILO, 1981 for an exception to the latter rule). It is consequently tempting to suggest the following interpretation: *F. sanguinea*, a "slavehunter", has been observed to migrate from a given locality after having exhausted the host species *Serviformica* from the patch (OINONEN, 1956). A strategy of "harvesting" the host species at intervals would not function on a small island where the host could be easily driven to extinction. *F. sanguinea* is able to maintain its colonies without any "slaves" (ROSENGREN, unpubl.) but the competition ability of such colonies is probably reduced. A tendency to migrate in search for new host colonies would in addition favour ant competitors with a more stationary nesting pattern and consequently a better ability to utilize the *priority* effect. Those mechanisms would be reinforced if *F. sanguinea* or *Serviformica fusca* or both have a poor recolonizing ability (poor dispersal in the archipelago was suggested for the latter species by VEPSÄLÄINEN & PISARSKI, 1982).

It seems probable that the archipelago islets studied by us simply were too small to support competitively efficient "supercolonies" of *F. polyctena* and *F. aquilonia* as those species are common on large forested islands far off from the coast (e.g. Pörtö and Sibbo Fagerö in area 3) and thus may be good dispersers. Another factor is that pine growing rock might not be an optimal habitat for permanent nests of *F. polyctena* and *F. aquilonia.* The relatively abundant occurence of those species in our mainland patches was clearly due to "leakage" from polydomous colonies situated in richer forests surrounding the rocks examined. The "hairy" species *F. rufa* and *F. lugubris* have very similar habits in the archipelago (observe that the latter, which in southern Finland is monodomous to olygodomous, is highly polydomous in the Swiss Jura mountains, see CHERIX, 1981). It is therefore interesting to note that those species tend to substitute each other in different parts of the archipelago (cf. area 2 and 3, table 1). Both area 1 and 3 contained several nests of a deviant phenotype of *F. lugubris* characterized by long antennal hairs in the workers (cf. a slightly similar form of the species described by CHERIX (1981, 1983) from the Jura mountains). COLLINGWOOD (1979) tentatively suggested the name *F. nylanderi* to this form if distinguished as a new species. The latter, which we have found also in other parts of the Finnish archipelago (including the Åland islands, specimens sent to us by L. PAULIN) has here been lumped together with the normal form of *F. lugubris* (which occur in the same areas and even on the same islets as "*F. nylanderi*"). Our sampling area 1 included one colony of *F. truncorum* with a deviant chromosome number (ROSENGREN, *et al.*, 1980). Such oddities could indicate a tendency for genetic drift in the archipelago habitat. They could also indicate a low competition pressure.

There is some ground for the latter hypothesis. A crude estimate based on the assumption that each *Formica* colony is able to defend a circular area with a radius of 30 m (this is clearly an underestimate for populous nests of *F. polyctena* but an overestimate for smaller colonies of e.g. *F. exsecta,* see also VEPSÄLÄINEN & PISARSKI, 1982) show that only 31% of the available area (66 of 212 ha, data in table 1) is occupied in the archipelago against 44% on mainland rock. This difference is however mainly due to *F. sanguinea* while the nest density of *rufa*-group ants may be higher in the archipelago (table 1). Another measure of the same point is that 22% of the 49 archipelago islets against 7% of the mainland patches had no *Formica* species at all (except *Serviformica*) and thus represented "empty squares in the checkerboard" (DIAMOND, 1975). Application of the formula of WRIGHT & BIEHL (1982) for the "shared island null hypothesis" of single species pairs gave the following results when applied to the pairs *F. truncorum* versus *F. rufa*-group (treated as a collective) and *F. truncorum* versus *F. exsecta.* Comparison *truncorum-rufa*: of 49 islets included in table 1 a total of 16 harboured *rufa* but no *truncorum*, 7 harboured *truncorum* but no *rufa*, 14 both the "species" and 12 neither "species". Inserting those values in the hypergeometric equation of WRIGHT & BIEHL (1982) gives a probability of $P = 0.19$ for the pattern being due to chance alone. The same applied to the species pair *truncorum-exsecta* (4 islets with only *exsecta*, 14 with *truncorum* but no *exsecta*, 6 with both species and 25 with neither species) giving a probability of $P = 0.11$ of the pattern being due to chance alone. We can conlcude that the results neither indicated significant associations between the species pairs nor gave evidence of a competitive "checkerboard" (as far as whole islets are concerned). The material was however fairly small making it selfevident that the results cannot be generalized. Studies carried out in archipelagos of other regions, on a larger array of ant species, indicate both statistically significant competition and (although much rarer) associations between species pairs (BARONI-URBANI, 1974).

Less than half of the archipelago islets investigated (20 of 49) harboured any nests of *F. truncorum* while the mean density of all the islets was 0.3 nests/ha (table 1). While this is high compared to our mainland patches (only 2 patches of 15 inhabited, mean density: 0.08 nests/ha) it is low compared to the islands mapped in fig. 3. The mean for the latter area is 5 *F. truncorum* nests/ha but some of the larger islands of the group included densely forested parts, not suitable for the species, while our "control" islets were selected with the aim of minimizing unsuitable vegetation. We have found other islands inhabited by dense nest populations of *F. truncorum* (fig. 7, not included in table 1 because the islands fell outside the size class or we knew of the colonies beforehand) but the occurence of 6 densely inhabited islands (fig. 3) close to each other can hardly be a coincidence.

Reproductive strategy and dispersal

Periodicity

F. truncorum alates of our study area usually emerged between mid-July and mid-August 1–3 months later than in true *rufa*-group species (except *F. pratensis* which according to our notes often has a second generation of sexuals in August) but at the same time as in *F. yessensis* in northern Japan (ITO & IMAMURA, 1974; HIGASHI, 1980, 1983). As in the latter species (see HIGASHI, 1983) sexuals were observed on the surface of nests only in the morning and usually disappeared before 10–11 a.m. We observed this activity rhythm also in a semi-natural nest (natural leaf litter, natural light conditions under plate of glass, nest container in a shady place) where the winged queens regularly appeared on the nest surface each morning but usually hide in the nest material before noon. An example: 8.00 (17°C) 50 alate ♀, 9.00 (17.8°C) 43♀, 10.00 (19.5°) 29♀, 11.00 (20.2°C) 6♀, 12.00 (19.7°C) 1♀. This periodicity in virgin queens of the species is in contrast to the case in *F. polyctena* where alate females were observed to leave nests by flight between 9 a.m. and 16 p.m. (ROSENGREN & FORTELIUS, 1986). A demarcated activity rhythm in the sexuals can be expected to synchronize the mating flights of alates from different nests.

Orientation

Our observations of alate males and females of *F. truncorum* leaving natural nests using their wings were too few to allow firm conclusions about orientation but the alates observed steered against light openings in the pine stands or rose high in the sky following a spiral path. Males were observed to fly longer than females many of which bumped to the ground a few meters from the nest. Females were also observed to climb small trees surrounding the nest (cf. CLARK & COMANOR, 1972) and sitting there for hours without taking flight during the observation period (some hours). All of 37 alate females and 21 males released from 2 different containers placed on a small treeless skerry far out in the sea flew straight downwinds (see also CLARK & COMANOR , 1972) until the vanishing point (wind velocity measured with a Lamprecht 34 hand cup anemometer was 1.5 to 2 m/s, the containers with ants shielded from wind during the experiment). A repetition of the latter test on the leeward shore of a forested islet (wind velocity 0.5–1.0 m/s) showed again that all tested females started to fly downwinds against the sea. But in this case 4 out of 11 tested females later changed their direction and returned to the islet along a curved path. This was probably not a homing reaction because a single queen followed by binoculars was observed to similarly approach another forested islet before it disappeared from sight. Our field experiments are still too few to admit firm conclusions but they suggest the following hypothesis. The queens starting from the nest fly against the lightest parts of the canopy thereby avoiding obstacles in the immediate vicinity of the nest. The orienting reaction may, however, later change so that the ants approach visual silhouettes contrasting against the sky and the sea. Such a spontaneous preference for a dark pattern contrasting against a light background was demonstrated in red wood ant workers (Rosengren, 1971) and occurs in several flying insects e.g. the "hypsotaxis" described by Schneider (1967). Hypsotaxis toward the silhouettes of forested islands appeared probable also in *Camponotus* females released from a boat (Rosengren, unpubl.). There can be no doubt, in spite of the possibility that alates of *F. truncorum* may approach island silhouettes when flying over the sea, that both males and females in the main are positively phototactic. Ants of both sexes were thus observed to fly against the windows when released in the laboratory and we happened to see several flying *F. truncorum* males circling a lamp for more than one hour after "light on" in an artificial light-dark cycle. The few flights observed in calm weather did however suggest an arbitrarily set orienting angle to the sun rather than a tendency to steer directly against it. Nothing in our observations support the hypothesis that males actively orient to females (or *vice versa*) through pheromones acting at a distance; males and females in the field tests discussed above were housed in different buckets, 2–5 m apart, but in no case was an alate observed flying toward a bucket containing alates of the opposite sex. Neither were flying males and females observed to approach each other in the air as claimed for the related *F. haemorrhoidalis* (Mackay & Mackay, 1984).

