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Insular ecology of the red wood ant *Formica truncorum* Fabr.

I. Polydomous nesting, population size and foraging.

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A polydomous colony of *Formica truncorum* FABR. occupying a 3 ha pine-forested offshore islet in the Gulf of Finland was studied with respect to nest building, population size, foraging, hibernation, internest movement and enzyme genes. The polygynic population inhabited 50–60 nests in summer containing a total of 1.2 million workers. 60% of those nests were desolated in autumn, the ants transporting nest mates with hypertrophied fatbodies to hibernation sites shared by ants from several nests. Internest drifting was high and ants from neighbour nests shared the same foraging area. The frequency distribution of worker size was skewed toward workers of large size representing nest defenders and hunters.

The significance of polydomy as a patch monopolizing strategy is discussed. It is suggested that flimsy nesting and a high degree of internest mobility is a consequence of the rocky habitat which necessitates thermoregulative migrations.

The now classic species equilibrium model of MACARTHUR & WILSON (1963) considers the species pool on islands as a dynamic equilibrium between immigration and extinction and thus emphasizes the turnover rate of species. Insects compared to vertebrates generally have a high turnover rate (SCHOENER, 1983) and some studies of insular ants agree with that view (LEVINS *et al.*, 1973). But it has been postulated that some ant species may have a low extinction rate due to priority effects, a phenomenon likely to introduce a stochastic element in the composition of the insular ant assembly (VEPSÄLÄINEN & PISARSKY, 1982).

Nest reproduction by fissioning may lead to a polydomous colony, a cluster of communicating nests, as described for several *Formica* species (MARIKOVSKY, 1962; SCHERBA, 1964; KNEITZ, 1964a; ROSENGREN, 1969, 1979; ITO, 1973; DOBRZANSKA, 1973; PISARSKI, 1973; KLOFT *et al.*, 1973; ZAKHAROV, 1974; CZECHOWSKI, 1977; HIGASHI, 1978b, 1979; WERNER *et al.*, 1979; MABELIS, 1979a; CHERIX, 1980, 1981; CHUDZICKA 1982, MACKAY & MACKAY, 1983). While the «supercolonies» of some species require large habitat areas (CHERIX, 1981) nest agglomerations in other species tend, due to the small distance between each individual nest unit, to be very tight and thus may be fitted to the small dimensions of archipelago islets (ROSENGREN & PAMILO, 1983). The latter type of small scale polydomous colonies can in some respects be compared to a «supranest» (DOBRZANSKA, 1973) associating to a single society obtaining a strategy of decentralized nesting (HÖLLDOBLER & LUMSDEN, 1980). Such a decentralized social unit would theoretically be an ideal vehicle for monopolizing an islet (HÖLLDOBLER & WILSON, 1977). We here describe social organization, population size and foraging tactics of supranesting *F. truncorum* on a forested islet in the archipelago of the Gulf of Finland. Our aim was to analyse the proximate and ultimate causes behind a possible

case of the priority effect. The ecology of *F. truncorum* has contrary to the case with other European «red wood ants», remained practically unknown and we try to fill this gap. But the crucial questions of mating strategy, dispersal and interspecific competition will be discussed later, in the second part of our study (ROSENGREN *et al.*, 1985).

MATERIAL AND METHODS

The species

It is understandable that the «red wood ant» *Formica truncorum* FABR. (= *F. truncicola* NYL. 1846), a member of the subgenus *Formica* s. str., is usually included in the *rufa*-group (LANGE, 1958; BETREM, 1960; KUTTER 1977). *F. truncorum* (including the form *F. dusmeti* EMERY) is however very divergent from other European members of the subgenus both with respect to morphology (YARROW, 1955; COLLINGWOOD, 1979) and biochemical criteria (PAMILO *et al.*, 1979; JAN LÖFQVIST personal communication). SEM-studies reveal a qualitatively distinct chitin microstructure common to both *F. truncorum* and *F. yessensis* FOREL (from eastern Asia) and we now have evidence that some of the nearctic *Formica* s. str. listed by KROMBEIN *et al.*, (1979) also belong to the «*truncorum*-group» (ROSENGREN & CHERIX, 1981 and unpublished SEM micrographes of nearctic samples). The latter group appears to have some ecological features in common which include a preference for xerothermic habitats and very plastic nesting habits (e. g. WHEELER & WHEELER, 1981). The annual cycle and phenology of *F. truncorum* is the same as in *Formica yessensis* from northern Japan (ITO, 1973; ITO & IMAMURA, 1974). Alates of both those species emerge between mid July and mid August and the alates have a flight time restricted to early morning (cf. ITO & IMAMURA, 1974 and ROSENGREN *et al.*, 1985). This is exceptional in Palearctic *Formica* s. str., where the alates usually are produced in spring or early summer and where the diel flight time of alates, at least in polygynous species, is not restricted to the morning (HIGASHI 1983, ROSENGREN & FORTELIUS, 1985). Polydomous colonies of *F. truncorum*, while very rare in central Europe (KUTTER, 1963; PREUSS, 1979), are common on pine forested islets in the archipelago of the Gulf of Finland, an area from which WILLIAM NYLANDER 140 years ago collected his type specimens of *F. truncicola* NYL.

Study site and habitat

The small offshore islet Lilla Träskön situated 2,6 km from the nearest mainland and 40 km west of Helsinki was selected for the present study. The archipelago of the Gulf of Finland abounds with similar islets but the present one had an unusually dense population of *F. truncorum* suggesting a situation close to the carrying capacity. The rather flat islet covering an area of nearly 3 ha (28350 m²) consists of sparsely pine-forested rockbed of granite (fig. 1). The pine-stand broken by exposed patches is concentrated to the central parts of the islet leaving a 10–40 m broad border of naked rock against the sea (fig. 1). Up to 80 cm thick beds of mineral earth (moraine of small stones, gravel and sand) cover in part the middle of the islet and its northern shore. The ground under the pines is covered by xerophilic vegetation-carpets mainly consisting of *Empetrum nigrum*, *Arctostaphylos uva-ursi* and *Festuca*-grasses while *Calluna vulgaris*, *Vaccinium vitis-idaea*, reindeerlichens and junipers occur in less prominent patches. We found a total of 9 ant species other than *F. truncorum* on the islet represented by 136 nests. The species were: *Lasius flavus* (40%), *L. niger* (10%), *Myrmica ruginodis* (11%), *M. scabrinodis* (7%), *M. rubra* (3%), *Leptothorax*

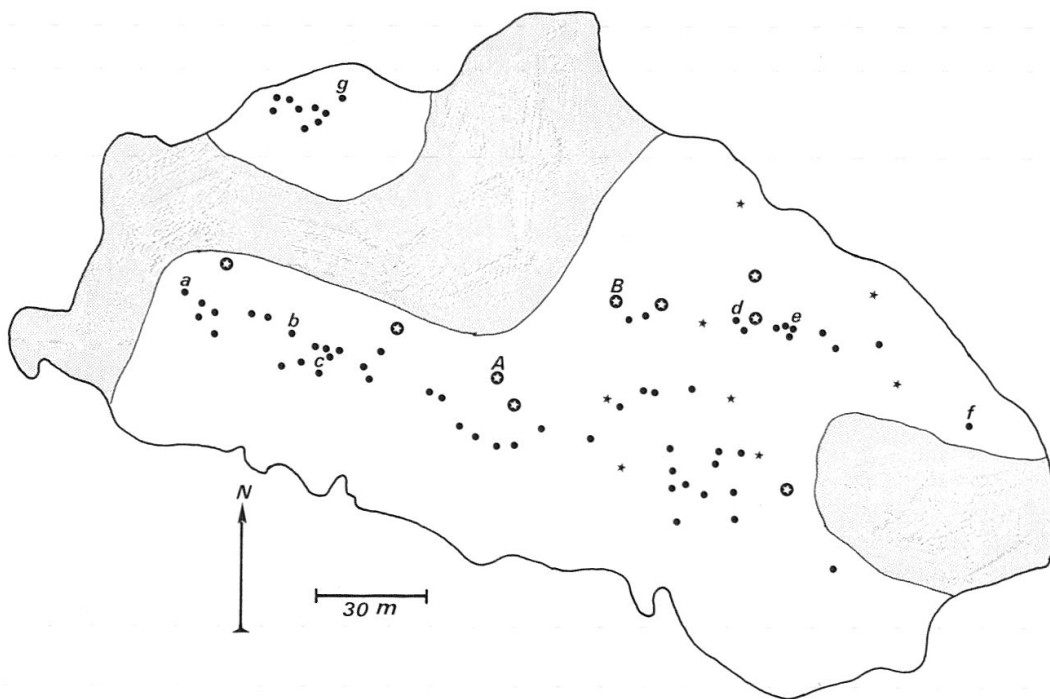
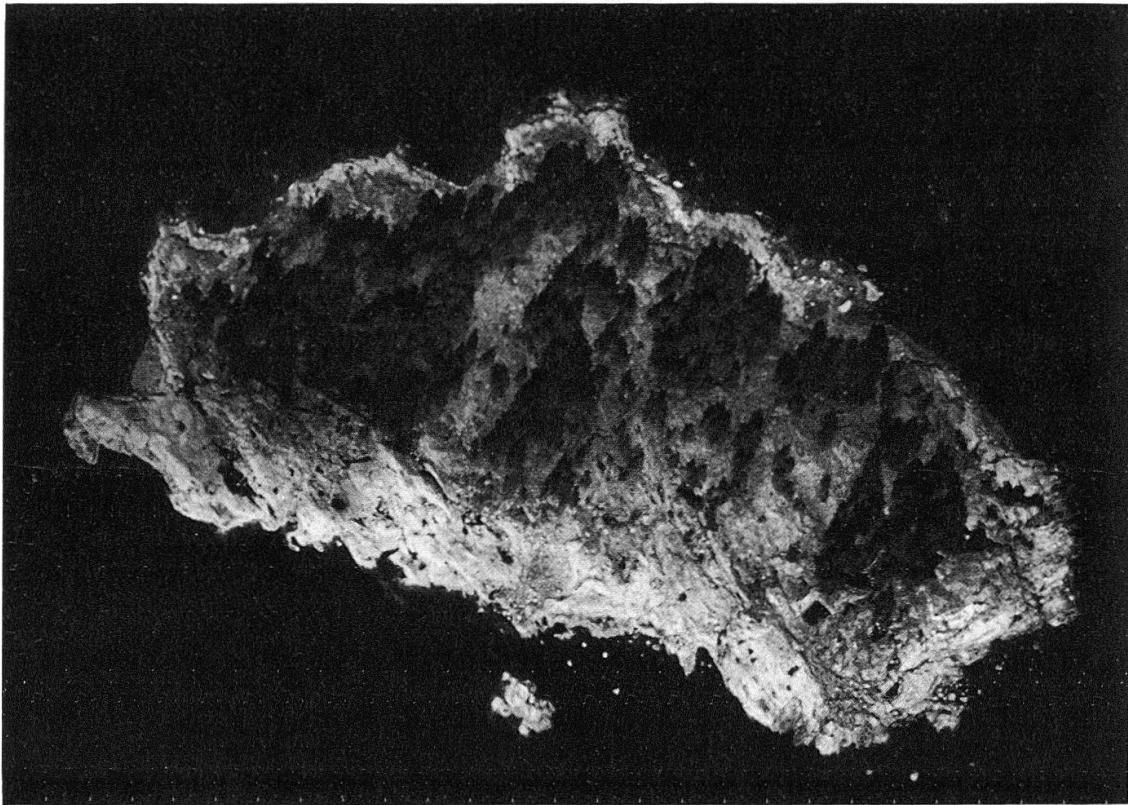


