

Life Histories of Subarctic Ants

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ABSTRACT. Ant species belonging to seven genera occur in habitats near the tree line in the Northern Hemisphere. An analysis of colony founding strategies suggests that in addition to physiological cold resistance, behavioral and sociometric adaptations might be important for survival and propagation of ants in subarctic biomes.

Key words: polygyny, budding, ants, Formicidae, *Leptothorax*

RÉSUMÉ. Des espèces de fourmis appartenant à sept genres vivent dans des habitats aux environs de la limite d'arbres. Une analyse des stratégies de fondation des sociétés suggère que, en plus d'une résistance physiologique au froid, des adaptations sociométriques et comportementales pourraient être importantes pour la survie et la propagation dans les biomes subarctiques.

Mots clés : polygynie, bouturage, fourmis, Formicidae, *Leptothorax*

INTRODUCTION

The ant fauna of boreal and alpine biomes consists of a monotonously small number of species and thus has been given little attention by myrmecologists (Gregg, 1972; Francoeur, 1983; Nielsen, 1987). Nevertheless, ants locally occur in high densities even near and beyond the tree line, suggesting that they play an important role in subarctic ecosystems, both as prey and predators (Nielsen, 1987).

Boreal ants have to cope with harsh environmental conditions, such as extremely low temperatures and long winters, but little is known about how they are adapted to life in the cold. Ants hibernate in a dense cluster of workers, queens, and in some species also larvae, and only few workers are found solitarily near the nest entrance and in other parts of the colony (Eidmann, 1943). Nest cavities of *Leptothorax*, subgenus *Leptothorax* (s.str.), may be partially filled with ice crystals, and even under protective snow cover temperatures in the nest may fall below -20°C (Berman *et al.*, 1982). Hibernating *Leptothorax acervorum* from Siberia are known to survive temperatures of -40°C by accumulating anti-freeze polyols (Leyrikh, 1989).

Recently it was suggested that in addition to physiological adaptations, changed life history strategies might facilitate the propagation of boreal ants (Heinze, 1991).

In the following, records of ants from areas near the tree line and data on their colony structures and colony founding strategies are summarized. Possible interrelations between life history traits and the occurrence in areas with long and cold winters are examined.

RECORDS OF ANTS NEAR THE TREE LINE

According to the sparse data scattered in the literature and from personal observation, species of seven genera of ants live near the tree line in northern Eurasia and America (Table 1), three belonging to the subfamily Formicidae (*Camponotus*, *Formica*, *Lasius*) and four to the Myrmicinae (*Formicoxenus*, *Harpagoxenus*, *Leptothorax*, *Myrmica*). All species are common throughout boreal coniferous forests, but only few reports document their occurrence beyond the

tree line in tundra habitats (e.g., Gregg, 1972). The ants ranging farthest north are taxa of *Leptothorax* (s.str.): a colony of *Leptothorax "muscorum"* was collected 80 km north of the tree line on Richards Island, N.W.T. (Brown, 1955); Arnoldi (1968, 1969) lists *L. acervorum* as the only species occurring in Russian tundra; and at least two *Leptothorax* species are common in tundra habitats in Quebec (Francoeur, 1983; pers. obs.). Of the other species, at least *Camponotus herculeanus* most probably does not advance far into treeless areas, as it requires wood as nesting material. Ants are completely absent from Greenland and Iceland today, but fossil *Camponotus* and *Formica* were found in the Plio-Pleistocene Kap København Formation in northernmost Greenland (Böcher, 1989).

LIFE HISTORIES OF BOREAL ANTS: LEPTOTHORAX

With a total length of less than 5 mm, *Leptothorax* (s.str.) are by far the smallest boreal ants and also have the smallest colonies. Typical nests contain from a few dozen to hundreds of workers (Fig. 1) and are built in cavities in decaying twigs, moss, or bark, or under stones.