Mating behaviour

Several copulation attempts but only two copulations were recorded in the field on the surface of nests (males and females probably emanating from the same nest). Captured sexuals copulated readily on the floor of glass vials during the morning hours when brought together in the laboratory, however. Mean copulation time was 3.1 ± 2.9 min (n = 16, range: 0.5 min–7.5 min) and thus appeared longer than in some other *Formica* s. str. (Rosengren, unpubl.). Freshly mated queens were still able to fly. The shortlived males were highly unselective "trying" to copulate with each other and even with workers, while females obviously "decided" if the numerous copulation attempts of males (often simultaneously entering the same female) failed or not. One female was observed in successive copulae with 5 different males (copulated males removed from the test vial which contained 10 males and 1 alate female) while a single male was observed in copulae with 3 different females (test vial with 10 alate females and 1 male). The above experiments were made in light. Can mating occur also in darkness e.g. within the nest if bad weather prevents the alates from leaving it? We divided winged females caught from a nest lacking male alates into 2 groups (6 females in each) both of which was kept in vials containing 10 males in each. One of the vials was stored for 3 days completely isolated from light while the other was kept in daylight. Examination of receptacula seminis gave the following result: 3 females of the group stored in darkness had mated against 2 females in the light group. The difference is obviously insignificant meaning that copulation behaviour is probably not influenced by light.

Dispersal

Some of our semi-natural flight tests with *F. truncorum* gave the impression that alates of this species were very efficient dispersers because most of the alates took flight within a short time span. This impression was strengthened by our observation of natural nests loosing all their alates within two days. Most of our trials to observe morning flights from semi-natural nests of *F. truncorum* failed however, which indicates that the conditions for flight in this species may be quite restricted. Flights were not seen if the temperature in the morning was too low (below about 20°C), if wind velocity was above 2 m/s or if the surface of the nest became too heated by the sun (the alates protected in the latter case within the nest) and we find it possible that air humidity too could have influenced the situation (we observed especially intense flights slightly before a thunderstorm). The required combination of climatic factors favourable for mating flight might not be present each season and especially not in the harsh environment of the archipelago. Conditions favourable for mating flights did not exist in July 1984 (rainy weather, mean temperature exceptionally low: 15.5°C) although the beginning of the season had been warm and the nests abounded with alates, some of which emerged unusually early this year (males were found in some nests already in the beginning of July). In the beginning of August some nests of a polydomous colony (islet A, area 2) contained wingless queens together with males and a few winged females all occuring in the uppermost part of the nests. Dissection of a sample of those dealated queens indicated that most of them were mated (7 out of 8 dissected queens had filled receptacula seminis) while their behaviour suggested they had de-alated a few days ago (older queens occur according to our observations in this and other *Formica s. str.* species mainly during the "sunning period" in spring in the upper part of the nest). A very similar case was during the same season independently observed by one of us (P.P.) on the Hangö peninsula (between area 1 and area 2 according to

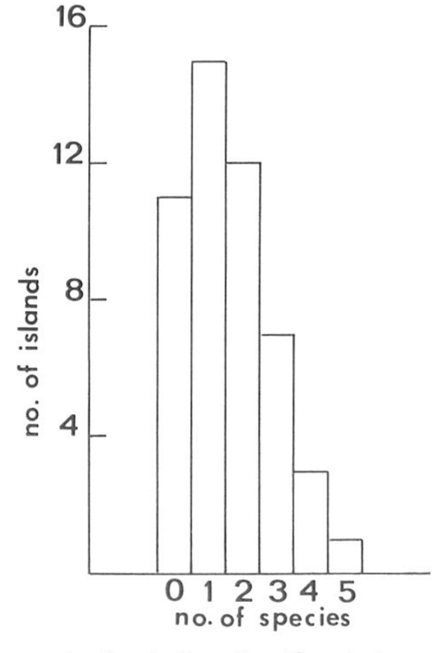

Fig. 5. Number of *Formica* species (excluding *Serviformica*) on pine-covered rock islets (pooled data for areas 1–3) in the archipelago of the Gulf of Finland.

fig. 1). Here one nest contained 20 de-alated females (together with 3 still alate females in the upper part of the nest). 18 of the de-alated females had filled spermatheca but the state of the ovaries including the corpora lutea suggested they had hatched during the same season. Another nest of the area harboured similarly 28 dealate queens in its upper part, 26 of which had mated. Only one of the mated queens had a corpora lutea stage suggesting that it may have hatched during earlier seasons.

There are several possible mechanisms explaining the development of polygyny in *Formica* ants (Rosengren & Pamilo, 1983). On the proximate level those explanations include a tendency of alate queens to strip their wings already before dispersal flight and mating (Gösswald & Schimdt, 1960). Such precopulatory wingstripping, although of high frequency in other polygynous species/ populations from southern Finland, is however of relatively low frequency in *F. truncorum* (Fortelius, in preparation). Our present observations make it tempting to suggest that narrow diel and/or climatic restrictions on the mating flight (perhaps reflecting a trend to syncronized matings) could also contribute to polygyny through a quite trivial mechanism: bad weather (forcing young queens to mate within the mother nest).

Both winged and wingless *F. truncorum* females floated on water for a time span which for unknown reasons was very variable (brackish water effect of sea waves "simulated" by shaking the container in which the queens were floating). All individuals in 3 groups of wingless *F. truncorum* queens (6–10 individuals in each group) sank to the bottom within a day. 3 of 8 queens remained floating for 4 days and in the fifth group 6 of 7 wingless queens still floated after 6 days (both differences in the origin of the queens and difficulty in standardizing shaking of the containers could have contributed to those variations). The wingless queens float on the gaster, which is shiny in many *Formica s. str.* but dull in *F. truncorum.* This probably explains why floating is better and less variable in wingless queens of *F. rufa* and *F. polyctena* (Rosengren, unpubl.) The wingless queens floating on the gaster (winged queens often float on thorax with the wings extended in the surface film) have their heads and thoraxes submerged and appear completely lifeless in this state. They usually recover completely within some hours. Wingless queens of *F. truncorum* and some other tested *Formica s. str.* species can actually be submerged completely for several days in cold brackish water without any apparent damage (Gyllenberg & Rosengren, 1984). The queens were found to survive submergence in a physiologically altered, apparently lifeless, state characterized by very low oxygen consumption (Gyllenberg & Rosengren, 1984). There is thus every reason to believe that hydrochoric transport is a potentially important dispersal mechanism in *Formica* queens especially when many other insects in the Baltic archipelago habitat also disperse by hydrochoric or anemohydrochoric methods (Palmen, 1944).