Fig. 1: Upper part: air photograph of the Lilla Träskön islet (scale as below)*. Lower part: map of nests and foraging areas (grey areas not visited by ants. ● = nests observed in summer 1979. ★ = new findings in 1980. ⊙ = hibernation nests (winter nests).

* Published with permission of the Finnish National Board Survey.

acervorum (7%), *L. muscorum* (2%), *Formica fusca* (20%), and *Camponotus herculeanus* (0,7%).

The diversity of this rather uniform habitat is increased by some elements of deciduous trees and by 5 rockpools. The Lilla Träskön islet, although protected from eastern storms by a long peninsula, faces the open sea in a southern and southwestern direction, thus exposing it to the winds prevailing during summertime in this area. Some of the pines nearest to the southern shores are consequently dwarfed and deformed. Storms were observed to wash ashore organic material e. g. *Fucus vesiculosus* meaning that the islet was not a nutritively «closed system».

Procedures

Counting and mapping of nests

The mound nests of *Formica s. str.* are usually easy to demarcate but *F. truncorum* is an exception from this. Digging out two apparently distinct nests situated 2 m apart from each other showed that the nests were interconnected by an underground gallery system. We tried to reduce this bias by counting two heaps of conifer needles within the same rocky crevice or two adjacent stones used as nest cover by the ants as only one nest. We are aware that our common sense criteria were partly arbitrary and that another observer may have reached another conclusion regarding the «true» number of nests. Each nest was plotted on a map with the aid of compass coordinates, marked with a numbered stick and photographed. Trees visited by the ants were similarly marked by numbered plastic labels through the season and the number of visitors measured on a 60 cm stretch of each trunk.

Colour markings

Inter-nest exchange of workers was studied by mass-marking the ants with «Magix» (formerly «Magi-Dyes») silver and light blue sprays for leather. The social and orientational behaviour of *Formica* ants is by this procedure, if applied correctly (see ROSENGREN, 1977b), disturbed to a surprisingly low degree (disturbance in orientation can be seen in a few individuals shortly after marking but not later, probably because too heavily marked individuals die and are thus eliminated). The method gives rather durable markings and a few marked *F. truncorum* workers were found in some of the nests still a year after marking (see CHERIX & ROSENGREN, 1980 for similar experiences in *F. lugubris*). Markings for CMR (Lincoln index) was made manually with silver paint. («Teoflux»).

Population estimate, method 1

Population estimates based on excavation or capture-mark-recapture (CMR) are difficult in *F. truncorum* because some of the workers and queens may hide in cracks or the nest may be too extended to allow unbiased marking and sampling. We used the following procedure. Each nest on the islet was in the beginning of the investigation classified according to an arbitrary scale running from nests inhabited by very large populations to nests inhabited by very small populations. The scale was based both on the number of workers pouring out from a nest when disturbed and the extension of the nest e. g. the amount of leaf litter accumulated by the ants. We later (August 1981 and 1982) selected nests suitable for excavation or CMR and corresponding to different grades of our semiquantitative scale. 4 of the nests were from the study islet

(Lilla Träskön) while 4 were from adjacent islets. The population estimate was in only one case based on pure CMR (Lincoln index). The procedure was as follows. A cylindrical column of nest material and ants, including both the upper and the deeper parts of a bell-shaped mound on sandy soil was removed. 700 ants found within this sample were marked manually with Teoflux paint and returned after drying. Similar samples were taken 2 days later and the frequency of marked ants determined. The primary estimate was multiplied with the correction factor 1.36 recommended by HORSTMANN (1982). All other population estimates were based either on excavations or on excavation combined with CMR. The procedure was as follows. Nests situated on sandy soil were dug out during rainy days. Nest material and ants were placed in large plastic containers (mound nest and earth nest in separate containers), the ants were anaesthetized with CO₂-gas led into the closed containers and the content was thoroughly mixed (after removal of stones). Several 1 dl samples were taken from each container (2–5 samples per 10 l material). Ants and pupae within each sample were counted while all of the material was searched for queens. Nest material and ants were after counting returned to the original nest site. Some of the foragers stay outside the nest even in rainy weather meaning that the estimate requires a correction factor. We found the required correction factor by the following procedure based on the fact that one nest classified as «very large» was completely confined to the inside of an old petrol drum at the shore.

500 foragers leaving or returning through the only exit of the drum were colour-marked with a spot silver colour (Teoflux) and the proportion of marked ants determined two days later through several 5 min traffic counts (ROSENGREN, 1977a; KRUK-DE BRUIN *et. al.*, 1977; BREEN, 1979). The Lincoln index method applied for this case underestimates the true number of foragers because foragers with a relatively short mean journey time are overrepresented (HORSTMANN, 1982 and personal communication) and the estimate needs a correction factor. We used the factor 1.28 found in *F. polycтена* (HORSTMANN, 1982). CO₂-gas was led into the drum which was cut open (rainy weather). The material (156 l in all) was placed in containers and mixed and sampled after additional treatment with CO₂. Marked and unmarked ants were counted separately within each sample. All the material was removed from the islet and the drum was filled with fresh leaf litter and placed in its original position. The drum was emptied 6 times and the ants counted and removed (last sample 9 days after the original excavation). The high frequency of marked ants in those additional samples indicated that they consisted of foragers from the original population. The procedure allowed two independent estimates of the number of foragers staying outside the nest during excavation (table 1) and thus an estimate of the required correction factor (1.17 or 1.16 according to table 1). All excavation results were corrected with the latter factor.

Population estimate, method 2

This method is based on a correlation between total worker number and the number of foragers visiting trees mainly for aphids (WELLENSTEIN, 1973; HORSTMANN, 1982). Assuming tentatively that the proportion of ants visiting trees is the same in *F. truncorum* and *F. polycтена* we would be able to estimate the population size of one of the species from the number of ants visiting trees provided we know the relation between tree visitors and total population size in the other species.

The total forager population of a large *F. polycтена* mound, which for methodological reasons was surrounded by an aluminium barrier forcing the traffic streams to

pass bridges (see CHERIX & BOURNE, 1980) had been thoroughly estimated during the same year by the Lincoln-index procedure for traffic data (ROSENGREN in preparation). We now compared the total number of tree visitors in both the colonies, counting the number of ants on a 60 cm stretch of each tree visited by ants (days with overcast sky and even temperature in early September). Ants in the colonies of both the species mainly visited aphids in pine during the time of comparison (mainly *Cinara pini* in both cases). It is perhaps not completely unreasonable to assume that individuals of two nearly related species cannot be completely different with respect to sugar consumption. The method is nevertheless highly hypothetical and we used it mainly because it offered a possibility to try a completely independent estimate of the total worker population of *F. truncorum* on our study islet.

Table 1: Calculation of correction factor for excavation data based on two partly independent methods. First excavation (a) was very complete in this case because the nest was confined within an empty petrol drum which was cut open after anaesthetizing the ants with CO₂.

| Excavation results | | | |
|--|---|---|--|
| a. Total no. of ants found in nest (first excavation) | b. Foragers outside nest during first excavation (sum of additional excavations) | c. Total no. of ants (a + b) | d. Correction factor of first excavation (c/a) |
| 62 501 | 10 816 | 73 317 | 1.1 730 532 |
| Combined CMR and excavation results | | | |
| e. No. of marked foragers | f. Marked/unmarked in extranidal sample (n = 3000) | g. Marked/unmarked in intranidal sample (n = 6000) | h. No. of foragers (uncorrected, Lincoln index) |
| 500 | 0.0490838 | 0.0022674 | 10687 |
| i. No. of foragers (corrected: $h \times 1.28$) | j. Foragers within nest (formula: $g \times a \times i/e$) | k. No. of true intranidal workers (a - j) | l. Foragers outside nest (i - j) |
| 13 679 | 3877 | 58 624 | 9802 |
| m. Total. no. of ants (a + l) | n. All foragers in % of all ants | o. % of foragers outside nest | p. Correction factor of first excavation (m/a) |
| 72 303 | 21% | 72% | 1.1568295 |

RESULTS

Nest architecture, nesting site and nest temperature

Ants of European *Formica s. str.* and *Coptoformica* usually construct paraboloidal or bell-shaped domes. Only 4% of the thatched mounds sampled on Lilla Träskön and surrounding islets of the same habitat type (table 2) approached the paraboloidal shape, the rest being highly irregular accumulations of pine needles and other leaf litter (fig. 2). The mounds of *F. truncorum* are messy in another respect too. The mounds in other species of *Formica s. str.* often have an obvious inner structure,