A comparative analysis of colony and population structures of leptothoracine ants from various biomes suggests a correlation between life in northern habitats and optional dependent colony founding strategies. The majority of the approximately 300 *Leptothorax* species live in temperate or subtropical biomes, such as the Mediterranean, the Near East, or the southern United States. In most southern species (subgenera *Myrafant*, *Temnothorax*, *Macromischa*, etc.) nests are obligatorily monogynous, i.e., they contain only a single inseminated egg-laying queen. New colonies are founded independently by young queens, which isolate themselves in small cavities directly after mating in midsummer (Table 2; see also Buschinger, 1968, 1974; Plateaux, 1970). In contrast, in colonies of all species belonging to the boreal subgenus *Leptothorax* (s.str.) and in many boreal and alpine *L. (Myrafant)* several inseminated queens may be present (e.g., Buschinger, 1968; Alloway *et al.*, 1982; Heinze and Buschinger, 1988; Stille *et al.*, 1991). Solitary founding queens have rarely been found. Direct observations and

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TABLE 1. Species list of ants from boreal habitats near the tree line†

	Ala	Ch	NQ	MLC	MW	FM	NR	NESib
<i>Myrmica</i>								
<i>alaskensis</i> ²	×	×	×	×				
<i>brevispinosa</i>	×							
<i>lobicornis</i> ^{1?}						×	×	(×)
<i>rubra</i> ²						×	×	×
<i>ruginodis</i> ³						×	×	×
c.f. <i>brevinodis</i>								×
<i>sulcinodis</i> ³						×	×	×
<i>rugulosa</i> ²								×
<i>bergi</i>								×
<i>Leptothorax</i> (s.str.)								
<i>acervorum</i> ²	×	×	×			×	×	×
cf. <i>canadensis</i> ²	×	×	×	×	×			
sp. A ²				×				
<i>wilsoni</i> ⁴				×				
<i>Leptothorax</i> (<i>Myrafant</i>)								
c.f. <i>tuberum</i> ³								×
<i>Formicoxenus</i>								
<i>quebecensis</i> ⁴				×				
<i>nitidulus</i> ⁴						×		
<i>Harpagoxenus</i>								
<i>canadensis</i> ⁴				×				
<i>sublaevis</i> ⁴						×		
<i>Lasius</i>								
<i>flavus</i> ³						×		
<i>Formica</i>								
<i>neorufibarbis</i> ²	×	×	×		×			
<i>subnuda</i> ⁴	×		×					
<i>whymperi</i>	×							
<i>podzolica</i>	×							
<i>fusca</i> ³	×							×
<i>lemanii</i> ²						×	×	×
<i>gagatoides</i> ³						×	×	×
<i>exsecta</i> ^{2,4}						×	×	×
<i>uralensis</i> ^{2,4}						×	×	×
<i>sanguinea</i> ^{2,4}						×		×
<i>truncorum</i> ^{2,4}						×	×	×
<i>picea</i>							×	×
<i>lugubris</i> ^{2,4*}						×	×	×
<i>aquilonia</i> ^{2,4}						×	×	×
<i>Camponotus</i>								
<i>herculeanus</i> ¹	×	×	×	×	×	×	×	×
<i>saxatilis</i>								×
<i>japonicus</i>								×

†Ala: central and interior Alaska (Nielsen, 1987; D. Ortius, pers. comm. 1991); Ch: Churchill, Manitoba (Gregg, 1972); NQ: Nouveau Québec (Francoeur, 1983); MLC: Mt. du Lac des Cygnes, Québec; MW: Mt. Washington, New Hampshire; FM: Finnmark, Norway (Collingwood, 1979; Holgersen, 1940); NR: tundra and forest-tundra of northern Russia (Arnoldi, 1968); NESib: northeastern Siberia (Kolyma Mts., Bolshoi Annachag; Berman *et al.*, 1980; Zhigulskaya and Berman, 1975). Colony founding strategies are indicated as follows (based on numerous references, e.g., Collingwood, 1979; Rosengren and Pamilo, 1983; Buschinger, 1974): ¹obligatorily monogynous, colonies founded by solitary queens; ²queen adoption and budding likely or observed; ³polygyny observed; ⁴social parasite or guest ant.

*The social structure of *F. lugubris* colonies shows geographic variation — nests from Central Europe are polygynous, but nests from Finland are mainly monogynous (Pamilo *et al.*, 1992).

seasonal fluctuations of colony structures in *Leptothorax* (s.str.) suggest that while some queens disperse and attempt independent colony founding immediately after mating, others are adopted into established nests.