The wind in summer usually blows from the south-west i. e. towards the mainland (northern winds are not only less usual but usually mean cold weather not likely to favour nuptial flight in ants). Both hydrochoric and anemochoric transport of *Formica* propagules may thus occur less often from the mainland towards offshore islets than in the reverse direction. This rather than distance *per se* could well be the main factor determining colonization probability and distribution pattern of *Formica* in the archipelago considering that a tendency to fly downwinds and an ability to float on water occur in other *Formica* too. The fact that our polydomous colonies of *F. truncorum* in area 2 (fig. 2) all lie along a south-western trajectory may thus not be a mere coincidence.

Sex ratio

A low frequency of nests producing alates in our polydomous colonies of *F. truncorum* can be contrasted against the high frequency of nests releasing alates in a sample of monodomous colonies of the species (table 2). Previous results (PAMILO & ROSENGREN, 1983) pointed to a difference between monodomous and polydomous colonies of *F. truncorum* with respect to sex ratio, polydomous colonies being male-biased while monodomous colonies had a population mean not significantly different from 1:1. Our present material (table 2 and fig. 6) confirm the latter rules. Why are polydomous colonies of *F. truncorum* markedly male-biased

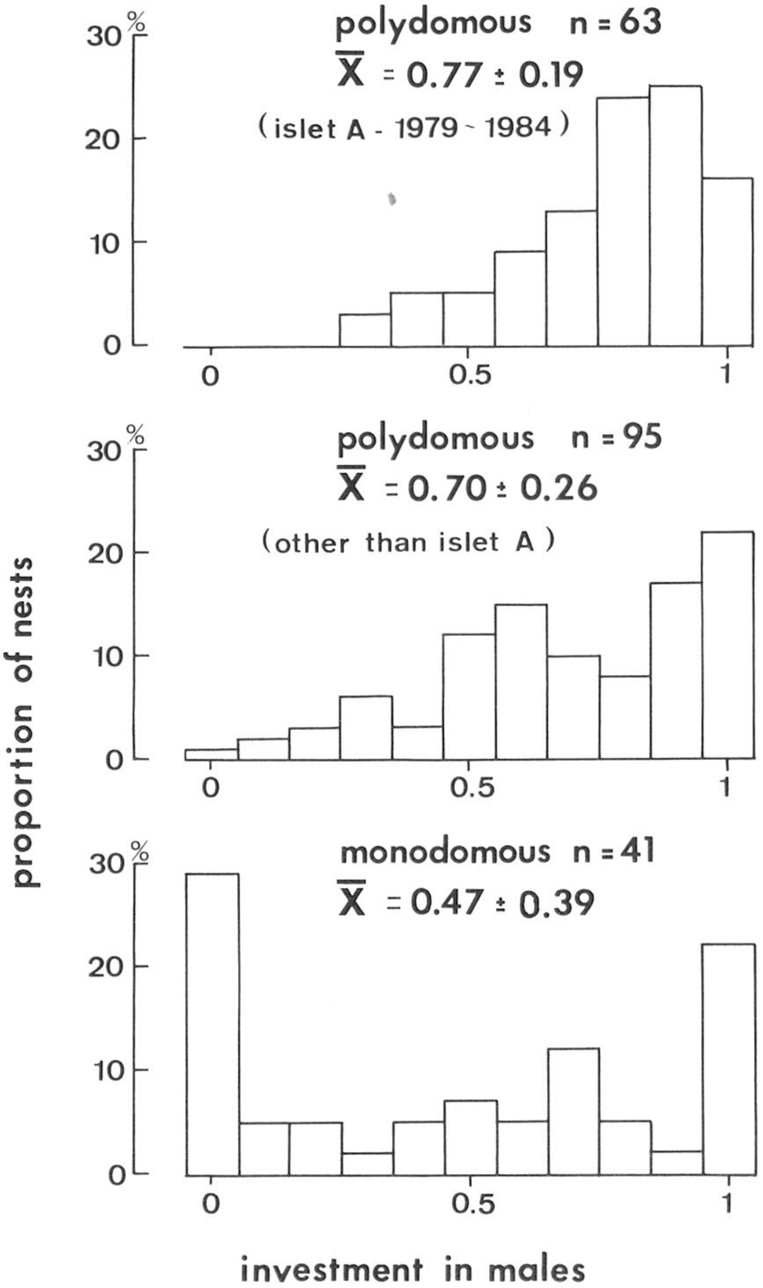

Fig. 6. Distribution of colony sex ratios given as PI in males (0 = all-female nests, 1 = all-male nests) and representing results for the *F. truncorum* populations listed in table 2 (data for different years and/or populations combined). X̄ ± SD gives population means for investment in males and n the total number of nests examined. The Wilcoxon rank test gives a significant deviation from an 1:1 investment ratio in the case of the polydomous populations only (polydomous population on islet A: R = 60, $P \ll 0.001$; polydomous populations from other sites: R = 969, $P \ll 0.001$; monodomous populations: R = 457, P = 0.73).

while polydomous colonies of *F. aquilonia* and *F. polyctena* by contrast often are markedly female-biased (PAMILO & ROSENGREN, 1983)? One reason could be the markedly patchy habitat in *F. truncorum* (rock and clearing patches) which means that polydomy easily leads to saturation of the local patch increasing sib competition among queens (truly forest-living species like *F. aquilonia* may in the boreal region retain the option of budding *ad infinitum*, see ROSENGREN & PAMILO, 1983, 1986). Both males and females can be used for dispersal (although males have a higher dispersal ability than the clumsy females) but males are smaller and thus "cheaper" to produce (bombcalorimetric measurements in *F. polyctena* indicate in addition that males contain about 3 J/mg less energy than females, ROSENGREN *et al.* unpublished). The proximate mechanism shifting the sex ratio toward a surplus of males may be quite trivial e.g. scarcity of food due to overcrowding when the supranest reaches the carrying capacity of the patch (cf. BRIAN, 1979).

Our data giving both frequency of males as a numerical population mean (table 2, see PAMILO & ROSENGREN, 1983 for calculations and sampling methods) and "parental investment" or PI (based on the dry weight ratio 0.85 males/females confirmed for this species, see PAMILO & ROSENGREN, 1983) indicate a lower frequency of nests producing mixed sexual brood in monodomous than in polydomous populations of *F. truncorum* (fig. 6). This difference may reflect a smaller number of reproducing queens per nest in monodomous than in polydomous populations of the species (if assuming that a single queen "decides" either to lay all-male or all-female sexual brood while multiple queens of a nest cannot "agree"). Numerical frequency of males appeared in some cases lower and the percentage of nests producing sexuals higher in 1984 than in 1983 (table 2) a difference possibly attributable to climatic fluctuations (cf. observations in ROSENGREN *et al.*, 1985).

Interspecific competition and coexistence

Major competitors

All species of *Formica s. str.* are generalists with respect to protein diet and thus should by expected to compete for the same booty insects as has actually been demonstrated for the species pair *F. rufa* and *F. truncorum* foraging in the same xerothermic island habitat (ROSENGREN *et al.*, 1985). They also use honeydew from the same tree-living aphid species (mainly *Cinara* sp. and *Symydobius oblongus* in southern Finland). The fact that different mound-building *Formica* species nevertheless often occur on the same small island (figs. 3, 5 and 7) is partly explainable by habitat heterogeneity, each species favouring different degrees of exposure, microclimate and vegetation. Islands G and D (fig. 3) demonstrate the latter point because here the nests of the *rufa*-group occur in more densely forested parts than the nests of *F. truncorum*, which concentrate on almost naked rock. Such habitat differences may occur between the centre and peripheral shore area even of smaller forested islets and the apparently very high degree of coexistence indicated by fig. 5 is at least partly due to habitat heterogeneity. Of 20 islets in the size class 3–6 ha harbouring *F. truncorum* (the same material as in table 1 and fig. 5) 16 (80%) thus had at least one other mound-building *Formica* species. This fact is by no means always explainable by habitat differences on the islet, as nests of *F. rufa*, *F. lugubris* and *F. exsecta* may occur in the same type of exposed archipelago sites typical for *F. truncorum*. Such cases are represented by the islands B, C and E according

