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Competition and coexistence in an insular ant community — a manipulation experiment (Hymenoptera: Formicidae).

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Colonies of the red wood ant *Formica truncorum* were transferred to offshore islets in the Gulf of Finland previously lacking this or other sg. *Formica* species. The result of this ecological manipulation experiment shows that *F. truncorum* by weakening populations of *Lasius niger* may at the same time boost the nest numbers of *Lasius flavus* and *Leptothorax* sp. The findings confirming previous notions of stable competition between *L. niger* and *L. flavus* indicate that *Leptothorax* sp. may also be involved in the competitive network. Such findings as the hostility between *F. truncorum* and *L. niger* are discussed.

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1. Introduction

The role of interspecific competition in structuring ecological communities has recently been hotly debated (see Simberloff 1982, Schoener 1982, Haila 1982 and Roughgarden 1983 for different attitudes). It is often pointed out that ecological manipulation experiments could represent a valuable complement or even an alternative to accelerating innovations within mathematical competition theory (Simberloff 1982, Schoener 1983, Connell 1983). Such experiments, often aiming at proving or disproving the "competitive exclusion principle" (Hardin 1960), have indeed been carried out (data summarized by Schoener 1983 and Connell 1983). A well established case is provided by long-term studies of *Lasius niger* (Linné, 1758) and *Lasius flavus* (Fabricius, 1781) showing that those ant species form permanent associations on British grasslands although competing for both nesting sites and food (Pontin 1961, 1963, 1969, 1982). I here utilize this species pair when trying to answer the question: What happens to an ant association based on stable interspecific competition (Pontin 1969) if a new, superior actor is introduced on the myrmechological scene?

Ants of the subgenus *Formica* are known to reduce nest numbers of other ant species within their territories (Skwarra 1929, Rosengren 1969, Higashi & Yamauchi 1979, Cherix & Bourne 1980). Do they affect all species equally? Previous observations suggest that *Formica truncorum* Fabr. forming vast polydomous nest-aggregations on some pine-forested offshore islands of the Gulf of Finland (Rosengren et al. 1985), may curtail populations of *Lasius niger* more strongly than those of some other species including *Lasius flavus* (Rosengren et al. 1986). My aim is not only to check the latter finding but to test a specific prediction. Suppose that *Lasius niger*, as observed by Pontin (1982), is competing with other minor ants of the assembly. Would we not expect cases where ant species repressed by *L. niger* are boosted by the introduction of *F. truncorum* to the habitat patch?

2. Habitats, ants and methods

2.1 Islets studied

The nonforrested skerries abounding in the Gulf of Finland, especially at a longer distance from the mainland, usually lack a layer of sand/humus supporting fields of grasses and herbs and are consequently poor in ants (species identification and nomenclature according to Collingwood 1979). The "Jack-of-all-trades", *L. niger*, usually dominate such barren skerries completely (Ranta et al. 1983) and is often the only species found (Vepsäläinen &

Pisarski 1982). The situation is, independently of distance from the mainland, very different on skerries covered by stony carpets of grasses and herbs. Here *L. flavus*, a species exclusively dependent on subterranean aphids (Pontin 1978), always occurs together with *L. niger* and may even dominate the assembly (Rosengren et al. 1986). *Myrmica* sp. (usually *M. ruba* or *M. ruginodis*), although patchily abundant at humid sites characterized by more luxuriant vegetation, is much less prominent in the stony grassland-type studied here. *Formica fusca* may in exceptional cases constitute up to 20 % of all nests on such grassland patches but is of sporadic occurrence. This is even more true of *Tetramorium caespitum*. Both species occur on Jussinkari and Iso Lamppukari 14 km from the mainland (the Söderskär archipelago; grid: 666:41) but were lacking on 6 other nonforested islets of the same vegetation type. The opposite pattern is found in the "miniature ant" *Leptothorax* sp. (mainly the species *L. acervorum* and *L. muscorum*) which occur in low frequency on all grassland skerries so far studied by me. Afforestation of islets appears to be correlated with an increased species diversity characterized by a larger share of *Myrmica, Leptothorax, Camponotus* and *Formica* (Pisarski et al. 1982, Vepsäläinen & Pisarski 1982, Rosengren et al. 1986). The following islets were used for the experiment.

