

## Scarcity of sites suitable for nesting promotes plesiobiosis in ants (Hymenoptera: Formicidae)

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Plesiobiosis is a rudimentary form of social symbiosis. It consists of the close proximity of nests of different social insect species. Numerous cases of plesiobiosis between ant species observed in a successional series of rocky habitats in S Finland are listed and the most interesting of them are described in detail. Among all *Lasius* colonies found within the whole successional series studied, as many as 8.4% were plesiobiotically associated with other ants. In the two earliest successional stages: the shore meadow and the open rocky outcrop, the proportion was nearly 12% and 10% respectively. The finding of numerous plesiobiotically related nests there is discussed in the context of the unique local habitat conditions.

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### 1. Introduction

Plesiobiosis [original term introduced by Wheeler (1901)] is the most rudimentary form of social symbiosis. It consists of the close proximity of colonies of different species of social insects whose nests border on one another. Typically, plesiobiotic colonies of two or more species may live under the same stone or in the same tree stump. However, their nests—even if they adjoin each other—remain separate as constructions, and individuals from different colonies do not mix. There is no biotic interdependence between them, and they are potentially hostile to one another. As a rule, the plesiobiotic partners differ from each other morphologically, ecologically and ethologically, and usually they represent systematically distant forms; they typically belong at least to different genera (Wheeler 1926, Wuorenrinne 1958, Hölldobler & Wilson 1990). Generally, they occupy lower, sub-

ordinate levels in the hierarchy of interspecific competition (Vepsäläinen & Pisarski 1982, Pisarski & Vepsäläinen 1989). Cases of plesiobiosis are included within the category of the so-called “compound nests” (distinct from “mixed colonies”) (Wasmann 1891, Wheeler 1926, Hölldobler & Wilson 1990); however, plesiobiotically related nests remain as individual units.

Several cases and aspects of plesiobiosis have been described recently (Czechowski & Rotkiewicz 1997, Czechowski & Yamauchi 1998, Czechowski & Czechowska 2000, Czechowski 2003), including rather unusual associations between wood ant (*Formica* s. str.) species and *Formica* (*Serviformica*) *fusca* L. (Czechowski & Vepsäläinen 1999a, b, Czechowski 2002). Apart from interesting theoretical implications regarding the evolution of social parasitism in ants [wood ants are temporary social parasites and *F. fusca* their host species; see Czechowski & Vepsäläinen



Fig. 1. A shore meadow (island Porsgrundet).

(1999a)], many cases of plesiobiosis point to nest competition as causality factor (Czechowski 2002). This in turn provides the basis for a more general hypothesis that plesiobiosis is especially frequent in habitats lacking from sites suitable for the nesting of ants.

Recent investigations on ecological differentiation of sibling species of the subgenus *Lasius* s. str. that were carried out in Finland by Czechowski, Radchenko, Savolainen and Vepsäläinen (in prep.) were an opportunity to test this hypothesis.

## 2. Material and methods

The study was conducted in the coastal region of southern Finland, on the Tvärminneön peninsula, Hanko, and on several islands of the Tvärminne archipelago, the westernmost part of the Gulf of Finland in the Baltic Sea. The local habitat spectrum consists mainly of different stages of primary succession ranging from the treeless open rocky outcrop to the mature moist pine forest. The rocky outcrop that is the prevailing form is intersected with crevices and interspersed with small patches of vegetation that are sites suitable for ant nesting (Savolainen & Vepsäläinen 1988, 1989). The myrmecofauna there has been studied by Vepsäläinen & Pisarski (1982 and unpubl.).

In 2003, nests of *Lasius* F. species were looked

for and registered in the habitats studied. A record was kept of every case of plesiobiosis noticed, not only those involving *Lasius* ants. Four successional habitat stages (not exactly linear) were distinguished: (1) rocks – an open rocky outcrop with poor herb vegetation in crevices filled with soil; (2) shore meadows – small patches or narrow strips of dense herb vegetation on wave-cut island, usually stony terraces (Fig. 1); (3) forest on rocks – a “park-like” sparse pine forest made up of scattered trees (in general, not very old) growing in rock crevices and in vegetation patches that interperse the rocky outcrop; (4) mature moist forest – a relatively thick pine forest with a herb layer growing in depressions with a well-developed soil stratum.

A total of 443 colonies of *Lasius* were found, including 273 colonies of *Lasius* s. str. sibling species, *L. niger* (L.) and *L. platythorax* Seifert, and 170 colonies of *L. (Cautolasius) flavus* F.