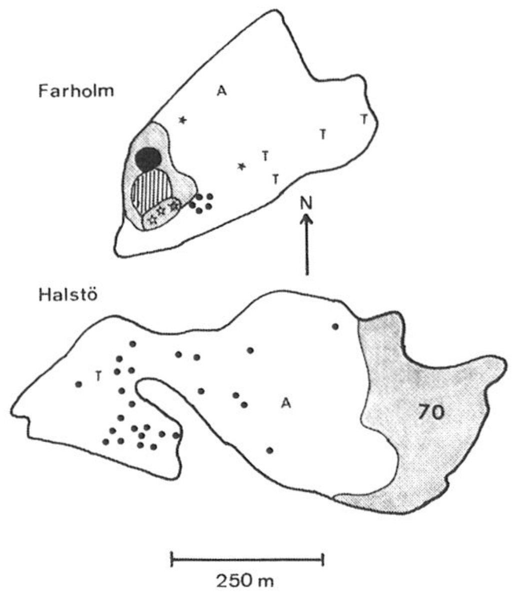

Fig. 7. Situation of *Formica* species on the forested archipelago islands Fårholm (area 3 in fig. 1) and Halstö (area 2). Grey and black areas: polydomous nest systems of *F. truncorum* (T = isolated foundings of *F. truncorum*). Empty stars within bordered grey area on Fårholm marks nests of *F. lugubris* later invaded by *F. truncorum* (filled stars: still intact nests of *F. lugubris*). The stretched area (Fårholm) marks a spruce thicket originally isolating *F. truncorum* (black area) from the rock inhabited by *F. lugubris*. Points = nests of *F. exsecta*. A = nests of *F. aquilonia*. For further explanations, see the text.

to fig. 3 and by the islands mapped in fig. 7. We may suggest stochastically determined priority effects (see VEPSÄLÄINEN & PISARSKI, 1982) with respect to different parts of one and the same islet as nests of different species often are separated only by distance. But even distance between heterospecific *Formica* nests were in some cases surprisingly short. The distance between a nest of *F. exsecta* and *F. rufa* (islet D fig. 3) was thus only about 20 m, and still shorter distance were in several cases found between flourishing nests of *F. exsecta* and *F. truncorum* (the nests only 5 m apart in two cases, see also fig. 7). *F. exsecta* was on the mainland not infrequently found together with *F. sanguinea* too, and it happens that all findings of *F. pressilabris* so far recorded in our study areas occur very close to nests of *F. exsecta* (see also two cases mapped in PAMILO & ROSENGREN, 1984). We even know of two cases on the mainland where monodomous *F. truncorum* nests were found on the same rock as *F. sanguinea* (measured distance between heterospecific nests: 23 m and 31 m) although results to be discussed indicate that the latter coexistence may be unstable. While we cannot exclude the possibility of mutualistic mechanisms in some of the cases listed above (the relation between *F. pressilabris* and *F. exsecta* appears to be a promising candidate) we would expect interference competition when foraging ranges of some of the species overlap. Interspecific contests are rarely seen in undisturbed habitats, however, and consequently we have only indirect evidences of competitive exclusion going on (see also VEPSÄLÄINEN & PISARSKI, 1982). Those evidences are:

1. In a follow-up study of monodomous *F. truncorum* colonies on the mainland we found that 8 out of 13 colonies died out in the patch within a 5 year period. This crudely corresponds to a yearly extinction rate of 10% (observe that we do not refer here to the abandoning of individual nests, a process with a still higher frequency). Two of those extinctions were accompanied by the previous *F. truncorum* nests be-

ing inhabited by *F. sanguinea* instead. Our sampling of sexual pupae in a larger material of monodomous *F. truncorum* nests gave further evidence for such substitutions because a *F. truncorum* nest producing sexuals in 1983 had "turned into" a *F. sanguinea* nest by 1984.

2. The more southern (and more exposed) of the two *F. rufa* nests situated on the island E (fig. 3) was found desolated in early summer 1983 while *F. truncorum* foragers which had previously avoided this part of the island were found on its surface. It seemed unlikely that the *rufa*-population of the desolated nest had migrated to the conspecific mound left (situated in a more shady position within a birch thicket) because our transfer experiments (below) showed that the two populations were mutually hostile. In summer 1984 the desolated *rufa*-mound was found inhabited by a *F. truncorum* colony and some new nest foundation of the latter species were recorded within the previously *truncorum*-free area of island E (fig. 3).

3. Our most impressive case was a rock patch on the Fårholm island of area 3 (fig. 1, fig. 7) completely monopolized by on oligodomous nest group of *F. lugubris* since at least 1967 (the xerothermic habitat and the colony described in Rosengren, 1971: 46). An adjacent rock patch on the island was similarly monopolized by about 10 nests of *F. truncorum* confined to this site (black area in fig. 7). A third, lower, rock area was inhabited by a small polydomous nest group of *F. exsecta* which had developed by fissioning from a single mound present in the late sixties (description of this nest and the habitat in Rosengren, 1971: 47). Although *F. lugubris* population on the rock patch (bordered in fig. 7) comprised 3 vigorous mound by 1975, it had disappeared without trace by 1981, at the same time as 5 large *F. truncorum* nests were found on the site. The latter species had gradually spread to other parts of the island too, probably mainly through fissioning from the original nest group, although a few nests clearly represented independant foundings, perhaps by individual foundresses from the original "beach head" (fig. 7). We counted a total of 25 *F. truncorum* nests on the island in 1981 and 39 in 1984, an increase attributable to the unusually high mean temperature of the summer preceeding the season of 1984 (see Rosengren *et al.*, 1985). Spatial expansion of the supercolony area had, however, in the main, reached its present maximum (fig. 7) already by 1981. The expansion of the supranest territory of *F. truncorum* brought this species into close contact with *F. exsecta* before 1981, but no clear effect on the latter species could be seen (the number of inhabited mounds was 5 in both 1981 and 1984, but had slightly decreased from the late seventies, when 7 nests were counted during a casual visit to the island).

The latter case study required a total observation period of 17 years but studies of species interaction can be accelerated by introducing excavated *Formica* nests to areas inhabited by other *Formica* species. This procedure is however rather artificial and the result sensitive to unknown variable and methodological errors. Conclusions of this "ecological experiment" can thus only be indicative.

A total of 43 *Formica* nests were transferred to pine-forested rock habitats in the archipelago (area 2 and 3 in fig. 1, 13 transfer sites shown in fig. 3) or to similar habitats on the mainland (the latter only when the contestant was *F. sanguinea).* The introduced colonies were placed around stumps, logs or large stones situated at a distance of 10 to 20 m from pre-existing *Formica* nests ("contestants" in table 3) while 6 transfers were made to small forested or semiforested islets lacking other *Formica* species than *Serviformica fusca.* The main difficulty in interpreting the results was that part of the introduced colonies responded to attack by migration from the spot. This did not bring them outside the reach of the contestant, however, although probably decreasing extermination probability. We made the following observations:

1. *F. truncorum* colonies introduced within nesting areas of *F. sanguinea* survived to a lower degree than when placed near nests of *F. rufa* or *F. exsecta* (table 3).
2. It seems tempting to postulate "enemy specification" (HÖLLDOBLER, 1979, 1983) between *F. truncorum* and *F. sanguinea* as the reciprocal test (*F. sanguinea* introduced into the area of *F. truncorum)* also led to rapid extermination of the introduced population (fig. 3, table 3).
3. The latter interpretation is complicated, however, by our observation that *F. sanguinea* in 6 out of 14 cases used a raiding technique against *F. truncorum* essentially similar to raiding of its host species *F. fusca*. Columns of *F. sanguinea* workers were thus observed in some cases approaching the introduced nests shortly after introduction. The attackers, although by and by killing workers and queens, concentrated on pupae which rapidly were carried away without efficient resistance from the defenders. Plundered pupae were stored living within the *F. sanguinea* nests in large heaps and probably gradually consumed as food (we did not notice any imago workers of *F. truncorum* hatching within the nests of the robbing species). Repeating the experiment at one *F. sanguinea* colony which had plundered and exterminated an introduced colony one week before did not result in raiding, indicating that this behaviour may indeed be predatory in function. Some other contestants too showed rapid extermination of introduced colonies (e.g. *F. truncorum* against *F. sanguinea* and *F. rufa*) but attackers concentrated on workers instead of pupae (which were usually not carried away before most defenders had been killed) and the fights observed resembled in some cases positional war, with clusters of fighting workers in the terrain.

