

**NEST TURNOVER IN A COLONY
OF *FORMICA PRESSILABRIS* NYLANDER, 1846
AS RELATED TO HABITAT QUALITY
(HYMENOPTERA: FORMICIDAE)**

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In a *F. pressilabris* colony in a primary habitat in NE Poland, an annual nest turn over-rate of 53% was found. Such dynamics are known for several ant spp. In this study, several known causes for colony dynamics were checked for *F. pressilabris*. Competition and nest microclimate change could be excluded as causes. Interspecific conflicts such as predation or competition were improbable, since nests in close vicinity to those of other *Formica* spp. were not abandoned, and *F. pressilabris* is foraging in young, aphid-infested *Populus* sprouts, whereas other *Formica* spp. forage in elder trees. There were no significant differences in development of vegetation density over the nests between persistent, abandoned and newly founded nests, this excluding change of nest microclimate. As a cause for colony dynamics, accidental and tempo-spatially unpredictable changes of food availability are proposed. 10-30 cm high sprouts of *Populus tremula*, potentially aphid-infested, grew interspersed between the colonies. Some of these potential food sources were browsed by game or cattle in irregular intervals and without spatial specificity. This stochasticity could be balanced by the satellite nest strategy. These small nests are always founded in the immediate vicinity of potential food sources. It is possible, if the food source is persistent, the satellite nest becomes a stem nest, if not, it is abandoned and new nests are founded elsewhere.

INTRODUCTION

The functional importance of ants in various ecosystems is well recognized since some time (e.g. PETAL, 1977, 1980; KJELLSSON, 1985;

HÖLLDOBLER & WILSON, 1990; KARHU & NEUVONEN, 1998). Therefore, ants are not only recognized bio-indicators, but also target species in numerous conservation measures (STEINER & SCHLICK-STEINER, 2002). Of all Middle European ant species, all (*Copto*)*formica* species in Germany and its neighbouring countries belong to the most endangered, many are threatened by extinction. Changes of land use or atmospheric eutrophication of the landscape (see BAKKER & HEERDT, 2005) are given as causes (e.g. SEIFERT, 1998; LAUTERER, 2003). This made and makes intensification of protective measures necessary (AGOSTI, 1989; GLASER, 1999; CZECHOWSKI et al., 2002; WESENIGK-STURM, 2002a; BÖNSEL & BUSCH, 2003). However, effective protection is difficult to achieve for these species, since knowledge about their autecology is sketchy. This can partly be attributed to the problem of taxonomic identification of colonies, which is possible only recently with certainty (SEIFERT, 2000). It is possible that some of the colonies referred so far to *F. pressilabris* will be identified as *F. foreli*, and vice versa. According to the present state of knowledge, habitat requirements of both species are very similar, even co-occurrence is possible. Both species are known to colonize oligotrophic habitats, of which *F. pressilabris* prefers the xerothermic ones (cf. KUTTER, 1956, 1957, 1966; SEIFERT, 2000). To preserve these highly endangered species in their respective localities, ecological habitat requirements as well as spatial dynamics of the colonies need to be known sufficiently. For the planning of maintenance measures such as mowing, grazing, burning or tilt cutting, it needs to be known whether the respective (*Copto*)*formica* species inhabits the same nest for longer periods, as do the large *Formica* species of the *Formica rufa-Formica polycтена* group (GÖßWALD, 1990), or whether there is a spatio-temporal variability of nest sites and which are the causes for that. Spatial dynamics is proven for several *Coptoformica* species, or at least tendencies are suggested, but the causes for colony movements are largely unknown (CZECHOWSKI, 1990; BÖNSEL & BUSCH, 2003; BLISS & PIEL, 2004; SÖRENSEN, 2004). Up to now, nest disturbance, nest microclimate change, competition or spatio-temporal dynamics of food availability are given as direct or indirect causes for colony dynamics in several species (e.g. WHEELER, 1926; HIGASHI & YAMANCHI, 1979; HERBERS, 1985; HÖLLDOBLER & WILSON, 1990). THERAULAZ et al. (2002) suggest that ants generally attempt to form spatial patterns, though in a highly manipulative experiment.

Here, a detailed ecological analysis of a *F. pressilabris* colony is presented. First, potential differences to the habitat requirements between *F. pressilabris* and *F. foreli* and the possible existence-threatening trends of

F. pressilabris should be discussed. Second, causes for colony movements, as listed above, and the pattern formation, as suggested by THERAULAZ et al. (2002) were checked.