## 3. Results

A total of 29 cases of plesiobiosis (i.e. such a number of couples or triplets of nests) was found: 26 of them were in habitats of the successional series studied (including 23 cases involving *Lasius* species) and another three were found on the verge of the road along the Tvärminneön peninsula. The most common pair of species was *L. (Lasius)*

Table 1. List of the cases of plesiobiosis registered within the successional seria of the rocky habitats (nrs. 1–26) and out of it (nrs. 27–29).

Nr.	Species	Locality	Habitat	Location of nest, or nest type
1	<i>L. niger/L. flavus</i>	Kvarnskärgrunden	Rocky outcrop	In rock crevice
2	<i>L. niger/L. flavus</i>	Kvarnskärgrunden	Shore meadow	Under stone
3	<i>L. niger/L. flavus</i>	Kvarnskärgrunden	Shore meadow	Under stone
4	<i>L. niger/L. flavus</i>	Kvarnskärgrunden	Shore meadow	Under stone
5	<i>L. niger/L. flavus</i>	Allgrundet	Shore meadow	In soil at rock
6	<i>L. niger/L. flavus</i>	Allgrundet	Shore meadow	Under stone
7	<i>L. niger/L. flavus</i>	Allgrundet	Shore meadow	Under stone
8	<i>L. niger/L. flavus</i>	Vikaskär	Shore meadow	Under stone
9	<i>L. niger/L. flavus</i>	Vikaskär	Shore meadow	Under stone
10	<i>L. niger/L. flavus</i>	Vikaskär	Shore meadow	Under stone
11	<i>L. flavus/F. fusca/M. rubra</i>	Tvärminneön	Forest on rocks	Under wood
12	<i>L. platythorax/L. flavus</i>	Tvärminneön	Forest on rocks	Overgrown soil mound
13	<i>L. platythorax/L. flavus</i>	Tvärminneön	Forest on rocks	In rock crevice
14	<i>L. flavus/F. fusca</i>	Tvärminneön	Forest on rocks	In rock crevice
15	<i>L. flavus/F. aquilonia</i>	Tvärminneön	Forest on rocks	<i>F. aquilonia</i> mound
16	<i>L. flavus/F. fusca</i>	Tvärminneön	Forest on rocks	Overgrown soil mound
17	<i>L. niger/L. flavus</i>	Kvarnskär	Shore meadow	Under stone
18	<i>L. niger/M. rubra</i>	Porsgrundet	Shore meadow	Under stone
19	<i>L. platythorax/M. rubra</i>	Porsgrundet	Forest	In rotten wood
20	<i>L. niger/L. flavus</i>	Munken	Shore meadow	Under stone
21	<i>L. platythorax/L. flavus</i>	Joskär	Rocky outcrop	Under stone
22	<i>L. platythorax/F. fusca</i>	Tvärminneön	Forest on rocks	In rotten wood
23	<i>L. flavus/F. fusca</i>	Tvärminneön	Forest on rocks	Under stone
24	<i>M. rubra/L. muscorum</i>	Porsgrundet	Shore meadow	Under stone
25	<i>F. truncorum/F. fusca</i>	Tvärminneön	Forest on rocks	In rock crevice
26	<i>F. lugubris/F. fusca</i>			
	<i>L. acervorum</i>	Tvärminneön	Forest on rocks	<i>F. lugubris</i> mound
27	<i>L. niger/M. rubra</i>	Tvärminneön	At road	Between asphalt edge and grass
28	<i>L. flavus/T. caespitum</i>	Tvärminneön	At road	Under stone
29	<i>L. platythorax/F. fusca</i>	Tvärminneön	Forest clearing	In and at rotten trunk

*niger/L. (Cautolasius) flavus*. For these, and other plesiobiotic associations, see Table 1.

Among all 443 *Lasius* colonies registered within the whole successional habitat series, 37 colonies (8.4%) were plesiobiotically associated with other ants. Most frequently, their partners were colonies of other *Lasius* species (always, however, of a different subgenus). *L. flavus* appeared to show greatest disposition to plesiobiotic relations, with 11.2% of its colonies living in plesiobiosis with another species. In *L. niger* that proportion was 7.1%, and in *L. platythorax* 5.6%.