In *Leptothorax muscorum*, *L. acervorum* from European populations, *L. (M.) curvispinosus*, and others, queen adoption leads to secondary polygyny, i.e., several queens lay eggs within a single colony. Though egg-laying rates of

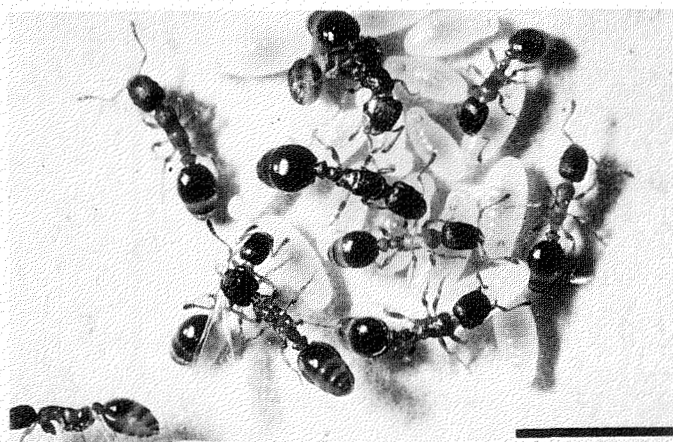


FIG. 1. Laboratory nest of *Leptothorax* sp. A from Quebec. Typical colonies of this ant consist of only a few dozen workers and may contain several queens. The large individual on top of the brood pile is a queen. The scale equals 5 mm.

TABLE 2. Colony structure (see Table 1) in ants of the genus *Leptothorax* from various habitats†

Subgenus	Species	Social organization	Geographical range
<i>Temnothorax</i>	<i>recedens</i>	1	Mediterranean
<i>Myrafant</i>	<i>ambiguus</i>	2	eastern North America
	<i>curvispinosus</i>	2	eastern North America
	<i>exilis</i>	1	Mediterranean
	<i>flavicornis</i>	3	Mediterranean?
	<i>interruptus</i>	3	Central Europe, Alps
	<i>longispinosus</i>	2	eastern North America
	<i>lichtensteini</i>	1	Mediterranean
	<i>melas</i>	1	Corsica
	<i>nigriceps</i>	1	Central Europe
	<i>nylanderi</i>	1/3	Central Europe, Mediterranean
	<i>parvulus</i>	1	Mediterranean
	<i>rudis</i>	1	California
	<i>tuberum</i>	3	Central Europe, Alps
	<i>unifasciatus</i>	1	Central Europe, Mediterranean
<i>Macromischa</i>	<i>allardycei</i>	1	Florida
<i>Leptothorax</i>	<i>acervorum</i>	2	boreal Eurasia, North America
	cf. <i>canadensis</i>	2	boreal North America
	<i>crassipilis</i>	3	alpine North America
	<i>gredleri</i>	2	Central Europe
	<i>muscorum</i>	2	boreal Eurasia
	<i>retractus</i>	3	boreal North America
	sp. A	2	boreal North America
	<i>sphagnicolus</i>	2	boreal North America

†Data from Buschinger (1968, 1974), Heinze and Buschinger (1988), Espadaler *et al.* (1984), Stuart and Page (1991), and unpubl. obs. *L. (Myrafant) nylanderi* is regularly monogynous, though polygynous nests have occasionally been found.

individual queens may differ significantly, there is no evidence of openly aggressive competition among nestmate queens (Bourke, 1991; Wilson, 1974; Lipski *et al.*, 1992). In *L. gredleri*, *L. sp. A*, and *L. acervorum* from Alaska, on the other hand, one queen more or less completely monopolizes reproduction. Other inseminated queens are tolerated in the colony only as long as they do not become reproductive ("functional monogyny"; Buschinger, 1968). It was observed that nestmate queens engaged in stereotyped

and openly aggressive interactions in early spring, resulting in the formation of rank orders. In each nest only the highest ranking queen began to lay eggs (Heinze and Smith, 1990; Heinze and Lipski, 1990; Heinze and Ortius, 1991).

In both polygynous and functionally monogynous *Leptothorax* (s.str.), spontaneous fractioning of colonies (budding) and queen emigration were observed in the laboratory. In *Leptothorax* sp.A and *L. cf. canadensis* from Quebec and New England and in *L. acervorum* from northern Norway and Alaska some inseminated queens left their nests directly after hibernation. Queens moved into empty nesting sites and were occasionally joined by workers from their maternal nests. The presence of very small colonies of *L. sp.A*, *L. gredleri*, and *L. acervorum* in early spring suggests that budding occurs regularly also in the field.

