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The largest polydomous system of *Formica* ants (Hymenoptera: Formicidae) in Europe discovered thus far in Romania

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Abstract. Polydomy is a rather general trait in ants. In Europe, mainly territorial mound building *Formica* species apply this strategy in the native fauna. Here we present the largest European polydomous system for *Formica exsecta* Nyl. which consists of 3,347 nests dispersed over ca. 22 ha in Transylvania, Romania. The whole population includes six additional smaller polydomous systems and comprises a total of 3,899 nests. Nest density shows considerable variations within the largest system. Ant nests are larger at the high nest density site. In addition, ant nest connectivity through shared aphid colony use with other nests can also reach extreme low (0 connections) and high (10 connections) values. These variations could reflect differences in the level of integration of single nests into a polydomous system.

Keywords: ants, aphids, connectivity, foraging, *Formica exsecta*, polydomy.

Introduction

Polydomous systems (colonies made up of multiple related nests) in ants develop in two main scenarios (Debout et al. 2007): (1) the exploitation of short-term ecological benefits in new, disturbed or empty habitats, in addition to ensuring successful nest founding – characteristic primarily of invasive, introduced polygynous species (see Holway et al. 2002 for a review); and (2) selection of cooperative nest networks due to their strong constraints on dispersal and progressive habitat saturation, exploitation of stable habitats, and better monopolization of food sources – characteristic primarily of native species (see e.g. Chapuisat & Keller 1999). Polydomy implies the existence of specific features in ant species (Seifert 2010): polygyny, reduction of male and gyne size, intranidal mating and/or shorter range gyne nuptial flights, and development of a nestmate recognition system, which diminishes nestmate discrimination and inter-colonial aggression. Polydomous systems involve also food-source sharing and frequent exchange of individuals and brood among nests (Pisarski 1982, Debout et al. 2007, Kümmerli & Keller 2007, Erős et al. 2009, Csata et al. 2012), consequently the level of aggression between non-nestmates in these systems is usually very low or aggression is completely absent (Chapuisat et al. 2004, Holzer et al. 2006, Martin et al. 2009, Kiss & Kóbori 2011).

Although worldwide many ant species are known to form large polydomous systems comprised of many interrelated nests (e.g. *Formica yessensis* and *Lasius sakagamii*), in Europe only a handful of ant species develop polydomous systems (Seifert 2010). Such 'supercolonies' are well-known in introduced ants as the invasive garden ant *Lasius neglectus* Van Loon, Boomsma et Andrásfalvy, 1990 (Espadaler et al. 2007) and the Argentine ant *Linepithema humile* (Mayr, 1868) (Giraud et al. 2002). In the native European ant fauna mainly species of two *Formica* subgenera are known to develop polydomous systems comprised of several tens or hundreds of interrelated nests: *Formica* s. str. (primarily *F. lugubris* Zetterstedt, 1838 and *F. paralugubris* Seifert, 1996 – e.g. Chapuisat et al. 2004, Torossian 1977) and *Coptoformica* species (e.g. Kümmerli & Keller 2007, Pisarski 1982). Nevertheless, these systems are nowhere near as large as those of invasive species (e.g. Giraud et al. 2002); they rarely exceed a few hectares, and only in exceptional cases consist of more than one-thousand nests.

Recently a large polydomous system of *Formica* (*Coptoformica*) *exsecta* Nylander, 1846 was discovered in Romania. Nest census revealed an exceptionally large nest number, making this system by far the largest known in Europe. Here we give a brief characterization of this supercolony, while also offering data on differences in ant nest density and nest parameters within the system. We also hypothesize that differences in ant nest density within a supercolony could result in differences regarding the number of connections an ant nest has with other nests e.g. through shared aphid colony tending (Erős et al. 2009, Csata et al. 2012).

Materials and methods

Formica (*Coptoformica*) *exsecta* Nylander, 1846 is a relatively common mound-building, territorial, Pan-Palaearctic ant species, inhabiting areas of mixed and deciduous forests mostly at forest edges, forest clearings or mountain pastures (Seifert 2000). Large polydomous colonies are known from the Alps, Central Europe and European Russia; these can comprise several hundred nests. Nests within such a system usually do not establish intra-territorial boundaries, there is permanent overlap of feeding grounds among neighboring nests, and food sources are permanently shared (Werner et al. 1979, Pisarski 1982, Erős et al. 2009, Csata et al. 2012).