Table 2: Sites of summer nests and/or permanent nests of *F. truncorum* on the Lilla Träskön islet (mounds in 1979 + new foundings in 1980) and on 9 other pine-growing granite islands in the Gulf of Finland.

| | Lilla Träskön | | other islands | |
|--------------------------------|---------------|----|---------------|----|
| | No. nests | % | No. nests | % |
| In rock crevices or on shelves | 29 | 41 | 99 | 38 |
| Under and around large stones | 12 | 17 | 54 | 21 |
| On roots of windfallen trees | 0 | 0 | 26 | 10 |
| Around stumps | 1 | 1 | 24 | 9 |
| Around roots of standing trees | 9 | 13 | 16 | 6 |
| Around and under logs | 0 | 0 | 12 | 5 |
| In moraine and/or sand | 11 | 15 | 14 | 5 |
| In tufts of <i>Festuca</i> | 8 | 11 | 11 | 5 |
| Within holes | 1 | 1 | 3 | 1 |

which in species like *F. uralensis* RUZSKY, typically consists of a conus of long twigs thatched by finer leaf litter. All traces of such an inner structure is lacking in *F. truncorum*, even in cases where the mound happens to be neatly bell-shaped. This messy nesting habit is probably connected to the highly variable nesting site (table 2) which appears to optimize only one quality: maximum collection of heat from the sun. Some nests form e. g. about 10 cm deep «sun-panels» covering the southern side of the almost vertical discs formed by the root systems of windfallen pinetrees (table 2). The most deviant feature is however that about 30% of the nests is built under cover e. g. logs, stones or *Festuca* tussocks or even situated within hollow trees (table 2, fig. 2). Ants nesting under cover usually border the cover with abundant leaf litter or fill the inside of a nest hole (e. g. an empty petrol drum found at the shore of Lilla Träskön) with a large amount of nest material (mainly pine needles). Large nests may be thatched with up to 200 l pine needles against 10 l or less for small nests but no absolute rule can be given. Nests used exclusively for hibernation do not have leaf litter at all and very little leaf litter was found even in large permanent nests if situated on beds of gravel and sand (nest 29 in fig. 2). It thus appears that the dynamic nesting pattern of *F. truncorum* is rather similar to the nesting habits of *F. yessensis* (ITO, 1973; HIGASHI, 1976), *F. haemorrhoidalis* (MACKEY & MACKEY, 1983, 1984) and *F. propinqua* (WHEELER & WHEELER, 1981).

F. polyctena and other species within the true *rufa*-group retain through spring and summer a high and even temperature within its mound nests (KNEITZ, 1964b; HORSTMANN, 1983). This thermal homeostatis, which is still sometimes confused with



Fig. 2: Nests of *Formica truncorum* on the Lilla Träskön islet. The 3 nests to the left (no. 28, 29 and 5) are permanent while the nests to the right (no. 14, 17 and 6) are temporary summer nests. Observe that nests 14 and 6 extend along all of the longitudinal axis of the photograph while nest 29 covers all of the vegetation-free parts of the stony field in the centre of the photograph. The size of the numbered shield is 15 cm × 15 cm.

external heating by insolation (SEELEY & HEINRICH, 1980), although it is often more clearly expressed in shady forest habitats than in exposed sites (ROSENGREN *et al.*, 1979 and unpubl.), is due to metabolic activity of the ants (KNEITZ, 1964b; MARTIN, 1980) and perhaps also to aerobic microbes favoured by the nest architecture (COENEN-STASS *et al.*, 1980). We selected among the largest size class of *F. truncorum* nests on Lilla Träskön and adjacent islands (table 2) 6 mound nests which approached a parabolic shape and thus appeared comparable to mound nests among other species within *Formica s. str.* The temperature within nests of this group was compared to the temperature within 12 mounds of *F. rufa* L. situated in the same island habitat (see ROSENGREN *et al.* 1985). The measurements for both of the species were made in the evening after

an overcast, rainy day in mid-June 1984 (ambient temperature $12 \pm -1^{\circ}\text{C}$). 6 mercury thermometers were situated at a depth of 10 cm to 50 cm within each nest and the highest reading used for comparison. The mean temperature in *F. truncorum* was $18.5 \pm 7.6^{\circ}\text{C}$ ($n = 6$, range: 15°C – 24°C) which is well above the ambient temperature and indicates «endogenous» heating. The corresponding value for *F. rufa* was $25.2 \pm 1.2^{\circ}\text{C}$ ($n = 12$, range: 23°C – 27°C). This difference is statistically significant (U-test, $P < 0.05$). We conclude that *F. truncorum*, although probably not exclusively dependent on insolation for warming its nest, has a lesser ability than *F. rufa* for maintaining thermal homeostasis and may be more dependent on external heat for raising its brood. Our temperature measurements thus supported our impression that *F. truncorum* may maximize insolation at the expense of heat preservation and that the flimsy nest architecture of the species may be connected to this strategy.

Supranest organization

The number of nests on the Lilla Träskön islet counted in July during different years varied between 49 and 63 (table 3). Only about 40% of the nests were inhabited through all of a year. We found in addition a fairly constant number of very large hibernation sites located to the same beds of mineral earth each year. We call them winter nest to distinguish them from temporary summer nests and permanent nests inhabited in both summer and winter (table 3).

In contrast to typical winter nests all nests inhabited in summer (fig. 1) occurred in very sunny places. Combining records of nests from 1979 with new findings in 1980 give a total of 71 nests 48 (68%) of which were cliff nests while 23 (32%) occurred on beds of mineral earth (20% at the border between the forest and the shore cliffs and 12% in exposed openings within the pine stands). Only 6 cliff nests but nearly all nests inhabited in summer and situated on moraine were permanent. Some temporary summer nests on the cliffs, although crowded with pupae, appeared to lack aphid-colonies of their own but a strict classification into «pupal incubators» and «all purpose nests» proved impossible.

77% of cliff nests were on cliffs facing south. The southern cliffs were not only exposed to the southwestern winds but were flooded by water during heavy storms. It is thus understandable that nests on the southern side of the islet were not found at a distance shorter than 20–30 m from the water's edge (fig. 1). It is nevertheless hard to

Table 3: Nests of *F. truncorum* counted on the Lilla Träskön islet in different parts of a year and during different years. Nests inhabited in May or September are permanent. We get the number of temporary summer nests by subtracting the number of inhabited nests in May from the corresponding number in July.

| | July 1979 | May 1980 | July 1980 | Sept. 1980 | July 1981 | July 1983 | July 1984 |
|----------------------------------|--------------|-------------|--------------|---------------|--------------|--------------|--------------|
| Summer nests and permanent nests | 63 | 25 | 58 | 24 | 49 | 53 | 58 |
| Brood-containing nests | 57 (90%) | – | 42 (72%) | – | 32 (65%) | 33 (62%) | 47 (81 %) |
| Nests producing sexuals (alates) | 16 (25%) | – | 19 (33%) | – | 17 (35%) | 14 (26%) | 23 (40%) |
| Winter nests | – | 8 | – | 9 | – | – | – |

understand that the nests on the southern cliffs do not simply blow away. The ants in those exposed sites do not have the option of extending the mound nest in a vertical dimension but utilize a «creeping» nesting pattern. They are thus able to hide within «silent pockets» offered by rock crevice and shelves (fig. 2 nests 6 and 14). This could be one reason why the flexible nesting habit of *F. truncorum* could be especially adaptive in the archipelago.

While a high percentage of the nests produced brood only about 30% had brood of sexuals. The sex ratio calculated as a population means was significantly male-biased through 5 years of sampling (ROSENGREN *et al.*, 1985). Of a total of 16 nests producing sexual brood in 1979 8 produced sexuals also in 1981 indicating a certain retention of the «task» (nests producing sexuals were usually permanent). SCHERBA (1961) investigating a highly polycalic group of about 400 nests in *F. opaciventris* EMERY reached the value of 20–25% nests producing sexuals and interpreted the result as «reproductive division of labour» taking place on the integrated level of the nest group.

WHEELER & WHEELER (1981) observing the extinction of a tight nest agglomeration of *F. propinqua* suggested the possibility of a density-dependent population crash. Our 6-year follow-up studies of several monodomous and polydomous *F. truncorum* colonies make catastrophic population crashes caused by polydomous nesting appear less likely in the present case especially when the observations suggest a smaller extinction probability for polydomous than for monodomous colonies of the species (ROSENGREN & PAMILO 1983). We observed, however, clear short term variations both in the total number of nests and in the frequency of nests producing brood on our study islet (table 3). Our sampling procedures, especially the removal of sexual brood, may have contributed to those variations but we find it likely that the main reason was climatic. The colony appeared to suffer especially during the long rainy periods of 1981 when more than 50% of the worker larvae in several of the nests failed to make cocoons. 1984 was on the other hand a «good year» for the species as observed especially clearly in two originally less crowded polydomous colonies of the species surveyed in the archipelago 30–40 km east of Helsinki. One of those had 19 inhabited nests in 1982 but 33 in 1984 (the Havsudden peninsula on the large Emsalö island) while the other (Fårholm in the archipelago of Sibbo) had 25 nests in 1981 but 39 in 1984. This striking increase in nest number (single nests of the areas appeared in addition more vigorous than before) was probably connected to the exceptionally high thermal sum of the season 1983 (April to September). The thermal sum was 77.7°C in 1983 against 69.4°C in 1982, 72.7°C in 1981 and the average of 72.7°C for the total period of 1931 to 1960 (data based on records from the Kaisaniemi meteorological station in Helsinki). But the warm spring of 1984 (mean temperature in May 1984 12.6°C against 9.0°C in 1982, 10.8°C in 1981 and an average of 9.3°C for the period of 1931 to 1960) could have facilitated the effect. Such strong annual variations in nest numbers or population levels have not been observed in ants of the *F. rufa* group (ROSENGREN unpublished records from a 10 years period, see also CEUSTERS, 1980).