MATERIAL AND METHODS

STUDY AREA AND FIELD PROCEDURES – The study area is located in the Biebrza valley in northeastern Poland (53°19'N; 22°34'E, 109 m NN), in one of the last intact percolation mires of Europe (SUCCOW & JESCHKE, 1986) with a total area of 80.000 ha. Mean annual precipitation in the study area is 540 mm, mean annual temperature is 7.6°C (ZUREK, 1991). Here a colony of *F. pressilabris* inhabits a mineral outcrop covered with sand, which is isolated by the surrounding bog. It will be a polygynous colony, even if specific examinations of this problematic nature were not carried out. A permit for ditching in nests and looking for one or more queens was not given.

The study area covers 1.5 ha, 25% shaded by *Quercus petraea* and *Tilia cordata*. 5% of the area are open sandy patches. 70% are covered by an herb layer which can be subdivided in various sub-layers. Soil type and plant community can be classified as dry grassland (see BÖNSEL & RUNZE, 2000). Anthropogenic disturbances are low in intensity and frequency, they consist in occasional grazing of 12-21 heads per ha of cattle. This utilization is being maintained for centuries now (OKRUSZKO, 1990) and is comparable to that of game (WILMANN, 1997).

The study area was marked with a grid of 20×20 m cells. All *Formica* nests of the respective year (2000 and 2001) were recorded in August, marked with red pegs and recorded by tachymetry; existence of last year's nests was checked by tachymetry. Additionally to the nest locations, the macro-relief of the study area was surveyed, allowing for determination of nest exposition. Nest height and diameter were recorded. Vegetation density over any nests, including the ones abandoned in 2001, was calculated as the product of degree of coverage (%) and mean plant height of herb- and shrub layer (cm) (see SEIFERT, 1986). For example, 55% coverage and a mean plant height of 26 cm resulted in a vegetation density of 1430. It was calculated for an area exceeding the nest periphery by 10 cm.

PROCESSING OF DATA – The survey data of the study area and the nest locations, their height and diameter in 2000 and 2001 were transferred to a geographical information system (GIS). The vegetation was digitized of field map on which plant communities were mapped according to DIERSCHKE, (1994). This allows exact determination of exposition and position of nests in specific plant communities. Nests were assigned to yearly GIS-layers and superimposed to obtain an operationalized spatio-temporal model of the colony (BILL, 1996), which allowed for exact determination of persistence, foundation or abandonment of nests. Additionally, nests were classified by diameter to elucidate the spatial distribution of stem- and initial nests (Fig. 1). Nest height, diameter and vegetation density were compared with the t-test between the identical nests in 2000 vs. 2001 and persistent nests vs. abandoned nests or persistent nests vs. new founded nests.