The large polydomous system of *Formica exsecta* reported here is located in the southern part of the Giurgeului depression, in the Eastern Carpathians (Fig. 1, 46°36′N, 25°36′E, 780 m a.s.l.) in the vicinity of Voşlobeni village, Harghita County, Transylvania, Romania. Additionally, six smaller polydomous systems are also present in the vicinity of the large one (Fig. 1). All *F. exsecta* polydomous systems are located in wet meadows with *Molinia caerulea*, *Deschampsia caespitosa*, *Festuca pratensis*, *Briza media*, *Nardus stricta*, *Succisa pratensis*, *Filipendula ulmaria*, *Stachys officinalis*, and *Cirsium palustre* as the most abundant or characteristic plant species. Their area is overgrown with scattered small trees and saplings of *Betula pubescens*, *Picea abies*, *Frangula alnus* and *Salix* spp (Fig. 2). The meadows are fairly intensely grazed by cows for most of the year. A census of the largest polydomous system was carried out in September 2010. In 2009, nest census was conducted for five smaller systems; the sixth small polydomous system was discovered and a similar census was carried out in 2011. Only permanent nests were counted, including newly established filial nests, outstations used for guarding aphid sources (see Pisarski 1982) were not included. In order to assess variations in the connectivity of nests within the largest polydomous system, two sites were selected that clearly differed in the density of ant nests: a high density (HD) site with 40 nests on 807 m^2 (0.52 nests/10 m^2) and a low density (LD) site with 12 nests on 2113 m^2 (0.09 nests/10 m^2). The same sites were previously studied concerning different aspects of food source sharing among ant nests (Erős et al. 2009, Csata et al. 2012). The same large polydomous system was subject to other studies on several aspects of polydomy, such as relatedness (Goropashnaya et al. 2007) and intraspecific aggression vs. differences in cuticular hydrocarbon profiles among nests of the same system (Martin et al. 2009). Other smaller polydomous systems in the same population were studied with regards to the effect of distance and season on intraspecific aggression (Kiss & Kóbori 2011).

All plants with aphids and all *Formica exsecta* nests were recorded at both study sites in July 2009. Measurements of ant nest mounds were taken at both sites; the longest nest diameter ('d_1') and the length of the diameter perpendicular to it ('d_2') were recorded, as was the height of the nest mound (soil basis plus plant cover) ('h'). Based on these data the above-ground volume of an ant nest

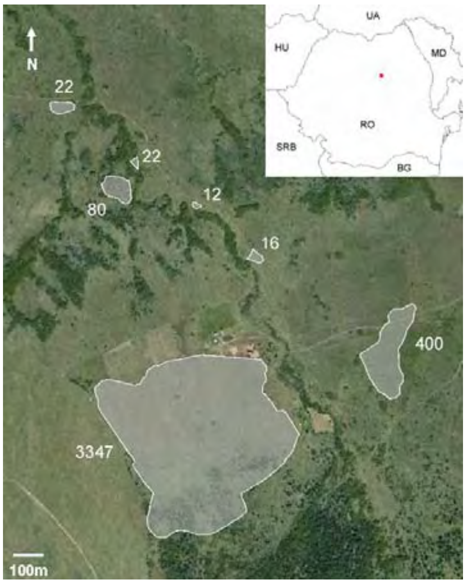

Figure 1. Map of the studied *Formica exsecta* population (46°36′N, 25°36′E, Harghita county) with the polydomous systems (with white outlines) and the number of nests (© Google Earth).

Figure 2. The largest *Formica exsecta* polydomous system (Voşlobeni, Harghita county, Romania) in mid-May 2009. (detail)

Figure 3. Typical *Formica exsecta* nest mound in the largest polydomous system (Voşlobeni, Harghita county, Romania) in July 2011.

was estimated according to Bliss et al. (2006): $V = 1/2 \times \pi \times r_1 \times r_2 \times h$, where '$r_1$' is the largest radius at bottom, that is half of 'd_1', 'r_2' is the radius perpendicular to 'r_1' (half of 'd_2'), and 'h' is the height of the mound above the ground (Fig. 3). The identity of aphid colony tending *F. exsecta* nests was determined on the basis of ant routes established between the ant nest and the visited aphid colony. This allowed us to establish how many ant nests were connected with any focal nest through shared aphid colony use.

