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PLESIOBIOSIS BETWEEN *FORMICA FUSCA* L. AND *FORMICA AQUILONIA* YARR. (HYMENOPTERA, FORMICIDAE)

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Abstract.— An unusual case of plesiobiosis of two competitive ant species, *Formica fusca* L. (non-territorial opportunistic form) and *Formica aquilonia* Yarr. (territorial form), is described. *F. fusca* was nesting on the edge of the latter's mound, after the *F. aquilonia* colony had experimentally been transferred to the site. We discuss the possible significance of our finding to the evolution of social parasitism in ants.

Key words.— Ants, *Formica fusca*, *Formica aquilonia*, competition, plesiobiosis, compound nests, evolution of social parasitism.

INTRODUCTION

Plesiobiosis is the most rudimentary form of social symbiosis in insects, falling within the category of «complex nests» (as distinct from «mixed colonies»). In plesiobiosis, the nests of different species touch. However, alien individuals generally make no contacts, there is no biotic interdependence between them and, potientially, they are hostile to one another. As a rule, they are taxonomically distant forms (at least belonging to different genera) and thus morphologically different (Wheeler 1926, Hölldobler and Wilson 1990); among ants, plesiobiotic species generally occupy lower, subordinate, levels in the interspecific competition hierarchy (cf. Vepsäläinen and Pisarski 1982).

Typically, colonies of two (or more) plesiobiotic ant species may live under the same stone. E.g., a frequent plesiobiont, *Formica fusca* L., may co-nest with *Lasius niger* (L.), *L. flavus* (F.), *Tetramorium* spp. or *Myrmica* spp. (Wuorenrinne 1958 and the authors' unpubl. observations). Here we describe a previously undocumented plesiobiosis between *F. fusca* and *F. aquilonia* Yarr., where one of the species is known of its fierce aggression toward individuals of alien colonies. Although most likely a rare phenomenon, this kind of plesiobiosis has interesting theoretical implications regarding the evolution of social parasitism in ants.

THE SPECIES

Formica (*Serviformica*) *fusca* is a non-aggressive species that defends only its nests against competitors. In accordance with the theory of hierarchic structure of ant communities (Vepsäläinen and Pisarski 1982) it represents the lowest level of hierarchy.

Formica (*Formica*) *aquilonia*, a member of the *F. rufa* L. group, is a species common in Finland. As all wood ant species it is a territorial form that defends its foraging area, and is therefore located at the highest level of hierarchy. Aggressiveness and abundant workforce of *F. rufa* group societies of ants secure them a dominant position in the habitat (Savolainen and Vepsäläinen 1988, Savolainen *et al.* 1989). Their colonies are organizing centres of ant communities, where subordinate species may nest at some distance from the mound of the dominant, the distance being inversely related to the distance between the species within the competition hierarchy (Pisarski and Vepsäläinen 1989).

Workers of *F. fusca* and those of the *F. rufa* group are similar in size and generally utilize the same food sources; thus competition between them is inevitable. Yet they are able to coexist because of different ways of foraging: workers of the *F. rufa* group communicate and cooperate very effectively and expansively, whereas *F. fusca* workers forage individually and opportunisticaly. Foraging workers of *F. fusca* avoid conflicts by evasive behaviour, which increases its possibilities to nest within the foraging area of territorial ants. However, the proximity of a large society of the dominant species has a negative impact on the population of *F. fusca* – the density of its nests decreases, foraging is less successful, and the production of offspring is reduced (Savolainen 1990, 1991).

CHRONOLOGY OF PLESIOBIOSIS

Colonization experiments of wood ants were started on the rocky islands of the Tvärminne archipelago in south-

Fig. 1. Situation of the *F. aquilonia* nest (V-aq-II) artificially established on Vikaskär; state in June 1998 (photo W. Czechowski).

ern Finland (westernmost part of the Gulf of Finland) in 1987. On the 2-hectare island of Vikaskär, mostly overgrown by pine forest, one of the colonies established was that of *F. aquilonia* (V-aq-II in see Czechowski 1990) (Fig. 1).

The moment they were released in a new place, *F. aquilonia* workers started to exterminate the numerous *F. fusca* colonies there. After a few days, the conflicts ceased and ants of both species peaceably, but in a dispersed manner, went up a large pine (ø = 80 cm) to reach aphids in its canopy – the main food source of the nearby colonies of *F. fusca*. The aphids had previously been shared only with *Camponotus ligniperda* (Latr.) that also was attacked by the transferred *F. aquilonia* (Czechowski 1990). A week after it had been established, the size of the fairly shipshape *F. aquilonia* mound was: ø = 110/90 cm, h = 30 cm. In the following season (1988), the colony was nesting 9.5 m from its original place, and the new mound measures were ø = 40 cm, h =35 cm.

Observations were resumed in 1992, when the *F. aquilonia* colony was clearly in regression and seemed to be dying out – probably owing to losing of its queen(s). The few hundred workers still present had abandoned maintenance of the mound that overgrown with plants. The crisis continued until 1994, when the colony slowly began to revive. In 1995, the still poorly inhabited mound measured ø = 80/60 cm, h = 30 cm, and the ants penetrated an area of about 540 m^2, exploiting aphids on nine old pines. In the following years, the abundance of the colony was permanently on the increase and the density and range of workers in the foraging area grew too.