The meaning of the concept «nest turnover rate» (HIGASHI, 1976; CEUSTERS, 1980; KLIMETZEK, 1980) is far from clear in the present case when 60% of the nests inhabited in summer are abandoned in autumn, most of them repopulated the following spring. 13 summer nests of a total of 63 nests inhabited in July 1979 were found empty in July 1980 while 8 new summer nests appeared in clearly new sites within the habitat (giving a nest mortality of 21% and a nest natality of 13%). A continuation of these statistics proved however less meaningful because many summer nests gradually shifted their position within the site (e. g. a rock crevice) during the course of the study and it became a matter of arbitrary choice whether to classify the nest as «new» or «old».

Seasonal migration

Ants from temporary summer nests migrated in autumn either to winter nests or to permanent nests situated on moraine (cf. IMAMURA 1974, 1978). Autumnal migration, reaching its peak at about the end of September, was very gradual and diffuse, the ants of a migrating nest carrying fellow-workers in their mandibles along more or less individual paths and usually to several hibernation sites. Distinct migration routes described in some other *Formica s. str.* species (ROSENGREN, 1971) were thus usually impossible to discern. 10 carrier ants were in late September separated from their burdens on the way from a temporary cliff nest to a winter nest. Dissection of the carried ants and their carriers (table 4) indicated that the former were *Innendienst* ants (SUDD, 1982) with well developed ovarioles (see BILLEN, 1982) and functioning as store animals due to accumulation of lipids in the fatbody. The store function of young workers in autumn and spring has previously been confirmed for *F. polyctena* (KNEITZ, 1964; KIRCHNER, 1964).

Ants from temporary summer nests did not only migrate to the winter nests mapped in fig. 1 but also to permanent nests situated on gravel and sand (e. g. the large nest 29, fig. 2). We thus recorded migration to 19 permanent nests in autumn 1979. The true winter nests were often situated in shady sites (an extreme was a winter nest found within a shrubbery of stunted spruce) and completely abandoned in late spring. They were repopulated each September when very large numbers of torpid workers were found crowding immediately below the surface (final hibernation occurred 20–70 cm from the surface as confirmed by digging in mid-November). Those strikingly populous winter nests appeared fairly well demarcated but we also observed that the population of some permanent nests hibernated in gallery systems diffusely spread through the soil around the nest. We found in addition a number of very small winter nests under *Festuca*-tussocks at the forest-border. Our major winter nests (fig. 1) are thus only «hot spots» in the distribution of the hibernating population. Migration back to the temporary summer nests started in May and appeared rather intense in warm weather with large number of workers carrying nestmates toward the cliffs. Before the onset of spring migration in 1980 the inhabitants of two large winter nests (A and B in fig. 1) crowding under stones close to the surface were marked with a separate spray paint for each nest. In mid-June, when the migration was completed, all nests

Table 4: The result of dissecting 10 ants carried between nests in late September and their carriers. Carriers all had yellow-grey fatbodies while the fatbodies of carried ants were whitish.

| | Carried ants | Carrier ants |
|---------------------------|--------------|--------------|
| <i>State of fatbody:</i> | | |
| Insignificant | 0 | 8 |
| small | 2 | 1 |
| large | 3 | 1 |
| very large | 5 | 0 |
| <i>Eggs in ovarioles:</i> | | |
| no | 4 | 10 |
| yes | 6 | 0 |

on the islet were searched for marked ants. Ants marked in the two hibernation sites had spread to 19 different summer nests, 6 of which contained marked ants from both A and B (fig. 3). The longest spreading distance was 105 m, but we do not know if this was the result of a single transport or of a stepwise migration through a chain of nests. We confirmed by similarly marking the inhabitants of two large nests in July that some of the ants from each of those permanent nests hibernated in different winter nests and that a given winter nest gets its inhabitants from more than one nest inhabited in summer (fig. 4).

Internest movement in summer

a. Carrying

We noted some nests as strongly inhabited in mid-June while poorly inhabited in mid-July and *vice versa* indicating a shift in the distribution of the population due to other causes than reproduction. Carrying of pupae and adults between summer nests, especially on the cliffs, was indeed frequently observed. Contrary to seasonal migration, internest carrying in summer very often took place in reciprocal directions (cf. ÖKLAND, 1931; MABELIS, 1979b), a phenomenon which has been interpreted as two parties of carrier ants «voting» about which nest is relatively more optimal (ADLERZ, 1886; ROSENGREN, 1971). It was anyhow clear that most of the carrying observed in summer could not functionally be interpreted as «recruitment» to a new nesting site (MÖGLICH & HÖLLDOBLER, 1974) because it took place between established nests and thus redistributed the population within an existing network of nests. We may speculate that the

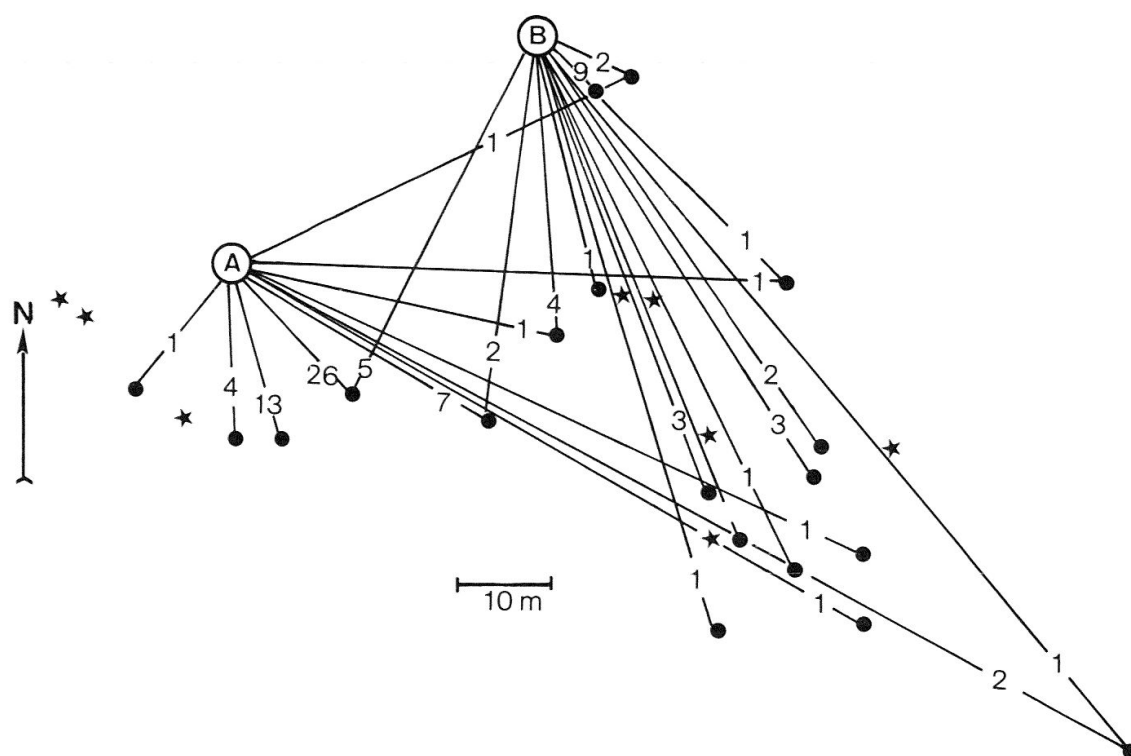


Fig. 3: Dispersion of workers marked in winter nest A (with silver spray) and in winter nest B (with blue spray) and recaptured in early summer in different summer nests (dots). The numbers in the figure refer to number of recaptures of each colour while stars are nests where no marked ants were found (other parts of the island were also searched for recaptures but without success).

population distribution by this means could be adjusted to temporal and spatial variations in the resource distribution including insolation and available room for brood and young workers within the nests. Space within the nest can as mentioned be a limiting resource in the present case because the windswept cliff habitat precludes much enlargement of an individual nest. The situation with ants carrying nestmates in different directions along the cliffs was too confusing to allow observations of a true nest fissioning on the study islet (although some new bud-nests were noted). A 47 m long migration route connecting a large *F. truncorum* mound with a newly founded bud-nest through a stream of one-way carriers was however observed in late June on another archipelago islet (the 2 ha islet which in 1978 harboured only one nest had 6 nests by 1983)

b. Drifting

Internest worker-exchange not attributable to transport of nestmates by carrier ants but to «visiting» (SCHERBA, 1964) or «drifting» (ITO & IMAMURA, 1974; HIGASHI, 1978a; MACKEY & MACKEY, 1983) of independently moving workers has been reported in some *Formica* species. We confirmed this phenomenon by spray-marking about 30% of the inhabitants of two large, permanent nests with a separate colour for each nest (fig. 4). Marking was done in July and sampling about 5 weeks later in August (fig. 4 shows in addition the result of sampling 2 hibernation nests in September). No carry-