A. Lilla Trädgårdsholm

The virtually treeless islet situated 6 km from the mainland (the Löparö archipelago in Sibbo; grid: 667:41) was about 6000 m^2 in size. The central patch used for sampling was about 2000 m^2 the rest being sterile beds of moraine or barren cliffs. The rather dry grassland patch was covered by "suitable stones" (below). With the exception of a single nest of *Myrmica ruginodis* no species other than *Lasius niger, Lasius flavus, Leptothorax acervorum* and *Leptothorax muscorum* were found. I call this islet "A" in the text that follows.

B. Tallkobben

The islet, 400 m^2 in size, was situated in the Ingå archipelago about 2 km from the nearest mainland peninsula (Kopparnäs; grid: 666:34). The islet, bearing a small stand of large scotch pines was separated by a narrow strait from a larger island harbouring about 30 nests of *F. truncorum*. The central part of the island covered by *Empetrum nigrum* was not suitable for the sampling method used here but the shore area contained suitable stones distributed over an area of 50— 100 m^2. The islet, representing a miniature version of a typical *F. truncorum* habitat (Rosengren et al. 1985), initially harboured the following species: *Camponotus herculeanus, Formica fusca, Lasius niger, Lasius flavus, Myrmica rubra, Leptothorax acervorum* and *Leptothorax muscorum*. I call this islet "B" in the text which follows.

C. Gråskär

The sparsely pine-forested islet situated 1 km south of islet A (7 km from the mainland in the Löparö archipelago of Sibbo; grid: 667:41) was 2 ha in size. The whole islet, sparsely covered by suitable stones, was used for sampling. The following species were found: *Lasius niger, Lasius flavus, Myrmica rubra, Myrmica ruginodis, Myrmica scabrinodis, Leptothorax acervorum, Leptothorax muscorum, Leptothorax tuberum* and *Harpagoxenus sublaevis*. I call this islet "C" in the text below.

Islets A and B were used for the transfer tests while islet C was used as a control with the aim of checking that possible trends in species abundancies observable when introducing a new competitor on islets A and B could not be explainable by climatic variables, specific to the year of sampling.

2.2. Methods

Lasius niger and especially *Lasius flavus* often build humus mounds in mainland habitats but are almost exclusively found nesting under stones on exposed archipelago islets. A switch to stone nesting appeared evident in the other species too. *Leptothorax* nests are e.g. often found in decaying twigs, stumps etc. but such objects were almost lacking on the nonforested islet A and were rare also on islet B. The central part of the latter islet was, however, covered with a dense *Empetrum* carpet on sandy soil and this area may have contained undetected nests of the species.

Nests were counted by simply examining "suitable" stones i.e. flat, not too heavy stones ($>$ 8 cm ∅) situated on humus and/or fine sand and not in obvious risk of being flooded by water. A nest was defined as any clearly inhabited unit situated 0.5 m or more from the nearest site inhabited by the same species. Even the latter precaution may have been insufficient, especially in *Lasius niger* and *Formica fusca*, considering that the same nest may have covered several stones. The method, although possibly overestimating the true nest number (the latter bias was unlikely in the case of the well-defined nests of *Leptothorax*) nevertheless gave a relative measure of population size. Stones occupied by invading *F. truncorum* or situated in the immediate vicinity of nests of that species were not included in the recording. The latter principle made it impossible to maintain the intended sample size on islet B (Table 1) because the number of suitable stones was very limited and too many became occupied by branch-nests of the expanding invader population. Stones were marked during the first sampling with small painted symbols (one for each species or species group), but the durability of the marking proved too poor for the intended purpose. Persistent traces of marking permitted, however, the localization of sites sampled in previous years.

The suitable stone method, as shown by the following examples, is sensitive to at least two kinds of bias:

1. Sampling 117 stones (46 inhabited) on the nonforested Ytter Ådgrund islet (grid: 665:34) gave 65 % *L. flavus* and 35 % *L. niger* (no other species). Extending sampling to virtually all suitable stones of the islet (examined: 1063, inhabited: 419) gave 56 % *L. flavus*, 41 % *L. niger*, 0.5 % *Myrmica rubra* and 2.5 % *Leptothorax* sp. (sampling did not include a humid cleft with tussocks containing a large number of *M. rubra* colonies). The ratio niger/flavus is not significantly higher in the large sample $\chi^2 = 1.0$, 1 *df*, $P > 0.1$) but the trend may indicate that the larger sample included proportionally more dryer, peripheral areas of grassland patches in which *L. niger* can be observed to predominate.

