REPLACEMENT OF SPECIES IN WOOD ANT COLONIES
ARTIFICALLY ESTABLISHED ON ISLANDS
IN SOUTHERN FINLAND

ABSTRACT: Wood ants, i.e. species of the subgenus Formica s. str., are known to be temporary social parasites of ants of the subgenus Serviformica For. However, not only Serviformica colonies are used by young wood ant queens to start their own colonies. They are also able to take over colonies, at least queenless ones, of related species of the subgenus Formica s. str. This study followed five experimental colonies of wood ants – three of hybrid Formica aquilonia × F. polyctena, one of F. aquilonia-like form, and one of F. polyctena – artificially planted on islands of the Tvärminne archipelago, S Finland. After some years, the species identity of all colonies was F. polyctena, i.e. four of them had been taken over by heterospecific queens, whose offspring gradually replaced the old workers. These findings, together with already documented existence of hybrids in wood ants, partly explain reasons for their difficult taxonomy.

KEY WORDS: ants, colony takeover, Formica aquilonia, Formica polyctena, Formica rufa group, hybrids, island ecology, mixed colonies, queen recruitment, species replacement.

Although societies of all ants consist of one or more reproductive queens and a number of workers, their colony founding varies a lot. In the basic mode, a single fertilised female – usually after dispersal flight – independently founds a colony, but occasionally a few females cooperate. In some species, colony founding proceeds through temporary social parasitism, where the young queen (foundress) takes over a usually heterospecific colony and exploits its workers in producing her own workforce (Hölldobler and Wilson 1990). Wood ants, which belong to the subgenus Formica s. str., typically found their colonies through temporary parasitism, usually exploiting species of the subgenus Serviformica For. Furthermore, in wood ants with multi-queen (polygynous) colonies, reproductive success of young queens is not any more contingent on colony founding, because after nuptial flight they may be re-adopted by their maternal colony, or by any other conspecific colony (see e.g. Keller 1991, Pisarski and Czechowski 1994).

Here, we report on still more versatile colony founding in wood ants, which in part explain reasons for their difficult taxonomy.

Wood ants of the F. rufa group (sensu Dlusskij 1967) originally consisted of four species: F. rufa L., F. polyctena Först., F. aquilonia Yarr., and F. lugubris Zett. The group was subsequently supplemented with
a fifth species: *F. paralugubris* Seifert (Seifert 1996a). In spite of the small number of recognised species, all living in the taxonomically well studied Europe, the *F. rufa* group still poses a taxonomic problem that often puzzles field researchers. Nearly 30 years ago, Vepsäläinen and Pisarski (1981) called the *F. rufa* group ‘a taxonomic enfant terrible’ among wood ants. They described the state of its taxonomy as ‘chaos before order’. Today, despite intense investigation and rich literature on the subject, these picturesque expressions are still relevant.

In wood ants, colonies are quite frequently found in which the identity of species is practically indeterminable, when using the commonly applied morphological criteria (for these criteria, see e.g. Dlusskij 1967, Dlussky and Pisarski 1971, Kutter 1977, Collingwood 1979, Seifert 1996b, Czechowski et al. 2002). Workers and even sexuals (Czechowski and Radchenko 2006) from the same nest may appear to represent different species or they exhibit intermediate species characters. In addition, the appearance of individuals within a colony may change over time, and nest samples from separate years may be identified as different species (Pamilo and Vepsäläinen 1977, Vepsäläinen and Pisarski 1981, Czechowski 1996). Recent investigations have cast some light on this mystery. First, temporary social parasitism has been documented within the subgenus *Formica* s. str., such that gynes (young sexual females, potential queens) invade orphaned (queenless) heterospecific wood ant colonies. For this reason, temporarily mixed colonies may arise (e.g. Pisarski and Czechowski 1994, Czechowski 1996). Second, species of the *F. rufa* group are able to cross-breed under natural conditions and individuals of intermediate phenotypes (Seifert 1991, 1999, 2010, Czechowski 1993, 1996, Czechowski and Douwes 1996, Goropashnaya et al. 2004, Sorvari 2006) two or more species-specific phenotypes (Korczyńska et al. 2010) are observed.

region of southern Finland (the Hanko peninsula and the Tvärminne archipelago in the Gulf of Finland, the Baltic Sea; Fig. 1) is especially well known for the unusual and often inexplicable variability among F. rufa group species, of which F. rufa, F. polyctena, F. aquilonia and F. lugubris can be found there. Evidently, the remarkable morphological spectrum seen here suggests mixed colonies or hybridisation within the local wood ant species (see e.g. Czechowski 1996).