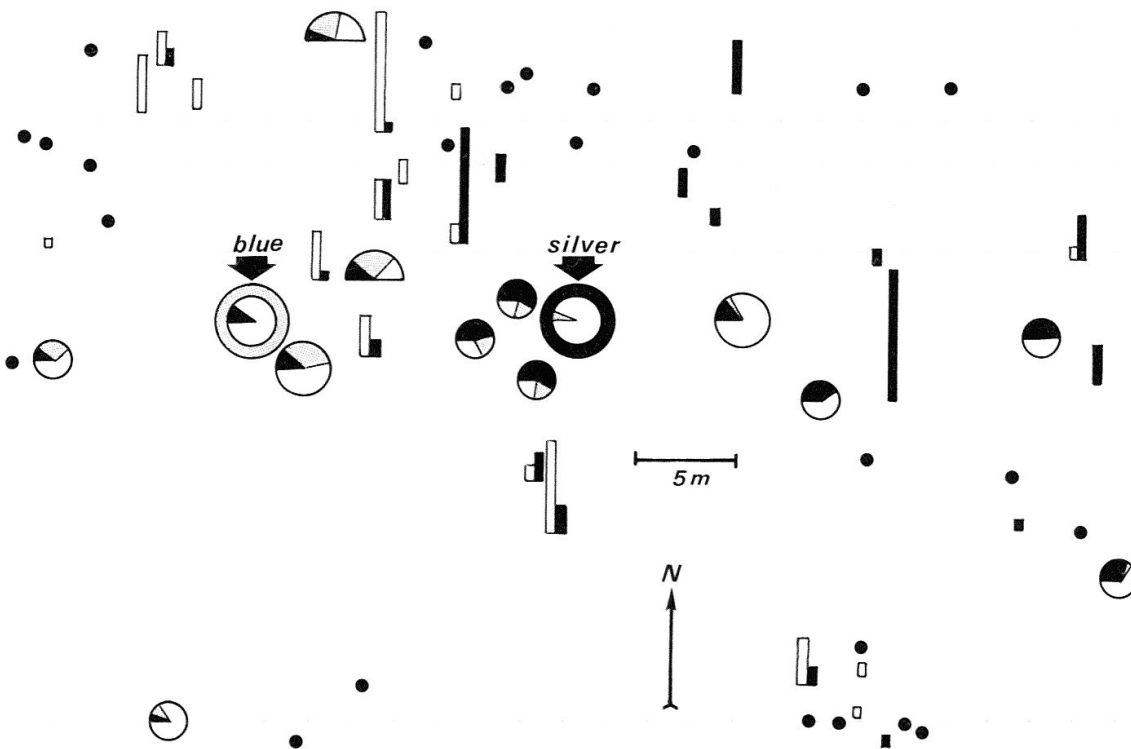


Fig. 4: The drifting index (DI, see the text) of ants marked in two nests with blue and silver spray respectively. Black sector within each circle (symbolizing a nest): DI for silver in each nest (DI for the originally marked nest population = 100%). Grey sector within circles: DI for ants marked blue. Semicircles: samples from winter nests. White staples = number of blue ants visiting trees for aphids (a stretch along the staple corresponding to its breadth = 1 marked ant, the values are based on pooling several examinations of the trees within 2 weeks after marking). Black staples: the same for silver ants. Staples close to each other mark the same tree (the staple is single if only one category of marked ants have been recaptured from the tree). Black dots: visited trees where no marked ants were found.

ing was observed in the interval between marking and sampling, but we cannot exclude this possibility. It seems, however, less likely that carrying took place from the nests in which marking was made because those permanent nests, which were the largest already at the time of marking (especially nest silver, fig. 4), appeared to grow relative to the others (most of which were temporary summer nests) toward late summer.

The drifting ratio (HIGASHI, 1978a) defined as number of recaptures in «wrong» nests as a percentage of all recaptures (HIGASHI counted the number of marked ants found on the surface of nests during a given searching time while we counted the marked ants found in samples of 400 ants taken from the inside of each nest) was 59% for blue ants and 77% for silver ants (based on a total of 153 blue and 255 silver ants from the 12 nests mapped in fig. 4). The percentual values used for fig. 4 are based on another measure, the drifting index (PAMILO & ROSENGREN, 1984), referring to the frequency of marked ants within each sample from a «wrong» nest divided by the frequency in the sample from the originally marked nest. On pooling the latter measures give 13% for blue ants and 30% for silver ants. Regression of the drifting index (DI) on distance from the point of marking (see fig. 4) gives a negative correlation which is statistically significant only for blue ants (blue: $r = -0.716$, $P < 0.01$, silver: $r = -0.519$, NS). The drifting ratio (DR) is of the same surprisingly high order of magnitude as found by HIGASHI (1978a) in *F. yessensis* (although the distance between nests was larger in our experiment). Those measures and especially the drifting index are however likely to give an exaggerated picture in the present case because the nests where marking was carried out were the largest ones (observe that even a modest addition of marked drifters from a large source of marked ants to a small nest may give a high drifting index while the same addition to a large nest population gives a low drifting index). It would theoretically be possible to correct for this bias but the data of table 6 appear too crude for this purpose. It seems nevertheless fair to conclude that drifting and/or visiting, in spite of the statistical bias of our method, must be of very large significance in *F. truncorum* and that the phenomenon appear much more pronounced in this species than in some other highly aggregated nesters studied by us by the same method (ROSENGREN, 1979 and unpublished; PAMILO & ROSENGREN, 1984). The highest DI for a single nest of a tight nest cluster of *F. exsecta* was thus only 13% (PAMILO & ROSENGREN, 1984) while seven nests in the present case had DI of 30% or higher (silver DI for 2 nests was higher than 50%).

The latter point speaks against the interpretation that the high DI observed in the present case was an artifact of the spray-marking procedure. We examined furthermore all marked recaptures for traces of paint on eyes and/or antennae but only 17 such individuals were found, 9 of which were within their original nests. The spray-marking method has in addition been used for the study of orientation in *Formica* s. str., spray-marked individuals usually retaining an excellent orienting ability based on a long-lasting spatial memory (ROSENGREN, 1971; CHERIX & ROSENGREN, 1980). The orienting capabilities of *Formica* ants suggest that the term «drifting», which is associated with a random event, may be less appropriate. We thus conclude that the inter-nest worker exchange observed is, most likely, neither an artifact of the marking procedure nor a natural error process (attributable to faulty orientation) but a function of a supranest organization favouring a high degree of social mobility. Marked *F. truncorum* workers observed on «alien» nests were in several cases observed to participate in building activity indicating they were not mere «visitors» but had changed their «home» nest (cf. HIGASHI, 1978a).

A few marked ants were found in nests situated outside the area mapped in fig. 4 but drifting in summer did not extend further than 45 m from the point of marking

(all nests in this part of the islet were searched for marked ants). Ants inhabiting nests on the eastern part of the islet could thus hardly have been in direct social contact with ants nesting 200 m away on the western part of the islet. We transferred groups of 500–2000 spray-marked ants from nest f to c, e to a, e to g and b to d (fig. 1). The transferred ants were in all cases accepted in the host nests and could be found in them still after several weeks (no case of a marked ant returning to its original nest was observed). The result proved however less relevant for the present problem than originally assumed. We found namely later that *F. truncorum* workers usually are accepted also if transferred between conspecific nests situated on different nearby islets of the archipelago (ROSENGREN *et al.* 1985).

Genetic structure

There are two aspects in the genetic development of a polycalic nest group as an «integrated unit». First, there is competition between such groups (competition against intruders, including invasions of other species, especially *Formica sanguinea*). Second, there is competition within the population between queens and individual nest units. Both aspects can be approached by analysing genetic differentiation between the social units in question, which reflects genetic relatedness among individuals within the units. If the adjacent nests of a polycalic system are genetically related to each other, this would allow us to explain the hypothetical «superunit» within the framework of kin selection theory and we do not need the much more controversial hypothesis of group selection. If ants from connected nest groups are genetically different, we face a problematic situation. Even if the worker ants from different nests behave in a friendly manner to each other and even if the hibernation process may function as a «genetical mixer», the queens compete with each other at the genetic level. Mixing the workers from different nests by «internest drifting» would only damp and obscure this process of hidden internest competition.

In order to analyse genetic population structures (see PAMILO & VARVIO-AHO, 1979; PAMILO & ROSENGREN, 1984) we made preliminary attempts to estimate genetic relatedness of worker ants within and between nests. We carried out electrophoretic analyses of 10 enzyme systems, encoded by 13 loci (for methods, see PAMILO *et al.*, 1978 and VARVIO-AHO & PAMILO, 1980). Samples from ten nests were assayed, but no variation was detected. The result might be considered as an indication for genetic homogeneity of the population, plausibly due to a small number of founders from which the present-day ants descend, although this interpretation may be premature as the level of genetic variation in *F. truncorum* is generally low (PAMILO *et al.*, 1978). If genetically homogenous, all the nests on the island could be treated as one supernest, subdivided on functional basis. The homogeneity might also smooth the effects of intrapopulation selection. We have no data from neighbouring islands, but observations from the species *Formica exsecta* and *F. fusca* show that populations on adjacent islands can genetically differ strikingly from each other (PAMILO, 1983). High genetic relatedness with reference to other populations does not remove internest competition, as the development of the social organization within the island depends on genetic relatednesses with reference to the population average. These relatednesses cannot be estimated from our monomorphic data, but observations on *Jdh* polymorphism in another *F. truncorum* population showed that the genotypes were rather uniformly distributed in the nests (both queen and worker material from three nests). The results indicate low differentiation between the nests, which might further reduce competitive internest interactions.

Estimate with method 1

Our method of combining estimation of the forager population by the Lincoln-index method with a complete excavation of the nest (table 1) allowed two independent estimates of the correction factor needed for excavation data (see methods). Table 5, based on both excavation and CMR data, gives the population number of each investigated nest (see methods), while table 6 presents a generalization of the data to all nests on the islet based on the situation in 1979. It is clear from our use of a semiquantitative nest classification that our estimate of the total number of workers on the islet (1.1 million workers) is at best a crude approximation. Our estimate of the total number of mated queens on the islet is even more tentative considering that our data do not indicate a correlation between number of workers and number of queens in the excavated nests (table 5). Assuming no correlation we get 6.3 queens/nest on an average which corresponds to a total of 400 queens on the islet. Summarizing both excavation results (table 5) and observations when gently examining all the nests in early summer gives 13 nests with 1 queen, 16 nests with 2–3 queens, 9 nests with 4–6 queens and 5 nests with more than 6 queens. Those numbers, however, represent pooled results for 3 years and we actually found no queens in the majority of gently – examined nests. Should this be taken literally? The presence of pupae (table 3) is no proof that a nest contains a laying queen because pupae were often seen carried between nests. But small larvae and/or eggs were not observed to be transported between nests and 42 of 57 brood-containing nests examined in 1979 (table 3) harboured this category (28 nests had eggs). This indicates that the majority of nests may have contained at least one queen.