2. Sampling the same area of a stony grassland islet both in late July and in late September the same year gave the niger/flavus ratio 49/54 for July and 22/64 for

September ($\chi^2=9.7$, 1 *df*, $P<0.01$). This significant difference is due to the fact that the thermophilous *L. niger* is an early hibernator while *L. flavus* (and *Leptothorax acervorum*) remains subterraneously active until the end of the season (Rosengren unpubl.).

Those errors were avoided by searching systematically through all parts of the islets containing suitable stones and by standardizing sampling time to late July.

About 200 litres nest material containing approximately 100 000 *F. truncorum* workers (estimate according to Rosengren et al. 1985) after the first sampling was transported to each of the islets A and B. Separately collected mature queens were added to transplanted nests. The introduced colonies flourished for all of the 3-year period and even produced sexuals. Expansion by founding of several branch-nests was stronger on the forested islet B.

Sampling was made using an interval of 1 year. The long intervals between samplings make it appear unlikely that the sampling procedure can have interferred with the results (each stone was, of course, carefully placed back in its original position). I avoided agitating *Leptothorax* by taking taxonomic samples from each nest (the small colony may in this case disperse, increasing the risk of queens becoming crushed when stones are replaced) and ants of this genus are therefore treated collectively.

3. Results

Islet C, used as a control, did not show any trends in nest numbers (or proportions of stones inhabited) in any of the species *L. flavus*, *L. niger*, and *Leptothorax* sp. (Table 1). The proportion between nests of different species (including *Myrmica*) was not significantly different in different years (1983 versus 1985: $\chi^2=1.7$, 3 *df*, $P>=.1$). The latter comparison gave highly significant differences in the case of the experimental islets A ($\chi^2=69.9$, 2 *df*, $P<0.001$) and B ($\chi^2=30.8$, 3 *df*, $P<0.001$). Islets A and B showed a significant decrease in the ratio inhabited/noninhabited stones (years 1 and 3 compared) for *L. niger* (A: $\chi^2=41.2$, 1 *df*, $P<0.001$; B: $\chi^2=29.8$, 1 *df*, $P<0.001$) but an increase for *Leptothorax* sp. (A: $\chi^2=15.4$, 1 *df*, $P<0.001$; B: $\chi^2=7.7$, 1 *df*, $P<0.001$). Islet A, but not islet B, showed a significant increase also with respect to *L. flavus* ($\chi^2=22.7$, 1 *df*, $P<0.001$). The small increase in the number of *L. flavus*-stones on islet B the second year (Table 1, Fig. 1B) was nonsignificant (year 1 versus 2: $\chi^2=0.33$, 1 *df*, $P>0.1$).

The introduced colonies of *F. truncorum* within 1−2 h were already vigorously attacked by *L. niger* workers which were probably mass-recruiting nestmates along pheromone trails to the points of intrusion. It is not really surprising that such an aggressive species cannot maintain its populations when confronted with an equally aggressive but physically stronger opponent (Fig. 1). Following the same logic it is even less astonishing that hypogoeic (Collingwood 1979) or cryptic species like *L. flavus* and *Leptothorax* may avoid extermination better (Rosengren et al. 1986). *Lasius flavus* and *Leptothorax* on islet A did, however, not only show a relative, but an absolute, increase in nest number (Table 1). The latter result is compatible with the idea of species equilibrium being maintained by competitive interaction (Pontin 1982). It is an unexpected finding, however, that *Leptothorax* is a participant in the game. The data from the forested islet B, while illustrating the latter point, is in another respect more difficult to interprete, especially when the sample sizes (Table 1) are quite small. It should, however,

Table 1. Results of sampling from under stones in the years 1−3 (1983, 1984 and 1985) on islets A (Lilla Trädgårdsholm), B (Tallkobben) and C (Gråskär). Large *Formica truncorum* colonies were introduced onto islets A and B immediately after the first sampling (July 1983) while C (no sg. *Formica* ants) represented the control. Absolute numbers of examined and inhabited nests are given but the column headed "Total" includes both the pooled number of nests and (in parenthesis) the percentage represented by these of all sites examined.