Species replacement in wood ant colonies (e.g. F. lugubris → F. polyctena, F. lugubris → F. rufa, F. lugubris → F. aquilonia; Czechowski 1996), and temporary existence of mixed colonies have already been documented in that region. Their existence has been explained by adoption of heterospecific queens by orphaned workers (Czechowski 1993, 1996, Pisarski and Czechowski 1994). Evidently, colonies most susceptible to be orphaned, and thus most susceptible to take-over by heterospecific queens, are monodomous and monogynous colonies, isolated from other conspecific nests. Colonies living under inappropriate habitat conditions that do not allow them to produce their own sexual brood may also replace the lost queen(s) with alien ones (see e.g. Czechowski and Vepsäläinen 2009). Such replacement is relatively fast; it comes to an end with the death of the orphaned workers which are offspring of the lost queen(s), i.e. within about three years. During this period a colony is mixed (bi-species).

Artificially created colonies, which may originally be queenless, are likely to be ‘high risk’ colonies, to be taken over by heterospecific queens. This assumption was supported by long-term field experiments within the Tvärminne archipelago, where wood ants of different species were artificially settled on islands where they were absent or scarce (for methodology, see Czechowski 1990). In the years 1987–1997, about a dozen experimental colonies were planted on islands, some of them providing extremely severe habitat conditions for wood ants. Of these, six survived until 2008, to the last control of their species-identity. Five of them are the subject of the present report; the origin of the sixth colony is uncertain.

Three of the colonies (#2, #3, #5 in Table 1) came from the Långholmen peninsula (Fig. 1), almost completely occupied by a polydomous system (several tens of big nests) of morphologically strange wood ants. Originally, in the 1970s and 1980s, they were regarded as atypical (less hairy) F. aquilonia (K. Vepsäläinen and B. Pisarski, unpubl.). Also Pamilo (1993) determined them, not without a doubt, as F. aquilonia. Only recent genetic (Saapunki et al. 2008, Kulmunen et al. 2010) and morphological (Seifert 2010) studies revealed the hybrid (F. aquilonia × F. polyctena) nature of that colony. The three artificial colonies, originally F. aquilonia × F. polyctena hybrids, were each settled on a separate island: Vikaskär, Kvarnskärsgrunden (one of the small islets blackened in Fig. 1) and Kvarnskär (Fig. 1). Gradually they transformed into pure (and typical) F. polyctena. Colony #2, established in 1987, was pure or almost pure F. polyctena already in 1992: in the nest sample (n = 24), maximally two specimens might be F. aquilonia × F. polyctena hybrids; the rest (92%) were unquestionably F. polyctena. Starting in 1995 (n = 22), colony #2 was produced per cent F. polyctena. Colony #3, established in 1987, appeared mixed in 1992 (F. polyctena 69%, hybrid-like individuals 31%, n = 26). The mixed phase lasted till 2002 – in 1993 F. polyctena 40%, hybrid-like individuals 60%, n = 20; in 1995 F. polyctena 73%, hybrid-like individuals 27%, n = 15. Afterwards no hybrid-like workers were seen in the colony. For a case study of colony #3 (identified as F. polyctena) in an ecological context, see Czechowski and Vepsäläinen (2009). The last hybrid colony, #5 taken from Långholmen in 1994, appeared typical F. polyctena in 2002 and kept this species identity until 2008 when last checked.

The maternal colony of the experimental colony #1 was located on the mainland, close to the Tvärminne Zoological Station (Fig. 1). This monocalic colony, which died out in the 1990s, a bone of contention amongst wood ant researchers visiting the station. Then, in the early 1980s, it was identified by B. Pisarski (pers. comm.) – on the basis of both workers and gynes – as F. aquilonia. Moreover, the workers of a nest sample collected in 1987 (the year of artificial colonisation of #1) were quite unlike the hybrids on Långholmen, by
Table 1. Changes of species identity of five wood ant colonies artificially established on islands of the Tvärminne archipelago – see Fig.1 (Year – year of artificial colonisation; Mound size measured in 2008).