   Although our observations of *F. sanguinea* attacking introduced nests of *F. truncorum* thus suggest predation rather than contest competition as the proximate cause, raiding could at the same time represent a mechanism for competitive exclusion (the ants at least do not make the distinction).
4. *F. sanguinea* exterminated most introduced *F. rufa* nests too, which accords with observations by LÖFQVIST (1976), while showing weaker response to *F. exsecta* (we do not know if contest in those cases was associated with predatory raiding).
5. We observed when watching *F. rufa* workers approaching an introduced nest of *F. truncorum* that contest in this case included both incidents of real fight and a "ritualized" element, attackers hesitating at an "invisible border" surrounding the introduced nest. Fighting behaviour, if observed at all, appeared weak when contrasted to the violent attack of resident *F. rufa* against an introduced conspecific nest. The *F. rufa* colony which was transferred from island G to island F (see fig. 3) was totally exterminated within 2 days while a *F. truncorum* colony introduced on the same islet and at the same distance from a *F. rufa* mound was not attacked within at least 2 months. This was not explainable by the size of the introduced populations as the introduced *F. rufa* colony was larger than the introduced *F. truncorum* colony.
6. The tendency of a *Formica* resident to win a contest was not clearly related to the sizes of the colonies involved. Some of the exterminated *F. truncorum* colonies were thus clearly larger than the *F. sanguinea* colonies attacking them. *F. sanguinea* also won its contests against larger colonies of introduced *F. rufa* although the latter species had larger workers in addition (see also LÖFQVIST, 1976). Human impressions about the "aggressiveness" of different ant species is probably an even poorer predictor of the outcome of interspecific conflicts among ants.

Tab. 3. Experiments with transfer of *Formica* nests to sites inhabited by other *Formica* species ("contestants") or to 6 "control" islets lacking such species (non *Formica*). Transfers were carried out in July (or early August) 1982 to 1984. Transferred *F. truncorum* colonies appear to survive better when the contestant was *F. rufa* compared to the case that the contestant was *F. sanguinea* but the difference is, possibly due to the small material, not statistically significant ($\chi^2 = 1.29$, 1 df, $0.3 > P > 0.2$).

Contestant	No. transfered nests	No. exterminated in 2 weeks	2 months	% survival
	F. truncorum			
F. sanguinea	14	6	10	29
F. exsecta	3	1	1	67
F. rufa	7	0	2	71
non Formica	6	0	0	100
	F. sanguinea			
F. truncorum	3	3	3	0
	F. rufa			
F. truncorum	2	1	2	0
F. rufa	1	1	1	0
F. sanguinea	3	1	2	33
	F. exsecta			
F. sanguinea	4	0	1	75

7. All of the six *F. truncorum* colonies introduced to islets lacking mound-building *Formica* species survived more than 2 months (table 3). 4 of those colonies had been introduced in 1982 and still lived in late summer 1984. Survival for more than a year was evident also in 3 out of 5 *F. truncorum* nests transferred to *F. rufa* territory and in 1 out of 2 cases transferred to an area inhabited by *F. exsecta.*

8. The *F. truncorum* colonies introduced to semiforested islets lacking mound-building *Formica* were initially vigorously attacked by *Lasius niger* in large numbers. The success of the mass mobilization of attacking *L. niger* was poor, however, and later the roles became reversed; *F. truncorum* clearing the vicinity of their nests of *L. niger* colonies. We observed on one of those islets a "fighting column" of large *Camponotus herculeanus* workers attacking one of the freshly introduced *F. truncorum* colonies in the evening. Those sluggish ants proved to be surprisingly efficient contestants, cutting large numbers of *F. truncorum* workers into pieces, but were, due to their small number, unable to kill more than a fraction of the introduced population.

The dramatic outcome of some of our experiments with introducing ant nests into new areas (see also ROSENGREN & PAMILO, 1983) raises the question why the same species which vigorously attack an introduced colony may nevertheless "habituate" to the presence of the same species during natural conditions. This process of "habituation" was seen also in our transfer experiments, the frenzied mass mobilization of attacking *L. niger* was e.g. seen only during the first days after introduction and faded away long before the population had been clearly reduced by *F. truncorum.* We may speculate that evolution may have favoured a "Blitzkrieg" tactic of using all available forces in exterminating a competitor. If this attempt fails, due to the strengths of the opponent, the next favourable option could well be defence of a territory by ritualized contest or even appeasement behaviour (see the cases of "interspecific trophallaxis" reported by BHATKAR & KLOFT, 1977; BHATKAR, 1983).

Another question is why *F. truncorum* did not naturally occur on our "control" islets if the species was able to thrive there. One reason could be that the host species, *F. fusca* (temporarily parasitized by the *Formica s. str.* foundress), occurred on only two of those islets and that the islets – all of which were rather exposed – abounded in *L. niger,* a species which, although usually too weak to exterminate mature colonies, may prevent *Formica* foundresses from settling by killing them before they find a host colony (killing of *Formica s. str.* queens by *L. niger* was actually observed during the course of the study although we do not yet know the significance of this factor).

It can be argued that our case studies and ecological experiments were "biased toward the detection of interference mechanisms" (ROUGHGARDEN, 1983). While this is literally true, interference, as pointed out by CONNELL (1983), is probably a good indicator of exploitative relations.

Minor competitors and prey species among ants

We used a sampling procedure based on the presence of fields of "suitable stones" (see methods) on some of the islands in order to assess the influence of *F. truncorum* on the ant assembly. We compared for this aim islands A and E (fig. 3) to other pine forested islets lacking *Formica* species other than *Serviformica fusca* (table 4). The "suitable stones" on the islet harbouring *F. truncorum* were situated in more exposed sites than was the rule on the forested control islets. We therefore included in the comparison also some nonforested or semiforested islets (only a few pines in the centre of the islet) representing the most sun-exposed fields of "suitable stones" (table 4). The latter group of islet was used also as a reference for the ecological experiment carried out on a semiforested islet (table 4).

Our forested control islets (1–4 in table 4) are not significantly different from each other with respect to the proportion of inhabited sites (χ^2-test, 3 d.f., $025<P<0.5$) while islet A (21 nests/ha of *F. truncorum*) had a significantly lower proportion of inhabited sites (excluding *F. truncorum,* 1 d.f., $P<0.0005$) than the control islet with the lowest proportion of inhabited sites (islet 1 in table 4). The data are however inconsistent as island E (15 nests/ha of *F. truncorum*) did not show a clear decrease in the latter respect. But A and E both show an obvious reduction in the proportion of sites inhabited by *L. niger* (compared to both forested and nonforested control islets). *Myrmica* sp. may have been reduced too, but the other species did not show clear evidence of a reduction (table 4) and the proportion of *F. flavus* was in fact higher on islet E than on any of the forested control islets.

The above tentative conclusions were supported by an ecological experiment carried out on one of the semi-forested islet. Most "suitable stones" on the 1.5 ha islet were examined in July 1982 shortly before the introduction of about 300000 *F. truncorum* workers (and 12 queens in addition to queens possibly present in the introduced leaf litter material) apportioned in 3 different places on the islet. The introduced colony flourished and even produced female sexual brood in the following year (the ants visited aphid colonies in *Chamaenerion angustifolium* in addition to the few pines, although aphids on herbs are not normally visited by this species).

Tab. 4. The effect of *F. truncorum* on minor competitors and prey species within the insluar ant assembly studied both during natural conditions and in an ecological field experiment (transplantation of a large *F. truncorum* population to a semiforested islet). The figures for given species refer to the percentage of nests of that species of all examined sites (stones) or to the percentage of nests of all species sampled on the islet (figure within parentheses).