Islet	Stones	Stones inhabited						
and year	examined	Total	*L. flavus*	*L. niger*	*F. fusca*	*Myrmica*	*Leptothorax*	*Camponotus*
A 1983	700	212 (30.3)	71	126	0	1	14	0
1984	700	247 (35.3)	135	80	0	0	32	0
1985	700	225 (32.1)	134	47	0	1	43	0
B 1983	300	94 (31.3)	13	64	6	1	8	2
1984	300	30 (10.0)	16	8	1	0	4	1
1985	150	26 (17.3)	5	2	3	0	16	0
C 1983	300	93 (31.0)	31	30	0	25	7	0
1984	300	86 (28.7)	27	26	0	30	3	0
1985	300	100 (33.3)	28	33	0	34	5	0

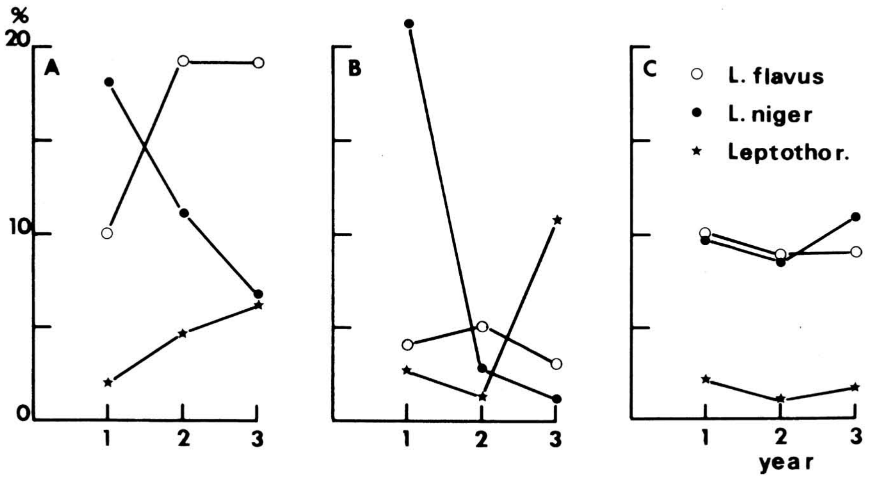

Fig. 1. Trends on islets A, B and C in the proportions of sampled stones inhabited by *Lasius flavus*, *Lasius niger* and *Leptothorax* during a 3-year period (see also Table 1). The first sample (year 1) was taken before, and the others (years 2—3) after, the addition of *Formica truncorum* to the ant association.

be noted that *Camponotus*, although a superior fighter in individual contests (Rosengren et al. 1986), was exterminated in the third year and that *Formica fusca* withstood the invasion (Table 1). The vigilant escape behaviour characteristic of *F. fusca* workers when encountering red wood ant foragers on shared food resources (Rosengren et al. 1986) could be one reason for coexistence.

4. Discussion

Flooding miniature islands with the aggressive red wood ant apparently represent a very extreme situation. Patches with very dense populations of *F. truncorum* occur, however, under natural conditions, too (Rosengren et al. 1985), although all gradations between high and low densities may be found. A reduction in the population numbers of *L. niger* by *Formica* s. str. considering the gradation in densities could theoretically represent one of several mechanisms switching the early succession stage of an ant assembly to a stage of higher species diversity (cf. Paine 1966), although the role of vegetational succession should not be underestimated.

The hypogoeic *L. flavus*, although not observed to be engaged in escalating battling with *F. truncorum*, is preyed upon by individual *F. truncorum* hunters digging openings in its nest (Rosengren et al. 1985). This implies that *F. truncorum*, when occurring at extremely high density, will gradually curtail the population size of *L. flavus* too, although reducing nest numbers of *L. niger* more strongly. Boosting as a net effect may thus be observable only if the restricting effect of *F. truncorum* on *L. flavus* remains smaller than the reduction in competition pressure caused by the extermination of *L. niger* by *F. truncorum*. This interpretation is compatible with my observations. Islet B was a poor *L. flavus* habitat when compared to islet A and individual colonies appeared weak even before the transfer. The very high density of invaders in this situation may have exerted a sufficiently strong predation pressure to eliminate net boosting of *L. flavus* (Fig. 1B). Predation pressure was probably, at least initially, much weaker on islet A because of the larger size of the latter (observe that the transfered populations were approximately equal) but the introduced ants may gradually have exhaused *L. flavus* nest on this islet too, thus limiting any further increase in nest numbers (Fig. 1A). An additional difference was that suitable stones were a much more limiting resource on islet B, while *L. flavus* colonies driven away by *F. truncorum* expanding its nesting area on islet A could select new sites of equal quality. *L. flavus* colonies driven away by *F. truncorum* occupying suitable stones on islet B clearly did not have the latter option open to them. The limited number of stones also lead to methodological difficulties in maintaining criteria for suitability considering that the best sites gradually become occupied by *F. truncorum*.