<table>
<thead>
<tr>
<th>№</th>
<th>Year</th>
<th>Site of origin</th>
<th>Destination</th>
<th>Species identity</th>
<th>Mound size Ø/h; cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>#1</td>
<td>1987</td>
<td>mainland</td>
<td>Vikaskär</td>
<td><em>F. aquilonia</em>-like</td>
<td>100/35</td>
</tr>
<tr>
<td>#2</td>
<td>1987</td>
<td>Långholmen</td>
<td>Vikaskär</td>
<td><em>F. aquilonia x polyc-ena</em></td>
<td>80/35</td>
</tr>
<tr>
<td>#3</td>
<td>1987</td>
<td>Långholmen</td>
<td>Kvarnskärsgrunden</td>
<td><em>F. aquilonia x polyc-ena</em></td>
<td>110/60</td>
</tr>
<tr>
<td>#4</td>
<td>1987</td>
<td>Halsholmen</td>
<td>Porsgrundet</td>
<td><em>F. polyc-ena</em></td>
<td>80/20</td>
</tr>
<tr>
<td>#5</td>
<td>1994</td>
<td>Långholmen</td>
<td>Kvarnskär</td>
<td><em>F. aquilonia x polyc-ena</em></td>
<td>90/35</td>
</tr>
</tbody>
</table>

being much more hairy, and certainly they were not *F. polyc-ena*. The nest sample taken in 1995 from colony #1, *i.e.* after eight years after its colonisation on Vikaskär (Fig. 1) (and all further samples from there), revealed that the colony was pure and highly typical *F. polyc-ena*. For the history of colony #1, including its temporary regression – probably owing to having lost its queen(s) – see Czechowski (1990) and Czechowski and Vepsäläinen (1999) (in these papers, the colony is identified as *F. aquilonia*).

The last experimental colony, #4, originated from a *F. polyc-ena* colony on the island of Halsholmen and was settled on a nearby island, Porsgrundet (Fig. 1). It maintained its species identity through the whole study period 1987–2008.

Gynes of wood ants are rather poor fliers (*e.g.* Pamilo *et al.* 1978, Rosengren and Pamilo 1983), but with wind they may cover distances of a few kilometres from the nest (Mäbelis 1994). During extensive study of ant assemblages within the Tvärminne region (Pisarski *et al.* 1982, Vepsäläinen and Pisarski 1982, Ranta *et al.* 1983, Pisarski and Vepsäläinen 1989), young fertilised woodant gynes were seen during their nuptial periods even on remote islands of the archipelago, where wood ants were absent (K. Vepsäläinen and B. Pisarski, unpublished). Although there is, as far as we know, no documented information on flight abilities of particular wood ant species, gynes of monogynous and monodomous species (*e.g.* *F. ruga*) are believed to be better dispersers than those of polygynous and polydomous forms (*including F. polyc-ena*) (Seifert 2007, 2010). Without doubt, however, *F. polyc-ena* gynes do at least some times disperse by flight. For example, in the Tvärminne archipelago, one winged gyne of *F. polyc-ena* was documented on a woodless skerry (within the Spikarna island group), over two kilometres from the closest wood ant colony (Lindholm 1983).

The most probable source of *F. polyc-ena* gynes for the artificially planted wood ant colonies that underwent transformation to *F. polyc-ena* was Joskär – a 10 ha island, highly elevated from the sea, and densely populated by morphologically standard *F. polyc-ena*. The three islands under discussion – Vikaskär, Kvarnskärsgrunden and Kvarnskär – are only about 250 m, 250 m and 390 m away from potential source colonies on Joskär, respectively (Fig. 1). In the 1980s, only two colonies of *F. polyc-ena* lived on Joskär – much earlier they had been one bicalic colony of mother and daughter nest (K. Vepsäläinen, unpublished). Then, during the 1990s and later the colonies rapidly expanded their territories by establishing numerous daughter nests, and – together with additional new *F. polyc-ena* colonies – monopolised most of the island area, locally driving out the most competitive species, *F. lugubris, F. aquilonia* and *F. truncorum* F., and, in lesser extent, also *F. exsecta* Nyl. (K. Vepsäläinen and W. Czechowski, unpublished). One of the local colonies of *F. lugubris* was taken over by
Replacement of species in wood ant colonies

F. polyctena (see Czechowski 1996), after going through a period of mixed F. lugubris and F. polyctena workforce (K. Vepsäläinen, unpublished).

We conclude that heterospecific colony takeover in wood ants – and probably also conspecific, though difficult to document – ought to be considered as temporary social parasitism, parallel to the better known exploitation of Serviformica workforce during colony foundation. The phenomenon seems to be conditioned by supply of and demand for young queens in areas with typically small-scaled mosaics of different habitats, populated by several related species.

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