Islets with F. truncorum	exam. sites	inhab. sites	% inhab. sites	L. flavus %	L. niger %	F. fusca %	Myrmica %	Leptoth. %	total no. species
A (21/ha)	880	136	15	6.1 (40)	1.6(10)	3.2(21)	3.2(21)	1.4(9)	9
E (16/ha)	224	65	29	14.3 (49)	1.3(5)	11.6(3)	0.9(3)	0.9(3)	6
Control islets :									
forested									
1	336	95	28	9.2 (33)	4.8(17)	0.0(0)	11.9(42)	2.4(8)	7
2	101	33	33	7.9 (24)	12.9(39)	0.0(0)	7.9(24)	4.0(12)	4
3	166	59	36	6.0 (17)	7.2(20)	3.6(10)	13.8(39)	4.8(14)	8
4	150	47	31	0.0 (0)	9.3(30)	6.0(19)	15.3(49)	0.7(2)	4
semiforested									
5	357	122	34	4.5 (13)	22.7(66)	2.5(7)	1.3(4)	3.1(9)	7
6	849	304	36	17.6 (49)	15.9(44)	0.0(0)	0.1(0)	2.2(6)	5
nonforested									
7	569	227	40	17.0 (43)	19.0(48)	0.0(0)	1.9(5)	1.9(5)	5
8	470	266	56	20.6 (36)	16.0(19)	10.6(19)	8.9(16)	0.4(1)	7
Experimental islet :									
- truncor -82	642	238	37	14.8 (40)	18.1(49)	0.6(2)	1.4(4)	2.2(6)	7
+ truncor -83	638	193	30	17.9 (59)	8.9(29)	0.1(0)	0.2(1)	3.1(10)	6

Foraging *F. truncorum* workers were found all over the islet when its stony fields were sampled (a year later) in July 1983 (stones inhabited by *F. truncorum* or situated close to bud nests of that species not included). The frequency of nests of *F. fusca, Myrmica* sp. and especially *L. niger* had decreased while the nest numbers of *Lepthothorax* sp. (mostly *L. acervorum*) and especially *L. flavus* had increased (table 4). The latter increase could have been apparent (if assuming that predation by *F. truncorum* split the colonies into smaller subunits) or it may have been real. We can thus not prove that the extermination of about 50% of the *L. niger* nests on the islet by *F. truncorum* reduced the competition pressure on *L. flavus* although this hypothesis is attractive when considering the strong, although stable, competition between the two *Lasius* species observed by PONTIN (1961, 1963, 1969). The reason for stability of two competitors sharing the same resources and inhabiting the same patch is according to PONTIN stronger intraspecific than interspecific competition. We do not doubt this ingenious explanation but our observations point to an additional possibility; *L. flavus,* a week contest competitor, is less dependent on warm weather and has been observed to produce brood and alates much later in the season than the thermophilic *L. niger* (ROSENGREN, unpublish.). *F. flavus* could thus compensate its relative weakness in interspecific contest by utilizing stages of the season when *L. niger* is less active. It is obvious that such a delicate balance may shift in favour of one of the species within the pair if a third contestant attacks the other species by preference. *Leptothorax* sp. and *L. flavus* are nonaggressive or hypogoeic (COLLINGWOOD, 1979), making them less vulnerable to strong contest competitors. *L. niger*, by contrast, is a very aggressive species observed to engage in escalating battling with *Formica* (ROSENGREN, 1969; CZECHOWSKI, 1979) and may therefore have difficulties in coexisting with superior contestants of that genus. The latter explanation may explain the observed reduction in the nest numbers of *Myrmica* sp. also while *F. fusca,* a "timid" ant which avoids direct confrontation with *F. truncorum* represent a more complicated case. *F. fusca* competes with *F. truncorum* for both nest sites and food and is in addition a host species for the major competitors of *F. truncorum* (meaning that its colonies represent a potential "fifth column" within the patch). But ants of *Formica s. str.*, while aggressive against *F. fusca,* may at the same time protect its colonies against slave-hunting *F. sanguinea* and we could even interpret the "timid" behaviour of *fusca* as a tactic for dealing with aggressive *Formica s. str.* species like *F. truncorum.* We have thus regularly observed *F. fusca* workers as "pilferers" on sugarbaits placed in the vicinity of *F. truncorum* nests and of 29 trees on islet A visited by individual foragers of *F. fusca*, 11 were regularly visited by *F. truncorum* too. (*Myrmica* sp., which also visited trees for aphids, was in no case observed to visit the same tree as *F. truncorum.*) The *F. fusca* foragers were observed to flee "nervously" or drop to the ground from a visited tree as soon as approached by a *F. truncorum* worker. While those observations point to coexistence between the two species, observations of *F. truncorum* exterminating nests of *F. fusca* (without much resistance) were made on our experimental islet (table 4) and the nest number of the latter species had within a year dropped from 4 to 1 (observe, however, that the situation was partly artificial, the habitat suddenly being "flooded" by *F. truncorum*).

Tetramorium caespitum, Harpagoxenus sublaevis, Camponotus ligniperda and/or *Camponotus herculeanus* occurred on some of our study islets but the nests were so few that we have noted them only in the column "total number of species" (table 4). There occurred however 5 nests of *Camponotus herculeanus* on our semiforested experimental islet, 4 of which were still inhabited a year after the introduction of *F. truncorum.* It was obvious that *F. truncorum* had difficulties in invading nests of *Camponotus* (see above) and our observations one year after the transfer indicated that *F. truncorum* later avoided the area inhabited by *Camponotus* although moving freely at nests still inhabited by other species.

Polydomous *Formica* colonies have been claimed to posess an ability to clear a jointly defended habitat patch of competitors, especially other ants (SKWARRA, 1929; ROSENGREN, 1969; HIGASHI & YAMAUCHI, 1979; CHERIX & BOURNE, 1980). We can, summarizing our present observations, conclude that this capability of extermination is directed only against some species of the ant assembly while the populations of other species may not be reduced at all and may possibly even be reinforced. The most spectacular hypothesis actualized by our findings is that *F. truncorum*, while reducing the nest numbers of *L. niger* by fierce contest competition, may actually be protecting one of its long-term food reserves, *L. flavus* (see ROSENGREN *et al.*, 1985). We also conclude that the pattern of insular coexistence and competition among ants is to a high degree predetermined by behavioural reactions (see also LEVINS *et al.*, 1973 and VEPSÄLÄINEN & PISARSKI, 1982).

Intraspecific aggression

It has been reported that intraspecific, heterocolonial contest in Italian population of *F. lugubris* and *F. rufa* is ritualized (no damage being inflicted) and thus contrast with the strong type of aggression expressed in interspecific encounter (LE MOLI & PARMIGIANI, 1982; LE MOLI *et al.*, 1982). We do not doubt those data although they do not agree at all with our own observations of the same species from southern Finland (see also page 80). We found, by applying the "graft test" (see methods), that transferred conspecifics were as a rule killed within a time-span of a few hours even in cold autumn weather (the introduced batch was in the latter case observed to result in a massive recruitment of defending workers from the deeper parts of the recipient mound). Of a total of 18 grafting tests made within a small part of area 2, between pairs of *F. rufa* mounds, only one resulted in some acceptance of the introduced workers within the host nest. Rapid killing of heterocolonial conspecifics was the rule also when the mounds were situated close to one another on the same islet. *F. rufa* ants from islets E and F (fig. 3) thus did not accept conspecific grafts from the same islet and of 6 nest pairs tested on islet D only 1 showed mutual acceptance. The 3 *F. polyctena* colonies on islet D, while totally rejecting *F. rufa* grafts (3 tests with graft material from *F. rufa* mounds on the same islet), all accepted grafts from each other. Similar grafting tests carried out between *F. polyctena* mounds on the mainland indicated however that tolerance for conspecific grafts is limited in this species too; grafts from a longer distance than about 500 m were usually rejected (ROSENGREN & PAMILO, 1983; ROSENGREN, unpublished).