The shore meadows were the habitat type most conducive to plesiobiotic relations. As many as 11.8% of all *Lasius* colonies registered there (22 out of 186) were plesiobiotically related to other colonies, compared to 9.8% in the open rocky out-

crop (4 out of 41), and 5% (10 out of 200) in the forests on rocks. The only case of plesiobiosis in the latter seemed to be accidental and the ant association short-lived. The co-nesting was between an incipient colony of *L. platythorax* (a queen and 4 workers) and a mature colony of *M. rubra* (nr. 19 in Table 1). The *L. platythorax* colony had practically no chance of developing and surviving amidst the extremely abundant *M. rubra* population that occupied this part of the island. Another case of plesiobiosis between *L. platythorax* and *F. fusca* observed in the forest on rocks (nr. 22 in Table 1) was somewhat similar to the former. Both sides there were represented by incipient colonies.

There is a significant difference between the plesiobiotic/non-plesiobiotic *Lasius* nest ratios in the first and the one before last successional stages,





Fig. 2. Plesiobiosis between *F. aquilonia* (the top part of the mound) and *L. flavus* (the lower part of the mound) (the case nr. 15; see Table 1).

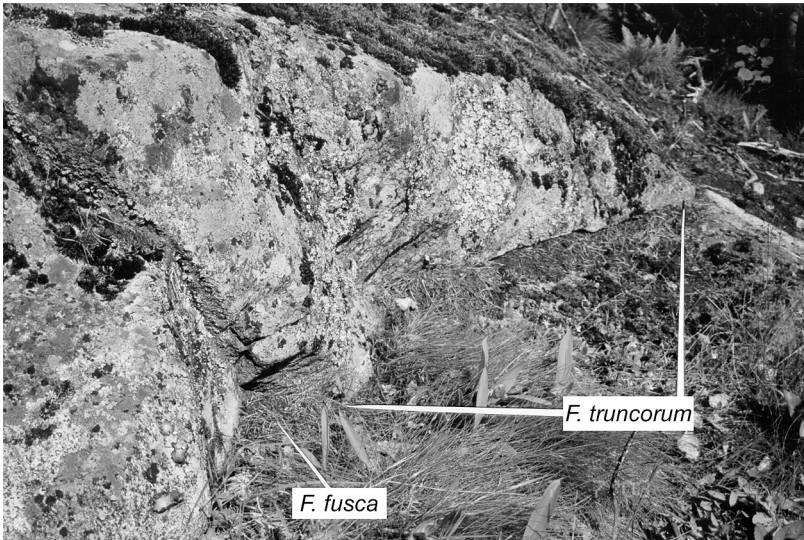


Fig. 3. Plesiobiosis between *F. truncorum* and *F. fusca* (the case nr. 25; see Table 1).

i.e. the shore meadow vs. the forest on rocks ( $\chi^2 = 6.71$ ,  $p < 0.01$ ). Analogous difference between the open rocky outcrop and the forest on rocks is not statistically significant ( $\chi^2 = 2.45$ ,  $p > 0.05$ ). The last successional stage (the mature pine forest) ought to be used for these comparisons, however the material obtained there was too scant and thus might be accidental.

Some particular cases of plesiobiosis (nrs. 12, 14, 15, 25, 26, 28, and 29 in Table 1) are remarkable as regards their form or expression, and due that they may be considered “untypical” ones – thus especially interested from the myrmecologi-

cal point of view. The first five of them were observed in the successional habitat series under discussion, and the two remaining ones were seen outside that area.

- nr. 12. *L. platythorax*/*L. flavus*. A compound nest in a rock crevice, with a soil mound overgrown with moss and grass (typical of *L. flavus*). The centre of the mound was occupied by a colony of *Lasius* sp., and it was encircled by an *L. flavus* colony.
- nr. 14. *L. flavus*/*F. fusca*. A linear, 2 meters long *L. flavus* nest in a rock crevice, interrupted in