The drastic drop in the percentage of sampled stones inhabited on islet B (cf. islets A and B according to Table 1) may at least partly be due to the latter bias, which probably could not be compensated for even by drastically reducing sample size (Table 1).

Leptothorax, claimed to be chemically invisible to both *Lasius* and *Formica* (Pontin 1982), is probably less exposed to predation by *Formica truncorum*, although cases of killing of *Leptothorax* workers by red wood ants have been noted in the laboratory (Rosengren unpubl.). Furthermore, *Leptothorax* may, owing to the small size of the nest (often less than 2 cm in Ø) be less sensitive to a reduction of suitable stones and could in the case of islet B have been favoured by the absent boosting of *L. flavus*. The decrease in nest numbers of *Leptothorax* the second year followed by a strong increase the third year (Fig. 1) raises the possibility that the polygynous colonies split into small fragments hiding in cracks, etc. Those buds, due to relaxed competition pressure from *Lasius*, may then have developed into larger entities easy to detect in the third sampling. However, it is also possible that *Leptothorax* colonies living in earth nests on the central parts of the islet migrated to the areas at the shore when sites under the stones became empty. The data from islet A (all inhabitable parts of the islet sampled) are thus in several respects less amibiguous.

F. truncorum was observed to systematically clear the terrain of *L. niger* by raiding nest after nest, a behaviour suggesting contest competition rather than mere predation. Strong interspecific aggression or "enemy specification" (Hölldobler 1983) is considered characteristic of species pairs with overlapping habitat requirements and resource spectra. This explanation appeares far from convincing in the present case. *L. niger* and *F. truncorum* represent quite different options within the r-K spectrum (the former is the classical opportunist while the latter almost represents the opposite extreme) and *L. niger* cannot, as indicated by my experiments, constitute a serious threat to a mature colony of *F. truncorum*. These species, although both above-ground food generalists, should furthermore be well partitioned by the large difference in worker size, making intense competition for trophic resources appear unlikely. How then can one explain the aggressive reaction of *F. truncorum* toward *L. niger*? The tentative explanation advocated below is based on the observation that the polygynous *F. truncorum* of the Gulf of Finland shows a distribution pattern characterized by polycalic nest groups clustering together on adjacent islands (Rosengren et al. 1986). Workers and queens from one island are accepted in colonies on nearby islands, although they are killed if transfered to islands located at greater distances (Rosengren et al. 1986); a situation suggesting kin-selection in family-structured (Mishod 1982) or viscous (Pamilo 1983) populations.

Formica truncorum differs from other European sg. *Formica* species by its extreme preference for open, xerothermic habitats (this is why the transfer of this "red wood ant" to the nonforested islet A was not an entirely artificial situation). The xerothermic habitats preferred by *F. truncorum* are originally dominated by *L. niger*. This means that an isolated *F. truncorum* foundress may encounter a large risk of being harassed and killed by *L. niger* before it can find the more scantily occurring nests of its host species *F. fusca*. The interpretation is supported by accidental observations of freshly dealated sg. *Formica* queens surrounded by clusters of attacking *L. niger* workers (Rosengren unpubl.). Both the beach head strategy of dispersal and the low level of intraspecific aggression (Rosengren et al. 1986) could represent mechanisms dealing with this problem. The fitness of a given female leaving the nest by flight could thus be improved if adjacent habitat-islands have been cleaned from *L. niger* by previously settled colonists representing the same deme or nest group. The hypothesis of constraints on colonization due to *L. niger* could also explain why the vast majority of pine-forested, xerothermic islets, representing the vegetation type preferred by *F. truncorum*, do not harbour any nests of that species (Rosengren et al. 1986). Islet B, although situated close to a *F. truncorum* beach head, harbouring several nests of the host species *F. fusca*, and (as demonstrated by the experiment) offering excellent living conditions for a mature colony of the species, illustrates the above point.

The boosting of *L. flavus* and *Leptothorax sp.* following weakening of *L. niger* supports the general notion of interspecific competition between coexisting ants (Pontin 1982). Pontin reached the plausible conclusion that coexistence between *L. niger* and *L. flavus* is due to stronger intra- than interspecific competition.

There may, however, exist additional mechanisms in this case. The hypogoeic life style of *L. flavus*, compared to *L. niger*, favours not only a given amount of resource partitioning but also seasonal partitioning. *L. flavus* may thus be able to compensate for a weaker competing ability in summer by a stronger ability to utilize resources in autumn.

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