A total of 30 mature queens, representing several spotsamples from several years, were dissected and found to contain sperm in *receptaculum seminis*. This does not prove functional polygyny but we observed several times more than one

Table 5: Results of population estimates in 8 nests of *F. truncorum* based on excavation and/or CMR. Correction factor for excavation data calculated for nest 1 (see table 1). Value corrected by this factor (see methods for correction factors used for CMR data).

| size class | nest | workers | pupae | queens | method |
|------------|------|---------|--------|--------|-------------------|
| very large | 1 | 72 303 | 19 920 | 15 | excavat. + CMR |
| large | 2 | 41 199 | 28 742 | 6 | excavat. |
| | 3 | 31 253 | – | – | CMR |
| medium | 4 | 10 273 | 5 156 | 6 | excavat. |
| | 5 | 7 133 | 4 055 | 0 | excavat. |
| | 6 | 7 413 | – | 3 | excavat. |
| small | 7 | 3 103 | – | 14 | excavat. |
| very small | 8 | 314 | – | 0 | excavat. |

physogastric queen in the same nest (even in the same nestchamber) indicating that the brood emanated from more than one queen. Genetic evidences indicate that polygyny in other *Formica* s. str. species too tends to be functional (PAMILO & ROSENGREN, 1983), although CHERIX (1983) concluded that different queens of a *F. lugubris* nest tend to lay eggs at different times of the colony cycle. If several *F. truncorum* queens occurred within the same nest they tended to be close together, one extreme being 14 queens found within the same chamber of the nest. The above observations of mature queens were all made in mid-summer after the completion of migration to the temporary summer nests. We counted in early spring 72 queens under a flat stone covering a large permanent nest. Similar high numbers have incidentally been observed in other areas too (64 *F. truncorum* queens, all of which had mated, were observed in a single nest). We observed later in the spring migration from the highly polygynous nest to temporary summer nests making it likely that some of the queens were later distributed among several nests (see also KIM & MURAKAMI, 1980). We find it probable that the species, although often harbouring several mated queens in its nests, is, as a rule, less markedly polygynous than in some other members of *Formica* s. str. (see ROSENGREN & PAMILO, 1983; ITO, 1973). But variations are likely to be high, as cold weather during the mating period may force the ants to intranest copulations (ROSENGREN *et al.*, 1985) thus increasing queen number, at least temporarily.

Estimate with method 2

Ants of our study colony of *F. polyctena* visited a total of 63 trees in early September against 112 trees in our supercolony of *F. truncorum*. Two different samplings of tree visitors (pooled values for all trees of a colony, see methods) gave almost the same ratio (*polyctena/truncorum*) 0.8 (339/436 and 259/318) indicating that the method gives repeatable results. Our colony of *F. polyctena* had in late June to early July a forager population of 408726 ± 15046 individuals (mean of 4 total traffic counts using the Lincoln-index method, data corrected with the factor 1.28 given by HORSTMANN, 1982). A new marking procedure using the same methods gave only 213489 still active foragers in mid-September. Dividing those values with the ratio 0.8 gives (provided our assumptions are correct) 510907 *F. truncorum* foragers for early July and 266861 for mid-September. Our estimate of the proportion of foragers in *F. truncorum* is from mid-August (21% according to table 1) when neither eggs nor larvae were any longer present in the nests. This 21% estimate, which closely agrees with data from *F. lugubris* (CHERIX, 1983), is here used as an approximation for the situation in late summer to early autumn. The calculation, using our estimate of forager number for mid-September, gives a total of 1.3 million *F. truncorum* workers on Lilla Träskön. It seems however reasonable to assume that the proportion of foragers was higher during the peak of the season in July (many of the workers counted in our excavations in mid-August were light coloured, indicating they had newly hatched, and the proportion of this category which cannot function as foragers during the same year obviously increased toward autumn). We have no estimate for the proportion of foragers in *F. truncorum* during peak activity in July but HORSTMANN (1982) suggests 43% foragers in *F. polyctena*. Using this as an approximation for the situation in July gives 1.2 million workers on our study islet. We admit, however, that our argumentation is somewhat far-fetched and that the close fit between the estimates with method 1 and method 2 could be a happy accident.

Using our excavation data (table 6) and the fact that the population utilized slightly less than 2 ha of the islet (the rest being too shady for this thermophilic species)

we get an average density of 56 worker ants /m². Workers from the upper parts of the nests weighed in September on an average 7.7 mg/ant while workers from the deeper parts of a permanent nest (representing the torpid category of «early hibernators» with an obviously swollen abdomen and a tendency to form clusters) weighed 9.0 mg (based on groups of 100 ants weighed in toto). Using 8.3 mg/ant as a compromise gives a total worker biomass of 8.9 kg freshweight on the islet.

Table 6: Classification of population size within each nest based on observations in 1979 and numerical population estimate based on generalization of data from table 5.

| size class | no. on nests of each class | workers/nest | workers in all nests |
|--------------|----------------------------|--------------|----------------------|
| very large | 7 | 70000 | 49×10^4 |
| large | 7 | 40000 | 28×10^4 |
| medium | 20 | 10000 | 20×10^4 |
| small-medium | 12 | 5000 | 6×10^4 |
| small | 12 | 3000 | 36×10^3 |
| very small | 5 | 500 | 25×10^2 |
| | | Sum: | 1 068 500 |

Foraging and worker size

The pattern of foraging

F. polychteta, nesting in a rich forest habitat, may harbour 1 million workers and several hundred mated queens in a single nest (ROSENGREN, 1977a; HORSTMANN, 1982). This is due to an effective foraging system based on partitioning of foraging grounds among workers, recruitment of naïve workers and actively cleared trunk trails functioning as conveyor belts for food (ROSENGREN, 1971; ROSENGREN & PAMILO, 1978). Increasing the size of a «central place» colony by increasing mean foraging distance may nevertheless drive the system toward a point of diminished return. This point is likely to be reached earlier in a nutritionally poor habitat, making decentralization rewarding as suggested by the results of CHERIX (1980, 1981). Nest decentralization as a territorial strategy increasing net profitability of foraging follows from the model developed by HÖLLDOBLER & LUMSDEN (1980, see also BERNSTEIN, 1982). It would thus be tempting to consider the highly integrated nest system studied by us as a vehicle for harvesting food from a poor environment.

The total foraging area of the *F. truncorum* colony was estimated as 19 100 m² leaving 9 250 m² empty (fig. 1). The single mound of *F. polychteta* mentioned earlier had, although harbouring nearly as many ants as our supercolony of *F. truncorum* a foraging area of only 2 500 m² (ROSENGREN in preparation). The comparison between those colonies showed furthermore that *F. polychteta* visited 63 trees in early September (mean density of visitors per m treetrunk : 9, range : 2–62) while the corresponding value for *F. truncorum* was 112 trees (mean density : 5/m, range : 2–40/m). Many of those trees may have been visited by individual hunters rather than by honeydew collectors and the main traffic was in both cases concentrated to only a part of the total

number of trees visited. In *F. polycтена* 9 trees (14% of all visited) accounted for 50% of the total traffic to trees while 21 trees (19% of all visited) gave the same percentage in *F. truncorum*. The most distant tree visited was situated 65 m from the nest in *F. polycтена* and 40 m from a single nest unit in *F. truncorum* (recording of colour-marked recaptures on tree trunks within and outside the area mapped in fig. 4). Those data do not contradict our working hypothesis that a decentralized population can utilize an area of low food density better than a «central place» colony of comparable population size. The main merit of a decentralized system is that the costs for foraging (time, energy expenditure) can be kept reasonably low.

Our marking experiments demonstrated that ants from different nests at least partly shared the same trees as foraging areas (fig. 4) and this lack of territory borders between nests probably also means that ants from different nests exchange liquid food by trophallaxis when encountering in the terrain (KLOFT, 1967; WILKINSON *et al.*, 1978, ROSENGREN, 1979). Internest visiting and carrying of store animals between nests could be other agents for nutritive homeostasis at the level of the supercolony.

The nests on our study islet lacked in most cases obvious foraging routes, foragers dispersing all over the visited area. A large bell-shaped mound of *F. truncorum* found on another island had however 6 fairly distinct foraging routes running through the moss-covered ground. We marked the ants of 3 routes (angular distance between adjacent routes more than 90°) with a separate spray-colour for each route. A total of 182 marked ants (106 silver, 40 yellow and 36 white) were found 2 weeks later when examining all the 6 routes of the system. 97% of the recaptures were found on the routes where they had been originally marked and thus obtained «route fidelity» (see ROSENGREN, 1971). The essence of the latter concept is not that foragers collectively follow fixed paths but that the individual forager, whether it follows a collective route or not, tends to return to a given searching area. Our marking experiment thus indicates that *F. truncorum* also when dispersing «diffusely» over the territory, has «partitioning of the foraging ground» (DOBZANSKA, 1958).

Foraging objects

There was a total of 1064 trees higher than 1 m on the islet 157 of which were visited during at least some part of a season. Of the total number 83% was *Pinus sylvestris* (16% of which was visited), 6% *Alnus glutinosa* (0% visited), 4% *Populus tremula* (7% visited), 3% *Sorbus aucuparia* (28% visited), 1.5% *Betula* sp. (31% visited), 2% *Picea abies* (0% visited) and 0.5% *Salix caprea* (17% visited). Birch and mountain ash were important sources for honeydew in spring and early summer while the ants almost exclusively visited pines (and a few poplars) later in the season. The ants preferred old but dwarfed pines (50% visited) to young pines of the same size class (less than 10% visited) and large old pines to mean sized, still growing pines. The ants visited *Symydobius oblongus* HEYD. on birch. With the exception of a small group of *Cinara nuda* MORDV. in the top of a young pine all aphids collected from pinet wigs visited by the ants were *Cinara pinea* MORDY or *C. pini* L. The ants continued to visit the dense colonies of the latter species long after the completion of the migration from the summer nests (ants visiting and watching the aphids were still found in mid-October if the autumn was warm). Predation on *Cinara* as observed by CHERIX (1981) in *F. lugubris* and by ROSENGREN *et al.* (1979) in *F. polycтена* was not seen in the present case.