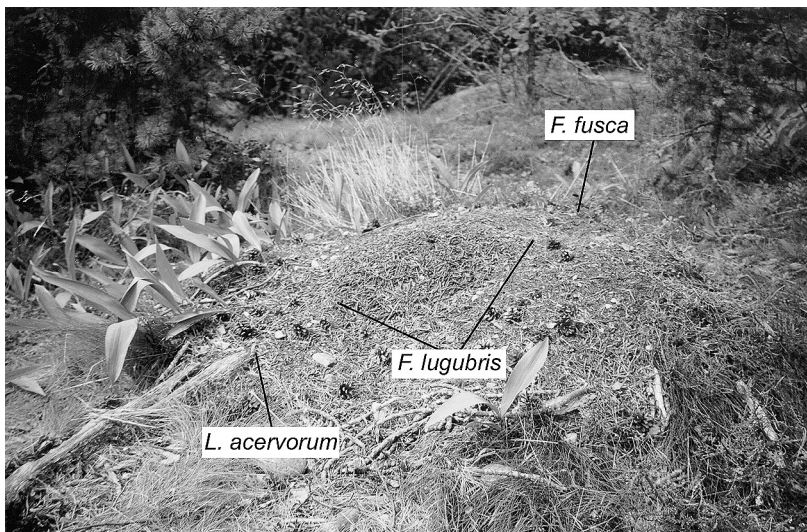


Fig. 4. Plesiobiosis between *F. lugubris*, *F. fusca* and *L. acervorum* (the case nr. 26; see Table 1).

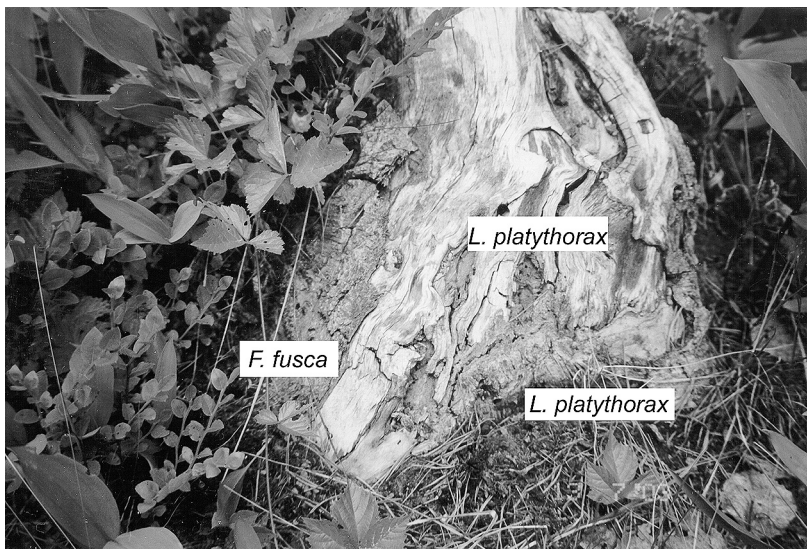


Fig. 5. Plesiobiosis between *F. fusca* and *L. platythorax* (the case nr. 29; see Table 1).

its central part by a nest of *F. fusca*.

- nr. 15. *L. flavus*/*F. aquilonia*. Originally a nest of *F. aquilonia* with a two-storeyed mound, situated on the top of the rocks and below, on a small ridge. Both parts of the mound were narrowly interconnected along a vertical rock crevice. In the observation period only the upper part was inhabited by a weak (dying out?) wood ant colony, whereas the lower one was occupied by *L. flavus* (Fig. 2).
- nr. 25. *F. truncorum*/*F. fusca*. Originally a linear, 1.5 meter long nest of *F. truncorum* in a rock crevice, wholly inhabited by wood ants in the

previous season. In 2003, one end of the nest, 25 cm long, was occupied by *F. fusca*, whereas the rest was still inhabited by *F. truncorum*. A route of the latter ants led over the *F. fusca* part (Fig. 3).

- nr. 26. *F. lugubris*/*F. fusca*/*L. acervorum*. Originally (as recently as the previous year) *F. lugubris* mound 1.1 m in diameter. In 2003, the wood ant colony distinctly declined and occupied only the central part of the mound, 40 cm in diameter, showing, however, great building activity. Colonies of *F. fusca* and *L. acervorum* nested vis-à-vis each other at edges

of the old mound, 40 and 30 cm away respectively from the part inhabited by *F. lugubris* (Fig. 4). On 8 July a nuptial flight of *L. acervorum* took place and this aroused no wood ants' interest.

- nr. 28. *L. flavus*/*T. caespitum*. A compound nest under a stone contained in an abandoned nest (a mound) of *Formica exsecta* NYL. at the road. During the previous season the nest was fully inhabited by *F. exsecta*.
- nr. 29. *L. platythorax*/*F. fusca*. A tree trunk in a grassy forest clearing with a nest of *L. platythorax* partly inside the trunk and partly at its foot, and a nest of *F. fusca* at the trunk foot. The compound nest was noticed on 11 July 2003, and on that day single *F. fusca* workers managed to get inside the trunk. They obstinately looked into holes and crevices, from time to time pulling out a *L. platythorax* worker. The victims were killed and carried to the *F. fusca* nest. This situation lasted till 13 July, when *L. platythorax* ants started to transfer their pupae from inside the trunk to the underground part of the nest (Fig. 5).