In June 1998, the mound had ø = 80/60 cm, h = 40 cm; most of it was almost normally saturated with ants and contained worker pupae – evidence of the presence of at least one queen. It also turned out that the nest was a complex one; the outermost part of the mound was occupied by a colony of *F. fusca* (Fig. 2). The weaker of the two *F. aquilonia* trails leading out run over the nest of *F. fusca*. When that part of the mound was mechanically excited, over a dozen *F. fusca* workers ran out, but they aroused practically no response in *F. aquilonia*.

DISCUSSION

F. fusca frequently moves into deserted mounds of wood ants. In this case, however, it settled into an uninhabited part of mound still inhabited by workers of *F. aquilonia*. Probably the queenless state of the wood ant colony had deprived the workforce of their typical aggressiveness and tendency to defend their nest and foraging area. Yet it is particularly intriguing that *F. fusca* remained in the mound even after the *F. aquilonia* colony had begun to revive and that it was still tolerated there. Our observation agrees with Sejma's (1971) conclusion: ants of different species living side by side and coming into contact every day become accustomed to one another so much that their mutual aggressiveness is lower than among alien individuals of the same species.

The plesiobiosis observed by us has interesting evolutionary implications. Wilson (1991) discussed the evolution of social parasitism in ants, and summarized his view in Fig. 19-3 (p. 361). The evolutionary schema is an extension of one evolved in a long sequence of contributions starting with Wheeler (1904). Essentially, Wilson suggests that, of the many variations of social parasitism, inquilinism (where the parasite spends the entire life cycle in the nest of its host; workers are either lacking or, if present, are usually scarce and degenerate in

behaviour) is a convergent phenomenon, reached independently by many different species following one or the other of at least three available pathways in evolution. Wilson's own contribution to the schema was to add the third one, the route starting with plesiobiosis, and potentially leading to inquilinism through parabiosis and xenobiosis (relations, in which the colony of one species lives in the nest of another species, still keeping their broods separate).

Fig. 2. Compound nest of *Formica aquilonia* + *Formica fusca*; the part occupied by *F. fusca* is marked with an arrow (photo W. Czechowski).

Although situations similar to our finding may be rare, its evolutionary significance seems clear. Co-existence of species pairs like *F. fusca* and *F. aquilonia* fits well the concept of evolution starting with plesiobiosis. These species are not closely related (they are classified to separate subgenera), and therefore lie ouside the domain of Buschinger's (1990) sympatric-speciation model of the evolution of various kinds of social parasitism.

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References

Buschinger, A. 1990. Sympatric speciation and radiative evolution of socially parasitic ants – Heretic hypotheses and their factual background. Zeitschrift für Zoologische Systematic und Evolutionsforschung, 28: 241–260.

Czechowski, W. 1990. Aggression of *Formica aquilonia* Yarr. to *Camponotus ligniperdus* (Latr.) (Hymenoptera, Formicidae) under the conditions of artificial colonization. Memorabilia Zoologica, 44: 83–91.

Hölldobler, B. and E. O. Wilson. 1990. The ants. Springer-Verlag, Berlin, xii + 732 pp.

Pisarski, B. and K. Vepsäläinen. 1989. Competitive hierarchy in ant communities (Hymenoptera, Formicidae). Annales Zoologici, 42: 321–329.

Savolainen, R. 1990. Colony success of the submissive ant *Formica fusca* within territories of the dominant *Formica polyctena*. Ecological Entomology, 15: 79–85.

Savolainen, R. 1991. Interference by wood ant influences size selection and retrieval rate of prey by *Formica fusca*. Behavioral Ecology and Sociobiology, 28: 1–7.

Savolainen, R. and K. Vepsäläinen. 1988. A competition hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos, 51: 135–155.

Savolainen, R., K. Vepsäläinen and H. Wuorenrinne. 1989. Ant assemblages in the taiga biome: testing the role of territorial wood ants. Oecologia, 81: 481–486.

Sejma, F. A. 1971. [On the problem of relations between territorial ant species], pp. 69–71. *In*: [Ants and forest protection]. Moskva (in Russian).

Vepsäläinen, K. and B. Pisarski. 1982. Assembly of island ant communities. Annales Zoologici Fennici, 19: 327–335.

Wheeler, M. W. 1904. A new type of social parasitism among ants. Bulletin of the American Museum of Natural History, 20: 347–375.

Wheeler, M. W. 1926. Ants, their structure, devolopment and behaviour. Columbia University Press, New York, xxv + 663 pp.

Wilson, E. O. 1971. The insect societies. The Belknap Press of Harvard University Press, Cambridge, MA, x + 548 pp.

Wuorenrinne, H. 1958. Über die gegenseitigen Beziehungen der Ameisenarten. Annales Zoologici Fennici, 24: 19–28.

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