We observed on several occasions both in spring and summer that dead *Gammarides* found by the ants at the shores constituted a conspicuous part of the

booty brought to the nests. Three spot samples of booty items collected on the southern cliffs in late June 1980 (n = 274), late May 1981 (n = 52) and mid-July 1982 (n = 170) thus contained 30%, 59% and 30% *Gammaridae* respectively (other main groups: *Porcellio scaber* 15%, *Chironomidae* 14%, *Formicidae* 12% and *Coleoptera* 12%). *Porcellio* was extremely abundant on the islet occurring under most stones not inhabited by ants. But we noted no killing of *Porcellio* by *F. truncorum* in the field, all items of that species brought to the nest representing dry carrions. A spot sample (n = 260) collected from the central pine stands in July gave however a more «normal» red wood ant diet (main groups: *Diptera* 29%, *Formicidae* 24%, *Lepidoptera* larvae 8%, *Coleoptera* 7% and *Psocoptera* 7%). That *F. truncorum* and *F. rufa* L. compete for the same booty was evident also from two spot samples collected simultaneously from *F. truncorum* (n = 75) and *F. rufa* (n = 90) respectively sharing the same islet and habitat in the Hitis archipelago (booty insects collected in August). The main groups were (nr. for *F. rufa* within parenthesis): *Diptera* 40% (22%), *Formicidae* 25% (22%), *Aranae* 17% (13%), *Psocoptera* 3% (22%), *Lepidoptera* larvae 3% (6%) and *Aphidoidea* 4% (2%).

Workers of alien ant species captured by *F. truncorum* as booty on the Lilla Träskön islet consisted of 50% *Myrmica* sp., 35% *Lasius flavus*, 11% *Lasius niger*, 4% *Leptothorax* sp. (pooling of several small samples from different parts of the season, pooled n = 121). We observed predation on *L. flavus* by large hunters of *F. truncorum* digging tunnels within a humus mound of that hypogoeic species. The most likely reason for the scarce predation on *L. niger* was that this species, being more exposed than *L. flavus* to contest competition from *F. truncorum*, had been reduced to a very low population level on the islet (ROSENGREN *et al.*, 1985). Winged queens and males of *Myrmica* sp. and *Lasius* sp. were occasionally from late July onwards the most obvious kind of booty. It may be that the islet situated in the middle of a bay constituted by long mainland peninsulas (map in ROSENGREN *et al.*, 1985) functioned as a visual swarm marker (see HUBBARD & NAGELL 1976) for alates of those species. To sum up our preliminary observations on protein food: it seems that a considerable part of the booty emanated from the sea (*Gammaridae*, *Chironomidae*) or from land areas outside the islet (alate ants). This explains why this and other apparently poor offshore islets can sometimes support surprisingly large populations of *Formica* s. str. and other ant species (see also VEPSÄLÄINEN & PISARSKI, 1982). An external source of food can be expected to be quite variable in amount (e. g. due to the wind conditions) and we would predict periods of protein shortage. Predation on conspecifics or «cannibalism» has been noted in polydomous colonies of *F. polyctena* during periods of protein shortage in the spring (MABELIS 1979a; ROSENGREN & PAMILO, 1983; DRIESSEN *et al.*, 1984) but we have so far not noted this phenomenon in *F. truncorum*.

Foraging and the size of workers

Although the foraging system, including site allegiance of individual foragers and social recruitment to food, may in principle be similar to that of other *Formica* s. str. species, one quantitative difference appears obvious. *F. truncorum* cannot to the same degree as in e. g. *F. polyctena* rely on mass effects in foraging and defence because each nest unit, regardless whether we have to do with a monodomous or a polydomous colony, is small and the probability of getting much help from nestmates in killing a booty item and transporting it to the nest would be low. This could mean that the size of the workers can be expected to be more critical in *F. truncorum* than in *F. polyctena*.

An increase in the mean size of workers would be a very expensive method of getting large workers while an increase of the variance may be a cheaper method. Our results are in accordance with those ideas.

Outer-orbital distance has been used as a measure of body size in *Formica s. str.* (HIGASHI 1974; KIM & MURAKAMI, 1980). We used this measure when comparing samples randomly taken from nests of *F. polyctena* and *F. truncorum*. Neither the means nor the variances were significantly different from each other in the two sampled colonies of *F. polyctena* but this species had a larger mean size (t-test, $P < 0.005$) and a lower variance (F-test, $P < 0.005$) and range than in our random sample of *F. truncorum* (table 7, fig. 5). The latter comparison is not quite adequate however because the size frequency curve although apparently symmetric in *F. polyctena* is skewed toward the larger size class in *F. truncorum* (observe the high n-value in fig. 5 making a statistical proof superfluous). The data thus indicate that *F. truncorum*, although still apparently monomorphic, has nevertheless entered the path towards true polymorphism (OSTER & WILSON, 1978).

We selected on behavioural criteria groups of workers from the same large nest which we had used for random sampling (table 7). Ants tending aphids 9 m from the nest and ants carrying and hiding pupae (when the nest was opened) were significantly smaller whereas hunters (carrying booty) and «aggressors» (ants pouring out from the nest and attacking the hand of the observer) were significantly larger than the mean for the random sample (pair-wise t-tests, $P < 0.001$ for all comparisons). Aggressors and hunters were significantly larger than pupae hiders and aphid visitors 9 m from the nest (t-test, $P < 0.02$ for each combination). Our results thus indicate a clear tendency for size-based polyethism in *F. truncorum* corresponding to previous findings in *F. yessensis* (HIGASHI, 1974; KIM & MURAKAMI, 1980). We are however less certain that the last-mentioned authors that ants fleeing with brood when the nest is opened are really identical with «nurses» (pupae hiding and attacking could as well represent two temporary roles in a defence strategy). We also disagree that aphid tenders are necessarily smaller than the mean for the population and our results actually show that ants visiting aphid colonies situated 20 m from the nest are larger than the mean for the nest population (t-test, $P < 0.001$). A correlation between foraging distance and

Table 7: No. of ants sampled (n), mean and standard deviation of outer-orbital distance in *F. polyctena* and *F. truncorum* workers from polydomous colonies. Random samples are from the upper part of nests (rainy weather) while selected samples were ants taken from nest or from the foraging area according to behavioural criteria.

| Random samples from nests: | n | \bar{x} (mm) | s |
|---|------|----------------|--------|
| <i>F. polyctena</i> | 129 | 1.57 | 0.1848 |
| <i>F. polyctena</i> | 251 | 1.54 | 0.1719 |
| <i>F. truncorum</i> | 1055 | 1.42 | 0.2200 |
| Selected samples (<i>F. truncorum</i>): | | | |
| pupae hiders | 90 | 1.28 | 0.1609 |
| aggressors | 153 | 1.53 | 0.2152 |
| hunters | 50 | 1.59 | 0.1910 |
| aphid visitors 9 m | 32 | 1.25 | 0.0753 |
| aphid visitors 20 m | 28 | 1.55 | 0.1133 |

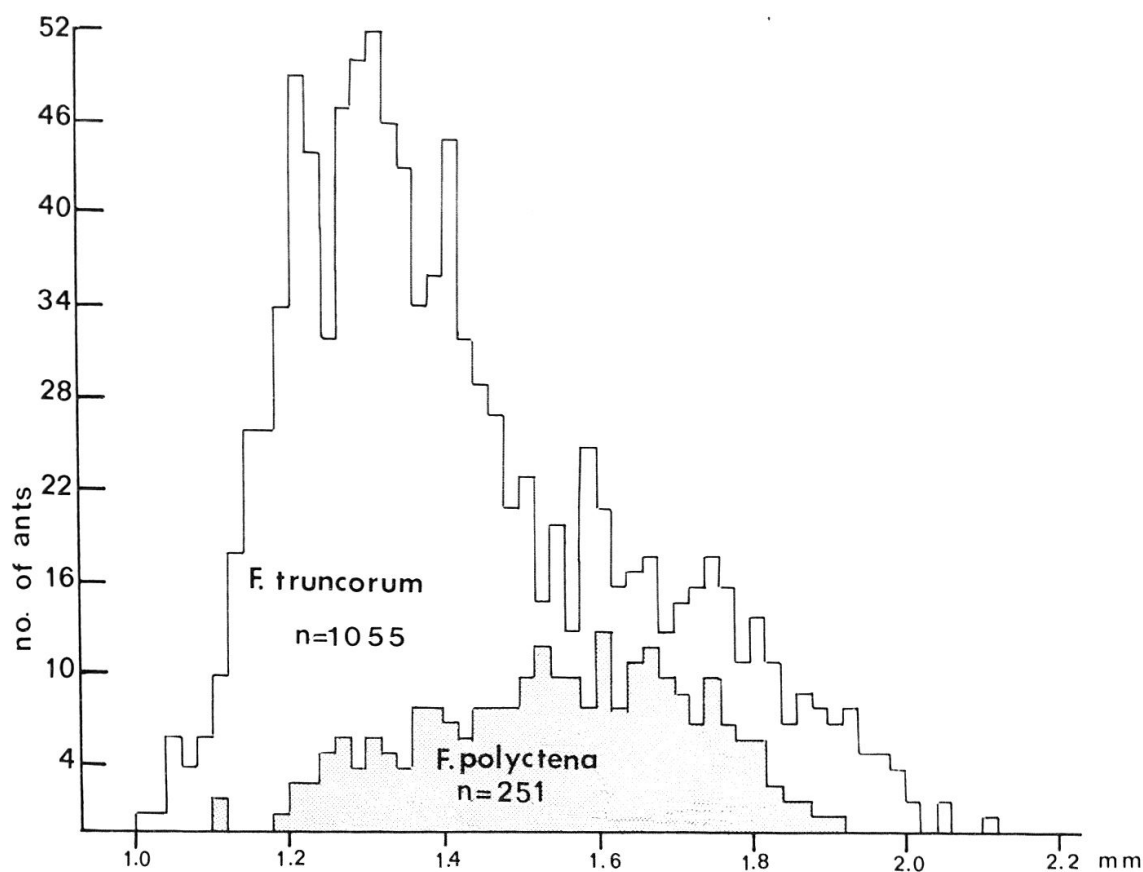


Fig. 5: The frequency distribution of outerorbital distances in workers (random samples from nests) of *F. truncorum* and *F. polycтена*. Observe the skewed size frequency distribution in *F. truncorum*.

size of workers was demonstrated in *F. polycтена* (HORSTMANN, 1972 and PARASCHIVESCU cited by HORSTMANN, 1972) although this species generally showed less size variation than in *F. yessensis* and *F. truncorum*. We find it possible that the correlation between foraging distance and size has a connection to the observation by BERNSTEIN & BERNSTEIN (1969) that larger *Formica* workers possessing larger brains and eyes have a better orienting ability than smaller workers. Size-based polyethism does not exclude age polyethism (OTTO, 1958; ROSENGREN, 1977a) and we have some indirect evidence that age polyethism is important in *F. truncorum* too. The ants within one of our study nests on an adjacent islet had been thoroughly marked with spray colours about two months before sampling in late August. 12.3% ($n = 200$) of ants caught outside the nest were still marked against 5.5% ($n = 1360$) for ants sampled from the inside of the nest. The latter group was stored in a refrigerated room in the laboratory ($\pm 6^{\circ}\text{C}$) which led to an obvious clustering by some of the ants. The percentage of marked individuals was only 1.1 ($n = 500$) in ants forming clusters (2×2 contingency tables; $P < 0.005$ in all comparisons). The result, which corresponds to results with other red wood ant species (ROSENGREN, 1971), is explainable by assuming that the «clusterers» (a group probably identical with early hibernating store animals, table 4) hatched from pupae after the marking procedure while extranidal workers were old.