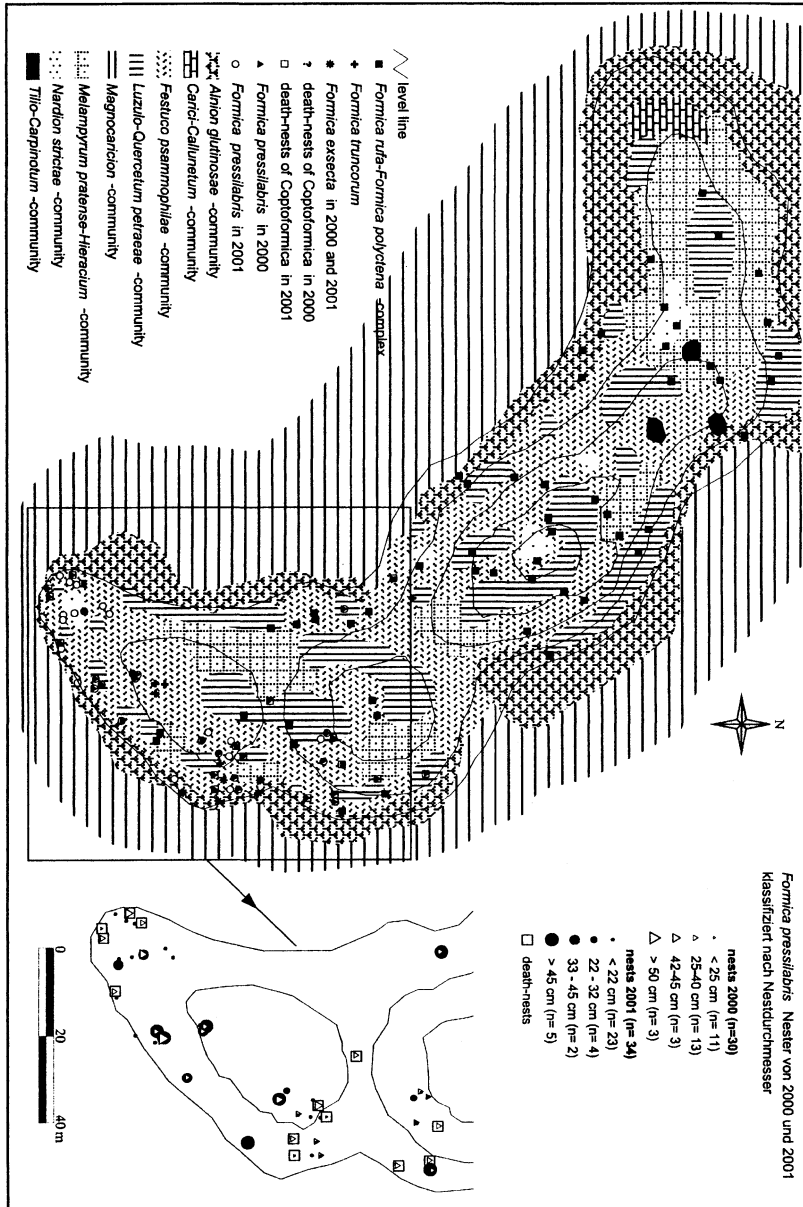


Fig. 1. Locality features and structure of the *Formica pressilabris* colony.

RESULTS

HABITAT CHARACTERISTICS AND NEST LOCATIONS

In both years, *F. pressilabris* nests were restricted to the southern part of the mineral outcrop. The south-exposed nests of *F. pressilabris* were situated in *Festuco psammophilae*- and *Melampyrum pratense-Hieracium* communities bordering on *Luzulo-Quercetum petraeae* communities (Fig. 1). Those plant communities showed 100% coverage, structural diversity was high due to species richness. Young shoots of *Populus tremula*, 10-30 cm high, grew in these plant communities, on some of them aphids and foraging *F. pressilabris* could be seen. This young shoots of *Populus tremula* were browsed by elks or cattle's. Thereby, dense vegetation such as *Calamagrostis epigeios* was reduced repeatedly, at least in the southern part of the study area and immediately over the nests, whereas in the northern part *C. epigejos* increasingly became established in spite of grazing. The effect of browsing was in irregular intervals and without spatial specificity. Before and afterwards to investigation elks and cattle's had grazed on this mineral outcrop. Therefore, all potentially aphid-infested *Populus tremula* sprouts per year was impossible assigned to GIS-Layers.

A colony of the *Formica rufa-Formica polyctena* complex predominantly colonized the northern part, few nests radiated into the southern part where they were situated below oak trees (Fig. 1). Nests of *F. truncorum* and *F. exsecta* were located immediately between nest clusters of *F. pressilabris* (Fig. 1). These *Formica* species did not change their nest locations in both years of the study, none were abandoned nor founded. Competition by these *Formica* species can be excluded, since especially the *F. pressilabris* nests located in immediate vicinity to nests of *F. truncorum*, *F. exsecta* or *F. polyctena* persisted in both years or even expanded (Fig. 1). This *Formica* species did forage on mature and ancient trees.

DEVELOPMENT OF THE VEGETATION OVER THE NESTS AND SPATIAL CHANGES OF NEST LOCATIONS

There was no correlation between vegetation density and nest diameter ($r = 0.067$) or vegetation density and nest height ($r = 0.222$). Vegetation density over the persistent nests in 2000 and 2001 did not change significantly ($p = 0.65$). Maximum vegetation density was 3800 in 2001, though in general was a decreasing trend over this nests (see Fig. 2). Mean vegetation density in 2000 was higher over the nests that were abandoned