#### 4. Discussion

Within the whole successional series of the rocky habitat studied in Finland, every twelfth colony of the genus *Lasius* was plesiobiotically associated with another ant colony. In the earliest successional stages of this series, i.e. on the shore meadows and the open rocky outcrop, the respective proportions were as high as one out of every eight and one out of every ten such *Lasius* colonies. While there are no proper quantitative data from (lowland) Central-European habitats, the author's own observations in Poland appear to indicate that plesiobiotic ant nests are much more difficult to find there. On the other hand, the data under discussion may be compared with very similar observations obtained in quite different habitat conditions in S Finland, namely in a sand dune complex with pine forest near the village of Tvärminne. About 30 ant species cohabit this dune complex (Gallé 1991; see also Czechowski 1999, 2000, 2001, Czechowski & Vepsäläinen 2001), with nest densities in various successional stages ranging from 2.0 to 37.4 per 100 m<sup>2</sup> (Gallé 1991).

In 2001, the occurrence of *Lasius* s. str. species was investigated in a series of successional habitats, from sand surfaces with very sparse grass or sedge cover to pine forest (Gallé 1991). A total of 112 nests of *Lasius* s.str. (*L. psammophilus* Seifert, *L. niger* and *L. platythorax*) were registered (Czechowski, Czechowska & Vepsäläinen in prep.). No case of plesiobiosis involving these species was revealed, and only one pair of plesiobiotic nests of other ants (*F. fusca*/*M. rubra*; Czechowski 2003) was seen in the course of that study. Each of the dune successional stages represented a habitat incomparably more homogeneous than rocky habitats are, and each of the former offered ants incomparably larger area suitable for nesting than the latter do.

Therefore, the scarcity of sites suitable for nesting may be suspected as a factor conducive to plesiobiotic relations (or rather forcing their formation) in ants that inhabit rocky habitats. The lack of sites was obvious in the open rock outcrop and also the forest on the rocks. Soil-dwelling ants can only nest there in rock crevices filled with earth, and the total surface of such microhabitats is very small, compared to the entire area. Despite apparent differences, the same applies perhaps even to a greater extent to the shore meadows. In this habitat, ants appear to nest almost exclusively under stones, and only in places that are not too moist (i.e. relatively far from the shore) and with a sufficiently thick layer of soil on the rock. On the other hand, the shore meadows are very attractive for ants, as they can be considered a habitat rich in food resources, especially in comparison with the adjacent open rocky areas. In the former, apart from the local soil, epigeal and epiphytic invertebrates, and honey-dew, staple food of ants, there are shore silts that are also rich in protein particles. The combination of these two habitat factors, a lack of nesting sites on the one hand, abundant food on the other, necessarily makes interspecific competition in ants especially intense. Plesiobiosis appears to be a way out of this situation, the phenomenon itself being possible due to differences in species' biologies and their positions in the competitive hierarchy.

Some particular cases of plesiobiosis are after all amazing in the light of earlier results. For example, *L. niger* and *M. rubra* actually compete with each other for food and nesting sites when

they live in seemingly optimum habitats (Czechowski 1985).

Finally, it is noteworthy that in the entire rocky area of the Tvärminneön peninsula, its neighbourhood and islands of the Tvärminne archipelago (including forests) there are virtually no empty mounds of species of the subgenera *Formica* s. str. and *Coptoformica* Müll. As soon as a colony abandons a nest or dies out, the nest is invaded by a colony of another species, usually *F. fusca*; sometimes the invasion takes place already during the removal or dying-out process (Czechowski & Vepsäläinen 1999a, b, Czechowski 2002 and unpublished observations). These findings complete our description of the nesting situation of the local ants.

Cases of (temporary) plesiobiosis between *F. fusca* and (declining) colonies of wood ants are of special interest, as the former is usually not able to nest close to mature colonies of the latter, or at least nesting within their territory, is subject to some restrictions (Vepsäläinen & Pisarski 1982, Savolainen 1990, 1991). On the other hand, it should be pointed out that *F. fusca* and wood ants are partners in temporary social parasitism (the former as the host, the latter as the parasite). Therefore, the possibility of plesiobiotic co-existence of pairs of such species may shed light on the evolution of social parasitism in ants, as it fits within the concept of evolution beginning with plesiobiosis (Wilson 1971).

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