Normality of data sets was assessed using the Kolmogorov-Smirnov test when performing parametric analysis. The mean diameter (average of 'd_1' and 'd_2') and volume of the ant nests were compared with Welch-test. All statistical analyses were carried out using the R 2.9.1 statistical package (R Development Core Team 2010).

Results

Altogether 3,347 permanent nests were counted on an area of ca. 22 ha in the largest polydomous system yielding a nest density of 153.25 nests/ha. The second largest system was also remarkably large, containing 400 nests dispersed over an area of ca. 1.93 ha with a nest density of 207.25 nests/ha. Together with the five other smaller polydomous systems (80, 22, 22, 16 and 12 nests, Fig. 1) the total nest number of the *Formica exsecta* population in the area comes to 3,899.

In the case of the largest polydomous system, in addition to within system differences in ant nest densities (0.52 nests/10 m^2 at the HD vs. 0.09 nests/10 m^2 at the LD site), the density of the aphid colonies also showed considerable differences between the two study sites (HD vs. LD): 485 aphid colonies were counted at the HD site (6.01 colonies/10 m^2) vs. 110 at the LD site (0.52 colony/10 m^2). Ant nests were significantly larger at the HD site based on their average diameter: $mean_{HD}$ 51.10 cm (1SD: 24, max 117.5 cm), $mean_{LD}$ 37.08 cm (1SD: 9.32, max 54.5 cm), Welch-test $t = 3.3$, $n_{HD} = 42$, $n_{LD} = 20$, $p < 0.01$. Parallel to this, the mounds also had a larger volume at the HD site: $mean_{HD}$ 24.96 dm^3 (1SD: 20.3, max 76.87 dm^3), $mean_{LD}$ 11.32 dm^3 (1SD: 7, max 26.69 dm^3), Welch-test $t = 3.89$, $n_{HD} = 42$, $n_{LD} = 20$, $p < 0.001$. Ant nests were known to exploit more aphid colonies at the HD site than at the LD site, and aphid colonies were also tended simultaneously by more ant nests at the HD site (see Erős et al. 2009 for a detailed analysis). This ultimately resulted in higher connectivity of ant nests through shared aphid colony tending at the HD site (Fig. 4). The maximum number of connections was 10 at the HD site versus three at the LD site. High connectivity of ant nests at the HD site suggests a higher probability of stable worker exchange at this site due to shared aphid colony tending.

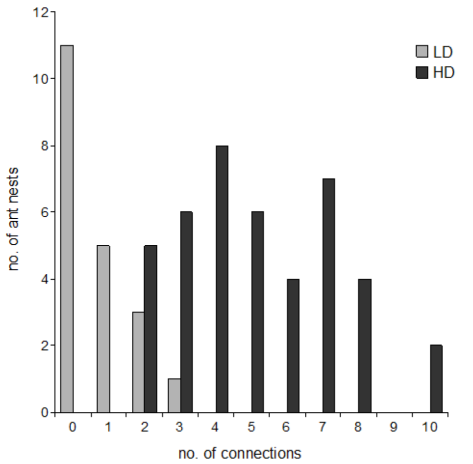

Figure 4. Distribution of the number of connections a *Formica exsecta* ant nest establishes with other *F. exsecta* nests through shared aphid colony tending at the two study sites.

Discussion

The *Formica exsecta* supercolony presented here is by far the largest known European polydomous system not just for this species, but most probably for all mound building territorial *Formica* species (Table 1). The entire population is remarkably large; it could well be one of the largest *F. exsecta* populations in Europe. On the other hand, the density of the nests was not exceptionally high, although local nest density could reach extreme values, as in the case of the HD site (520.45 nests/ha if extrapolating). The size of the nest mounds can also be considered within the range of normality. The diameter of *F. exsecta* nests can reach as much as 200-300 cm according to various literature data (see Seifert 2000) but in our case the maximum value of 117.5 cm was well below these extremes. In fact, the recorded nest parameters fit the available data on *F. exsecta* polydomous systems well: e.g. the mean nest diameter of the population studied by Bliss et al. (2006) was 41.7 cm (max 77.5 cm), while in the case of the mound volume the average was 23.9 dm^3 (max 82.5 dm^3), both of which are comparable to our data. In the exhaustive *F. exsecta* study of Pisarski (1982) the maximum nest mound diameter was also ca. 100