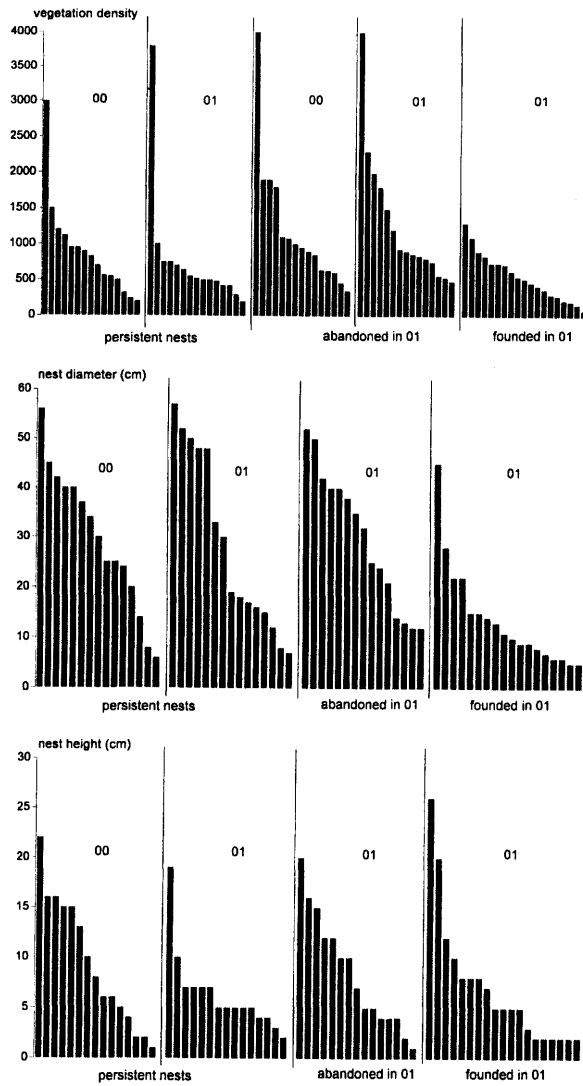


Fig. 2. Vegetation density, nest diameter and nest height of all persistent, abandoned and newly founded *Formica pressilabris* nests in 2000 and 2001.

in 2001 (see Fig. 2) and than over those persistent to 2001, though not significantly ($p = 0.15$). The reason for the abandonment of two nests is obvious, one was destroyed by wild boars, and the other was heavily shaded by a high grown birch. In all other nests, no direct influence for abandonment or foundation of nests could be found. New nests were generally founded at low vegetation densities (Fig. 2), though vegetation densities did not differ significantly between the persistent nests and newly founded ($p = 0.14$). Also vegetation density over the nests abandoned in 2001 was within the range of variability of the persistent nests in 93 %, and in 73% of the newly founded nests (cf. Fig. 2). Therefore, vegetation density can be excluded as a cause for abandonment or foundation of nests. The degree of browsing effects also did not give unequivocal hints towards the reason for abandonment, persistence or foundation of nests. These characteristics can change over the year, and all conditions could be found over all nests. There were no significant differences of the persistent nests diameter and height between the years (diameter $p = 0.86$; height $p = 0.13$), nor between abandoned and persistent nests between years ($p = 0.96$; $p = 0.73$). Only new nests had significantly smaller diameters than the persistent ones ($p = 0.004^{***}$) nor between those heights ($p = 0.64$).

In 2000, 30 *F. pressilabris* nests were recorded, 50% of which did persist to 2001, 50% were abandoned and 19 new nests had been founded in 2001 (see Fig. 1), corresponding to a turnover rate of 53%. Newly founded nests were always in the vicinity of persistent stem nests, and new nests often were founded in the immediate vicinity of abandoned nests, though there was no strict spatial exactness (Fig. 1, see the clusters). Persistent nests, abandonment or foundation of new nests was not correlated with any plant community, but in *Festuco psammophilae*-community, *Luzulo-Quercetum petraeae*-community, *Melampyrum pratense-Hieracium*-community or *Nardion strictae*-community with young shoots of *Populus tremula*. The arrangement of persistent, new and abandoned nests was neither a linear path nor it was following strictly any structure, such as the margin of a plant community (Fig. 1). Generally, the nests were mostly located in the southern part of the study area. A connection of the nest was not following any geometry, which makes spatial statistics inapplicable.