We here give the above informations for two reasons. Firstly, because they show that intraspecific aggression varies with the geographical region and, secondly, because they represent an obvious contrast to our present observations on *F. truncorum.* The data presented in fig. 8 are based on grafts made between *F. truncorum* nests situated on different islands mapped in fig. 3 (distances less than 1.5 km) and grafts transferred to nests of island E (fig. 3) from islands situated 5–80 km away. The graft tests made in early August included marking workers of the recipient nest with light blue and a batch of alien workers with silver spray. The frequency of silver was 30% to 70% in the initial sample (marked recaptures, n >100).

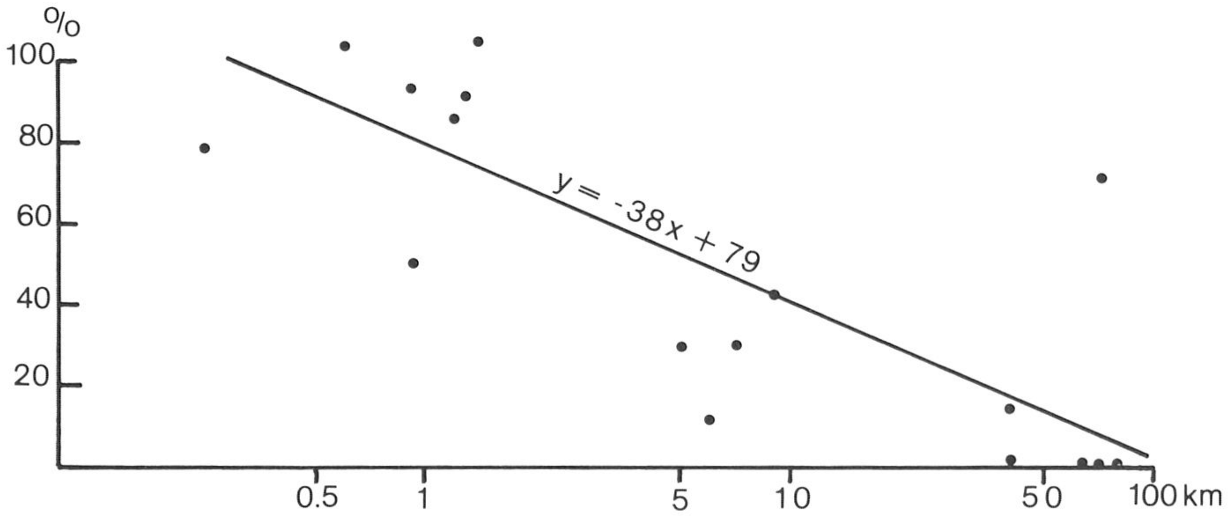

Fig. 8. Regression of acceptance index (percentages, see text) on logarithmic distance between donor mounds and recipient mounds (the latter all on island E, fig. 3) during "graft tests". All donor populations except 3 (5, 6 and 9 km) were, like the recipient population, polydomous.

A second sample was taken 2–20 days later but only samplings 20 days (for ants transferred a shorter distance than 1.5 km) or 10 days (for ants transferred a longer distance than 1.5 km) after grafting have been noted in fig. 8. The reason for combining data for 20 and 10 days in the same graph is that we made a complete sampling of grafts transferred a shorter distance than 1.5 km only after 20 days, and that intervening spot samples of this group did not indicate changes with time (e.g. ants transferred 1.4 km: 0 days 34% [n = 150], 2 days 32% [n = 154], 5 days 42% [n = 106], 20 days 36% [n = 71]). The samples taken after 10 or 20 days all included more than 40 marked ants.

We calculated, using the two samples taken from each nest, a simple measure of social tolerance expressed by workers of a nest towards introduced workers from an alien nest. This measure, the "acceptance index" or AI, is estimated according to the following formula:

$$AI = 100\, b^t (a^0 + b^0) / b^0 (a^t + b^t)$$

where b^0 is the number of alien ants in the sample taken immediately after transplantation (zero sample), a^0 is the number of ants from the recipient nest in the zero sample, b^t is the number of alien ants after time t and a^t the number of ants from the recipient nest after time t.

The regression of AI on the logarithmic value of the distance between donor nest and recipient nest (fig. 8) gave a highly significant negative correlation ($r = -0.786$, $t = -4.584$, 2-tail, $P<0.001$).

The fact that acceptance of a graft transferred from a distance of 70 km was good in one case (fig. 8) indicate that the "distance rule" (the negative correlation between AI and distance) is probabilistic rather than deterministic. We found, supporting the latter notion, that tolerance for heterocolonial grafts may vary with the recipient population because ants transferred from area 2 to area 3 appeared to be tolerated better than grafts made in the reverse direction (the experiment was however carried out in autumn when aggression may have been inhibited by low temperature). Our preliminary graft tests with *F. exsecta* also point to the probabilistic nature of the distance rule. We found in the latter species a case where a conspecific graft from the same islet was rejected, while ants from a colony situated 7 km away were accepted (ROSENGREN, unpublished). Using the same method in the Jura mountains in Switzerland SEEGER concluded that no aggression, measurable by this method, occurred between *F. exsecta* colonies situated between 1.5 km and 21 km apart (B. SEEGER, unpublished). Such apparent discrepancies become intelligible if assumed that olfactory discriminators determining social acceptance have a genetical background (see LENOIR, 1984 for evidence on kin recognition in ants) comparable to, say, histocompatibility alleles (see CROZIER & DIX, 1979 and HÖLLDOBLER & MICHENER, 1980 for discussion of alternative models). The probability that two nests related by descent have the same "compatibility alleles" may be high, especially if the degree of outbreeding is low (as may be the case in the archipelago with respect to some species). Areas characterized by introgession between populations from different source areas could on the other hand be expected to have a low probability of intercolonial acceptance. But even unrelated colonies from areas separated by a long distance could by chance have the same discriminator alleles. We would according to the above tentative model expect "viscous" populations (PAMILO, 1983) to reflect the distance rule of social acceptance more clearly than panmictic populations. This hypothesis does not exclude the possibility that different populations of the same species may show differences in the threshold for intraspecific aggression, meaning that some populations may accept less deviations in odour cues than others. That different species within the same area show striking differences with respect to "chauvinism" is already clear from the present account. Why is *F. truncorum* in our study area less "chauvinistic" than *F. rufa*? Our guess is that this has to do both with the local breeding structure including the level of polygyny and with the nesting strategy as a local adaptation. There is no theoretical hindrance to explain why the roles could not be reversed in another habitat type or another geographical region.

An important aspect of intraspecific aggression in ants is the attitude towards heterocolonial, conspecific queens. We found a total of 7 seminatural nests (large numbers of workers within natural nest material from their original nest). A total of 27 old mated queens and 4 virgins (all from islet 5, fig. 2) were distributed among the nests, 3 of which were from islet 5, 1 from islet 2, 1 from islet 7, and 2 from islet 1 (fig 2). The queens were accepted in all cases although 2 of the nests had queens of their own. The test was, however, made in mid-September and should be repeated during other parts of the season to permit general conclusions. The results nevertheless represent an obvious difference to our observations in *F. polyctena* where killing of mated queens by workers from a neighbour mound was noted during the same time of the year as in the present case (ROSENGREN & PAMILO, 1983).

DISCUSSION

Competition and coexistence

The results presented above appear contradictory in one important respect. Our distributional data show that several *Formica* species representing rather similar trophic levels may coexist on the same islet and even within the same habitat patch. Our follow-up studies of single cases indicate, like our ecological experiments, on the other hand, the existence of interference competition between those same species. If the latter were generally true we would predict that one species, say *F. truncorum*, would have long ago excluded competing *Formica* species from a given habitat type or we would expect a more or less stochastically determined checkerboard pattern based on the priority effect, with one species monopolizing one islet and another species another islet. Although cases suggesting a checkerboard (at least with respect to different parts of a single island, fig. 6) could be found, this was not a general rule. How to explain the enigma? The explanation we find most probable contains two main components:

The game theoretical argument

Suppose an ant colony A is threatened by a high probability that another colony B, representing a strong contestant, will invade the area of A. Suppose further that the probability of this happening will decrease if another colony C (which also is threatened by B), representing a less dangerous scramble competitor of A, is present in the patch. Would it pay for A not to drive away C and for C to accept A? The reason why such a mechanism does not necessarily evolve into true mutualism could be that the coexistence option between A and C could be conditional. Both the degree of "enemy specification" and "friend specification" could vary with the size of the colonies involved if the threshold for manifest aggression is correlated with the relative strength of an ant colony. It could e.g. pay for A to attack C if A later become sufficiently strong to resist the threat from B.