Table 1. Selective list of published data on largest European polydomous systems (in decreasing order of nest number within species) in mound building territorial *Formica* species with special reference to *F. exsecta.*

Species	Area (ha)	No. of nests	Density (nests/ha)	Country	Reference
F. bruni Kutter, 1967	0.56	250	442.95	CH	Seifert 2000
F. exsecta Nylander, 1846	**21.84**	**3347**	**153.25**	**RO**	*current article*
F. exsecta	2	408	204	D	Dewes 1993
F. exsecta	**1.93**	**400**	**207.25**	**RO**	*current article*
F. exsecta	3	400	133.33	CH	Kümmerli & Keller 2007
F. exsecta	n.a.	300	n.a.	CH	Brown & Keller 2000
F. exsecta	0.4	254	635	CZ	Bezděčka & Bezděčková 2008
F. exsecta	14	220	15.71	CH	Cherix et al. 1980
F. exsecta	1.39	220	305.56	D	Katzerke et al. 2006
F. exsecta	1.42	207	293.93	D	Katzerke et al. 2006
F. exsecta	>1000 m²	>100	n.a.	PL	Czechowski 1976
F. exsecta	0.48	49	23.76	D	Katzerke et al. 2006
F. exsecta	0.72	40	28.99	D	Katzerke et al. 2006
F. exsecta	0.0168	11	654.76	D	Bliss et al. 2006
F. foreli Bondroit, 1918	6.24	2550	408.65	D	Seifert 2007
F. foreli	0.54	605	1120.37	CZ	Bezděčková & Bezděčka 2009
F. foreli	0.25	100	400	D	Seifert 2000
F. forsslundi Lohmander, 1949	42	400	9.52	D	Seifert 2000
F. pressilabris Nylander, 1846	>1000 m²	>100	n.a.	PL	Czechowski 1975
F. pressilabris	0.13	74	592	PL	Czechowski 1975
F. pressilabris	1.5	30	20	PL	Bönsel 2007
F. paralugubris Seifert, 1996*	70	1200	17.14	CH	Cherix & Bourne 1980
F. paralugubris	n.a.	100	n.a.	CH	Chapuisat et al. 2004
F. truncorum Fabricius, 1804	6	130	21.67	FIN	Elias et al. 2005

*published as *F. lugubris*

cm, while in the vast majority of mounds it was below 40 cm.

The stable integration of an ant nest into a polydomous system can be achieved in the simplest way through a high rate of worker exchange among nests (Kümmerli & Keller 2007), which could reduce the variability of nestmate recognition cues and/or raise the threshold for discrimination (Martin et al. 2009). The common use of aphid colonies can serve this purpose as they act as stable meeting points for foragers from different ant nests based on our study (see Erős et al. 2009; Csata et al. 2012). Kümmerli and Keller (2007) have shown that even in a *Formica exsecta* polydomous system with an ant nest density similar to our LD site there is a high exchange rate of individuals among nests: the ratio of recaptured marked individuals in a nest other than their original one was 85.1% ± 7.7 after one month. Based on this we can assume that the exchange rate of individuals, and thus the degree of integration of a single nest into the polydomous system, is extremely high at the HD site, as also indicated by the high number of connections.

More or less permanent gene flow among nests through the adoption of young gynes originating from different parts of a polydomous system can also play an important role in integrating nests into the system. However, there could be considerable temporal and spatial variations in gyne production within a *Formica exsecta* polydomous system (Liautard et al. 2003), which could be biased even on population level. Due to limited dispersal of workers in *F. exsecta* (not more than 10 meters, see Sorvari 2009), the different polydomous systems in the population under study could only be ‘connected’ through mutual gyne adoptions at this moment, although the population seemed very compact at first, and some parts are only separated by a few hundred meters (see Fig. 1.).

The *Formica exsecta* population presented here seems extremely healthy and stable due to high ant nest density and ant nest number. Nevertheless, the recent changes in Romanian agriculture, which have caused a drastic decrease in cow numbers and consequently abandonment of traditional extensive grazing and haymaking techniques, may endanger the survival of this unique population in the long run, as proven in other related species (Bönsel 2007). Thus, only the implementation of an appropriate management plan could help the survival of this unique social system.

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