DISCUSSION

HABITAT AND EXISTENCE-THREATENING TRENDS

According to the law of similar habitat preference (see WALTER & BRECKLE, 1991), the habitat described here does not differ much from other habitats of *F. pressilabris* and *F. foreli*. Both species live in elder succession states of mesotrophic plant communities, interspersed by adolescent trees, the nests being south-exposed and little shaded (e.g. STITZ, 1939; CZECHOWSKI, 1975; COLLINGWOOD, 1979; WESENIGK-STURM, 2002a; 2002b; BÖNSEL & BUSCH, 2003). The statement of AGOSTI, (1989) is supported by the circumstance that *Coptoformica* species hardly differ in their habitat requirements since they all colonize long-lived mesotrophic grassland communities associated with forests (see KUTTER, 1956, 1957; PISARSKI, 1962; LAUTERER, 1968; HILZEN-SAUER, 1980; DEWES, 1993; BUSCHINGER & JOCHUM, 1999; GLASER & SEIFERT, 1999; BLISS et al., 2000; CZECHOWSKI et al., 2002). These grassland communities were promoted by anthropogenic utilization after the last glaciation until about 1950 (BRESINSKY, 1993; LANG, 1994; LITT, 1994; BEHRE, 2000); now then they are endangered by change of human management. These only are the existence-threatening trends of *F. pressilabris*. There seems to exist no endangering of these ant species by colony isolation, since primary and secondary habitats have always been isolated (see AGOSTI, 1989). How genomic impoverishment by isolation is avoided is not as yet understood (AGOSTI, 1989), but several sex- and behaviour-specific phenomena give first hints (AGOSTI & HAUSCHTECK-JUNGEN, 1987; AGOSTI, 1989; BROWN & KELLER, 2000). Such adaptations to isolation should, therefore, be subject of further studies on *Coptoformica* species, since they have also been found in other insects colonizing isolated habitats (e.g. BÖNSEL, 2004).

CAUSES FOR NEST TURNOVER

Competition by other *Coptoformica* or *Formica* species could be excluded as an endangering factor and cause for colony movements in this primary habitat. It is because these species forage on mature and ancient trees and *F. pressilabris* on young shoots of *Populus tremula*. Differences in behaviour might also explain coexistence of several *Coptoformica* species in similar habitats (BROWN & WILSON, 1956; AGOSTI, 1989). Such coexistence of several *Formica* species and even of closely related *Coptoformica* species has already been described by KUTTER (1957), who

also pointed to possible behavioural differences. Our evidence excludes nest disturbance and nest microclimate change as causes for colony dynamics. Significant differences in vegetation density over newly founded, persistent and abandoned nests have not been found, nor correlations between vegetation density and nest quality. On the other hand, the hypothesis of SEIFERT (2000) that nest turnover is specifically adapted to accidental and tempo-spatially unpredictable changes of food availability is supported by our observations. Permanent foundation of new nests in the vicinity of a stem nests is known for several ant species, though there is a broad spectrum of triggering factors and purposes (WILSON, 1958, 1959; NIELSEN, 1972; HIGASHI & YAMANCHI, 1979; VESPSÄLÄINEN & PISARSKI, 1982). Our habitat was sparsely covered by 10-30 cm high sprouts of *Populus tremula*, potential habitats of aphids. *F. pressilabris* has to concentrate on these young trees, since larger trees are foraged by other *Formica* species and aphids living on herbs produce less honeydew than those living on woody plants (KLOFT & KUNKEL, 1985). The potentially aphid-infested *Populus* sprouts are grazed by game and cattle in irregular intervals and without spatial exactness. Moreover, aphid colonies on young trees are known for their frequent and unpredictable changes of locality for manifold reasons (KLOFT & KUNKEL, 1985). Due to these irregularities, there is always the danger that potential food sources of *F. pressilabris* suddenly disappear, or unbrowsed *Populus* sprouts grow up. Ants can not predict whether food sources will be browsed or not, they try to found as many initial nests (satellite nest) as possible near young trees, i.e. food sources. If the nest location appears favourable, nests expand, offspring are raised and new small (satellite) nests appear, close to the potential new food sources. If food sources in the nest vicinity change in the course of the year or in the next year, nest locations are changed again. Since changes in conditions may take effect with time-lag, this can also happen in larger nests, as suggested by SÖRENSEN (1999). In fact, the organization of our colony remains cryptic. Considering the stochasticities responsible for colony dynamics here, the development of geometric patterns in ant colonies in their natural surroundings is questionable, though this may happen under experimental conditions (e.g. THERAULAZ et al., 2002). The existence of nest turnover in a colony of *F. pressilabris* and its very probable cause has implications for adequate conservation. It deserves wider recognition for further investigations.

ACKNOWLEDGEMENTS

I want to thank T. BUSCH, B. SEIFERT and N. HOBBHAHN for critical reading of the manuscript, and M. RUNZE and D. HÖNIG for their help in the field.

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Received 12 January 2007
 Reviewed and Accepted 29 April 2007