The mechanism sketched could be expected to be especially powerful in favouring coexistence between different ant species if A and B are colonies of the same species but A and C belong to different species. We got preliminary support for the latter case by our observation that monodomous *F. rufa* tolerated introduced *F. truncorum* nests within its territory while attacking heterocolonial conspecifics. *F. truncorum,* on the other hand, while practically lacking intraspecific aggression, did not tolerate nests of *F. rufa* within its jointly defended home range (table 3 and fig. 3). The point of our reasoning is that two species can be classified as "mutualists" or "competitors" depending on which other species occure within the assembly. We do not argue, however, that mutualism in a strict sense is common among archipelago ants (cf. Baroni-Urbani, 1974).

Climatic fluctuations or general harshness?

The above "Prisoner's Dilemma"-reasoning could possibly explain why monodomous species characterized by a high level of intraspecific aggression could coexist in a patch. But it does not explain why species capable of migratory expansion through nest fissioning have not already monopolized all of the inhabitable area. Why do we still find nests of *F. rufa* or *F. lugubris* within the habitat range of *F. truncorum* as proved by our observations of such nests being exterminated by expanding supercolonies of the latter species? Suppose a tendency for long-term fluctuations in the populations size of *F. truncorum.* This would lead to retreats followed by expansions of the supercolony area and thus explain our observations. An additional factor could be that *F. truncorum* and ants of the *rufa*-group may react differently on a given combination of climatic variable (long spells of sunny weather could e.g. make the rock habitat too hot and dry for *F. rufa* while *F. truncorum*, on the other hand, may be more hampered by rainy summers).

The observations of Wheeler & Wheeler (1981) in *F. propinqua* suggests that supranesting of the same type as found in *F. truncorum*, could lead to density-dependent population crashes. Our long-term observations of crowded supercolonies of *F. truncorum* did not support this, although indicating much stronger variations in nest number, as usually found in *Formica s. str.* (Rosengren *et al.*, 1985). The cause of those fluctuations was attributed to the flimsy and "opportunistic" nesting strategy of *F. truncorum* which was found correlated to a low level of thermal nest homeostasis (compared to the paraboloid mounds of the *F. rufa* group) and consequently a larger dependence of the developing brood on external climatic variables (Rosengren *et al.,* 1985). A single bad summer, although favouring competitors with more homeostatic nesting conditions, need not seriously crunch a *F. truncorum* population, firstly, because there is a time lag determined by the longevity of workers and queens and, secondly, because long periods of cold and rainy weather could actually, as mentioned above, increase the number of mated queens within the nest. The latter feed-back effect does not function, however, unless the bad summer is followed by a good one and several bad summers will probably reduce the population to a lower level. Supranesting as a technique for monopolizing the habitat could well be fairly insensitive to fluctuating population numbers because here too there is a time lag (other species cannot immediately "know" that defence of the patch has been reduced and it may take considerable time before recolonization in an island habitat can occur). But *F. rufa* and/or *F. lugubris* may be able to recolonize the rocks from shadier forest habitats on the same island as soon as *F. truncorum* is reduced below economic defensibilieity of the area. The fact that the archipelago habitat, both in autumn, when the rocks may be flooded by the sea, and in winter when the wind may remove the protecting snow-cover, represents a harsh environment, could indeed create empty space for colonizers. But an unselective "tabula rasa" of this type is more likely to favour polydomous residents than immigrants in the stage of establishing their colonies (cf. the "stochastic strategy" discussed in Rosengren & Pamilo, 1983).

The beach-head effect – priority extending through a multipatch system?

Sparsely pine-forested granite islets in the archipelago of the Gulf of Finland represent a notable stereotypic habitat type. It does not therefore appear likely that the unusually high nest density of *F. truncorum* common for a small group of islets (fig. 3) is attributable to vegetational or microclimatic characteristics. Local nest aggregations are usually explained with reference to budding and polydomy (e.g. Rosengren & Pamilo, 1983) but expansion by budding can of course not progress from one offshore islet to another.

The rule of thumb that flexible (and flimsy) nesting in ants indicates an "r-strategist" do not hold for patch monopolizing "supranesters" like *F. truncorum* (Rosengren *et al.*, 1985). But it should be admitted that *F. truncorum* by inhabiting dry clearings and areas of burnt off forest on the mainland could have adapted to more ephemeral habitats than is the rule in other *Formica s. str.* species. This does not nessesarily imply r-selection in the proper sense (Boyce, 1984) although commonly regarded as characteristic of "r-species" within a given r-K continuum (Southwood, 1977). We suggest that *F. truncorum*, relative to other species within the subgenus, could indeed represent an "r-species" *sensu* Southwood (1977). We may further speculate that a polydomous *F. truncorum* colony while monopolizing the local habitat patch by fissioning may at the same time increase colonization pressure on surrounding patches by assailing them with independent foundresses over a long time. Dispersal of propagules from a polydomous colony could, in spite of the low frequency of nests producing alates, be more efficient than from a monodomous colony representing a single isolated nest. There are several possible reasons for this. 1. A female from a polydomous colony may have a higher probability of finding a mate if males and females orient in the same direction (e.g. because of the wind) or if mating occurs before dispersal. 2. The colonization pressure may not only be a function of the number of alates spread to adjacent areas (by anemochoric and anemohydrochoric transport in addition to active orientation) but could also be a function of repetition of propagule dispersal from the same patch year after year. Polydomous colonies of *F. truncorum* have been observed to have a smaller extinction probability than monodomous colonies of the same species (ROSENGREN & PAMILO, 1983). A colony based on supranesting could thus function as a stable source area or "beach head" taking advantage of the possibility that competing species may have colonies less stable in time and space. An accidental extinction of the colony of a competitor could thus lead to establishement of a *F. truncorum* colony in the patch by an independent foundress. 3. Suppose the population has a low level of intraspecific aggression. This would mean that conspecific colonizers of a fresh patch could "cooperate" to a certain degree e.g. by protecting the same aphid species (which thus is likely to multiply within the patch) or by exterminating mutual competitors e.g. the ever-present *Lasius niger* which, although probably rather harmless for a mature colony of *Formica s. str.* may kill *Formica* foundresses. Colonization of an islet with *F. truncorum* could perhaps be expected to exhaust the number of nests of the host species *Serviformica fusca* available for additional colonizers. But the use of a host species is probably not the only option for freshly mated queens. The low level of intraspecific aggression observed by us in *F. truncorum* make it appear likely that queens are accepted in alien conspecific colonies of the species. Combining some of those potential effects would easily mean a threshold bound cumulative process where an influx of propagules from neighbour colonies speeds up the growth of a new colony, thereby decreasing its extinction probability. This in turn would decrease the extinction probability of the original colony (if fresh queens arrive from surrounding islets). 4. The pattern of wind, together with an unequal distribution of "stepping stones" (BARONI-URBANI, 1971), could facilitate the effect by concentrating polydomous colonies of mutually cooperating nests along bands of islets, as genetically closely related propagules may orient or be passively transported by the wind along given trajectories. The wind direction could in addition function as a dispersal barrier. This could partly explain why polydomous colonies of *F. truncorum* do not spread like wildfire in the archipelago but remain confined to certain areas. But also the recent genesis of the Finnish archipelago, which is still rising from the sea as the result of land uplift (HAILA *et al.,* 1982), could theoretically, like the irregular "tabula rasa effect" of a harsh environment, explain why the *Formica* assembly of the Gulf of Finland does not appear to be in equilibrium and why distributional discontinuances appear common among Baltic archipelago ants.

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