The old notion that ants inhabiting different nests of a polydomous colony may show nonhostile social interactions was supported by our observations. In fact the interactions appeared so intense in this case that the conception of an ant nest as a social and reproductive unit was undermined. An alternative to asking why different nests of *F. truncorum* «cooperate» is to ask why worker biomass and reproductives of a society are distributed in several different centres. An attempt to answer the latter question for a monogynous species was made by HÖLLDOBLER & LUMSDEN (1980) and the problemacy in polygynous species has also been discussed (HÖLLDOBLER & WILSON, 1977; ROSENGREN & PAMILO, 1983). The problemacy is full of nuances as both proximate and ultimate explanations have to be considered and a given species (e. g. *Formica truncorum*) may be exclusively monodomous and monogynous in one geographical region while polydomous and polygynous in another (ROSENGREN & PAMILO, 1983). When discussing interactions within polydomous colonies of different species we also have to consider differences of degree. Internest exchange of workers may in species like *F. polyctena* occasionally be very intense but tends to be a temporal phenomenon, the individual nest retaining a high degree of social integrity (MABELIS, 1979a; ROSENGREN & PAMILO, 1983). In species like *F. yessensis* and *F. truncorum*, on the other hand, the borders between individual nests become more or less blurred, making the term «supranest» especially pertinent (information in KROMBEIN *et. al.*, 1979 indicate that several nearctic red wood ant species possible also belong to this group of «supranesters», see also MAC KAY & MAC KAY, 1983, 1984). Supranesting in the *truncorum* -group within *Formica s. str.* appears associated with a very variable and plastic nesting architecture in which the inner structure and regular paraboloid shape characteristic for the mounds of other *Formica s. str.* species has degenerated or never evolved. The high degree of population stability in species like *F. polyctena* may be connected to «homeostatic nesting» making brood rearing less dependent on climatic fluctuations. The flimsy nesting habits of ants of the morphological «*truncorum*-group» appears to represent a more opportunistic or «r-selected» strategy and our observations of fluctuating population numbers in *F. truncorum* is compatible with this view. We may however look on the nesting habits of *F. truncorum* as simply another mean to gain homeostatic conditions for brood rearing. The abandoning of a heat-preserving (and/or heat-producing) nest architecture in *F. truncorum* and related species is probably connected to a pronounced tendency to rely on external heating of the nest and part of the nest movements observable in this species group is clearly thermoregulative in function (see SEELEY & HEINRICH, 1980 for similar observations in other ant species). Another factor preadapting the species for dynamic supranesting is the use of naked rock as a nesting site, because this limits the growth of each individual nest unit (for both nutritive and «physical» reasons) and necessitates an obligatory differentiation in summer nests (used for heating of the brood) and winter nests (used for hibernation within a sufficiently deep layer of soil). Adaptation to a specific habitat rather than true ecological «opportunism» can thus be the reason for the flexible nesting habits of *F. truncorum*. The most striking consequence of this flexibility is that *F. truncorum* is known as a nuisance in summer cottages in the Gulf of Finland where it, unlike other red wood ants, may nest within sun-exposed walls or under roofing tiles (several samples and descriptions of such cases communicated to R. ROSENGREN).

The above explanations, although stressing the role of trivial abiotic constraints of a specific habitat, do not exclude evolutionary consequences of polydomy or supranesting in interspecific competition within the ant assembly (HÖLLDOBLER &

WILSON, 1977). The latter consequences will later be considered in detail (ROSENGREN *et al.*, 1985) but we note here that severe competitors of *F. truncorum* e. g. *F. sanguinea*, may have considerable difficulties in establishing their colonies on an islet already occupied by an extensive supranest of the former species. Although the priority effect thus appears plausible, monopolization of the habitat by *F. truncorum* does not preclude some degree of coexistence with a majority of species within the ant assembly (it should be remembered that our study islet had a total of 10 ant species which is not clearly lower than usually found on Baltic archipelago islets of this size and distance from the mainland, see PISARSKI *et al.*, 1982).

Monopolizing an insular habitat by supranesting is likely to reduce the «extinction probability» not only of the ants but also of their aphids which were actively guarded by workers even at low temperature in the night. But the main effect of supranesting on foraging would be the ability to harvest booty from a larger area and thus compensate for a low density of prey (CHERIX, 1981). Decentralized nesting means that each nest unit becomes small making collective nest defence less effective and weakening use of trunk trails as «conveyor belts» for collective carrying of booty. We advocated the hypothesis that this higher degree of «individualism» in foraging *F. truncorum* workers (compared to *F. polyctena*) could have selected for the great size variation observed in the species. This if of course only one of several possible explanations.

It can logically be argued that polydomous nesting is evolutionarily rewarding because of strong interspecific competition (ROSENGREN & PAMILO, 1983) and that polydomy represents an adaptation to a low density of food. The problemacy is however very twisted as poor habitats may be scarce also in competing ant species normally restricting colony growth and budding. In fact BRIAN (1965) considered polygyny in *Myrmica* as an adaptation to a species-poor environment with few competitors (see also MARIKOVSKY, 1962). But supranesting as a «territorial strategy» in the sense of HÖLLDOBLER & LUMSDEN (1980) is rewarding exactly because there are many competitors. We are thus trapped in a paradox. It appears intuitively plausible that reduced interspecific competition in extreme habitats like the Jura mountains (CHERIX, 1981) or the offshore islets studied by us (see also ROSENGREN *et al.*, 1985) could favour the «ontogenic» development of polydomous nest aggregates (because colonies will more easily reach the «critical size» needed for budding if not inhibited by competitors). There is furthermore the argument of CONNOR (1980) that interspecific competition may be low in a harsh environment and we may add the rule of density compensation. Still another possibility is that polydomy and polygyny may be facilitated by a high degree of genetical uniformity in the local breeding community as actually can be expected in isolated regions like mountains or boreal archipelago areas. If the regional population is genetically heterogenous we could on the other hand expect marked olfactory differences between individual queens (and nests) with intraspecific aggression and territorial repulsion between nests as a result.

It is thus by no means necessary to look at polydomy as a «phylogenetic» adaptation directly favoured by natural selection especially when this view easily becomes «Panglossian» (see GOULD & LEWONTIN, 1979 and DAWKINS, 1982 for a discussion of those problems). Polydomy appears connected to polygyny in ants of the genus *Formica* and may thus be an indirect consequence of natural selection favouring alate queens avoiding risky dispersal (HIGASHI, 1980; ROSENGREN & PAMILO, 1983). Competition between queens staying within the same nest may in turn favour budding and polydomy which thus would represent only an epiphenomenon to polygyny. Dispersal of unmated *F. truncorum* queens could have a low probability of success in the archi-

pelago especially if the host species *Serviformica fusca*, as postulated by VEPSÄLÄINEN & PISARSKI (1982), have difficulties in colonizing offshore islets. *F. truncorum* is considered monogynous and monodomous in the lowland of continental Europe (LANGE, 1958; BETREM, 1960) but KUTTER (1963) observing a large polygynous and polydomous colony of the species in the Swiss mountains remarked that nest multiplication by budding (instead of by lonely foundresses usurping a colony of the host species) could be rewarding if *Serviformica* is locally scarce. The latter point was made also by HIGASHI adding that the risk encountered by dispersing *Formica* s. str. foundresses will increase if the host species too develop polygyny (HIGASHI, 1980, 1983). We have indeed observed oligogynous *F. fusca* colonies in the archipelago. There is however a nexus of possible reasons why dispersal of single foundresses could be relatively more risky in some habitats than in others (ROSENGREN & PAMILO, 1983).

The main points of the above discussion can be summarized in a logically more explicit although highly tentative form:

1. Polygyny may evolve in a given population inhabiting a given habitat type if dispersal is sufficiently risky to outweigh the fitness-reducing effect of several reproductives competing for resources within the same colony. The latter competition is reduced if the colony divides its reproductives between several nests within the local patch (polydomy).
2. It follows from the above point that polygyny which according to our view, evolves through selection acting on the level of individual queens, should evolve more easily if «colony level selection» (OSTER & WILSON, 1978) simultaneously favours a decentralized colony organization based on spatially separate subunits. Such a colony organization occurs in some monogynous ant species where it is known to increase the economic defensibility of the territory (HÖLLEDOBLER & LUMSDEN, 1980). Our present case study of *F. truncorum* indicates the presence of an additional mechanism: a given habitat type may «force» a colony to adopt decentralized nesting through such a simple mechanism as lack of space (e. g. for hibernation) or the need for wind-protection, thermoregulation etc. The resulting supranest may facilitate the evolution of polygyny also for proximate causes as reproductive daughters joining the mother colony can easily escape aggressive or manipulative interactions with the mother (primer pheromones repressing the reproductive capacity of subordinates are e. g. less likely to function efficiently between the parts of a highly dispersed supranest).
3. Supranesting combined with polygyny could, dependent on the type of habitat, have important evolutionary consequences on the reproductive output of the family-structured subpopulations involved. Those consequences could be negative e. g. if crowding of nests in the same patch increases susceptibility to contagious diseases or attracts parasites and predators (see ROSENGREN, 1979 and CHERIX, 1981 for a discussion of some of those points). An increased ability to monopolize an insular patch could in certain climatic regions or habitat types outweigh those supposedly negative effects.

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