SOCIAL ORGANIZATION OF OTHER BOREAL ANTS

Though data on colony and population structures of boreal ants are rare, queen adoption and budding appear to be common strategies also among other boreal genera (Table 1). Many *Myrmica* and *Formica* species are facultatively polygynous, and colony budding was reported from both genera (e.g., Rosengren and Pamilo, 1983; Czechowski, 1984; Uchmański and Pętal, 1982). Queen emigration is likely in *Myrmica* (e.g., Elmes, 1982). Though most species of *Lasius* (s.str.) are strictly monogynous, facultative polygyny was reported from *Lasius flavus* (Waloff, 1957).

A rather high percentage of boreal ants are social parasites — i.e., they depend on the help of other ant species at least during parts of their life cycles. Queens of temporary parasites, e.g., species belonging to the *Formica rufa* and *Formica exsecta* groups, invade nests of other *Formica* species, where they somehow eliminate the host queen. Host workers take care of the parasite's brood but are eventually replaced by the parasite queen's own workers. New nests may also arise through colony budding and nest splitting (e.g., Hölldobler and Wilson, 1990). *Harpagoxenus sublaevis* and *H. canadensis* are slave makers. Queens enter a *Leptothorax* (s.str.) nest and kill or expel all adult residents. Workers that eclose from the conquered *Leptothorax* pupae nurse the *Harpagoxenus* brood. *Harpagoxenus* workers are inefficient in brood care and do not forage; thus the parasites permanently depend on their hosts. New host workers are obtained in slave raids, during which *Harpagoxenus* workers pillage neighboring *Leptothorax* colonies (e.g., Hölldobler and Wilson, 1990). *Formicoxenus* are guest ants in the nests of *Myrmica* or *Formica*. Though they beg food from their hosts, they are typically capable of rearing their brood themselves. New colonies may be founded by budding within a host nest (Lenoir *et al.*, 1992).

Camponotus herculeanus appears to be the only boreal ant species in which new nests are founded independently by solitary queens. Mature colonies are typically monogynous. Queens are intolerant of each other, but occasionally two or more queens may coexist in different parts of the same colony ("oligogyny"; Hölldobler, 1962). In contrast to other ants, male and female sexuals of *Camponotus* are reared in late summer and hibernate in their maternal nests before

mating in spring or early summer (Hölldobler and Wilson, 1990). In Quebec, founding queens of *Camponotus* may therefore be found already in early June (pers. obs.), whereas in other species mating and colony founding takes place only in late July and August.

ADAPTIVE VALUE OF DEPENDENT COLONY FOUNDING

Generally, natural selection is thought to favor colony founding by solitary ant queens and the monopolization of reproduction by single queens (e.g., Hölldobler and Wilson, 1990). In southern ant faunas, a large percentage of species are strictly monogynous and new nests are initiated by dispersing queens immediately after mating in midsummer. Alternative strategies — queen adoption, polygyny, and budding — appear to be adaptations to special ecological conditions, such as unstable nest sites, habitat patchiness, or resource limitation (e.g., Hölldobler and Wilson, 1977, 1990; Bolton, 1986).

In six of seven boreal ant genera, independent colony founding is at least partly replaced by dependent strategies: queen adoption after mating and budding after hibernation or parasitic invasion of host species colonies.

As yet it is not clear whether the surprisingly high frequency of dependent founding among boreal species is accidental or causally connected with life in the cold. Several species of *Lasius*, *Formica*, *Leptothorax*, and *Myrmica* from temperate habitats are also facultatively polygynous, and *Formica lugubris* is mainly monogynous in Finland but polygynous in Central Europe (Pamilo *et al.*, 1992). Hence, it appears unlikely that dispersal strategies changed in all these genera as an adaptation to life in boreal biomes. Rather, already existing life history traits might have favored facultatively polygynous species during the colonization of habitats near the tree line. Colony fractioning might be facilitated in boreal biomes by the comparatively simple structuring of ecosystems, in which potential nest sites have little diversity but occur in high densities. Furthermore, resource limitation and the shortness of summers in taiga and tundra might have favored species that produce few queens with a "safe" colony founding strategy rather than numerous dispersing queens with a high rate of founding failure.

In addition to budding, boreal ants might benefit also from another aspect of their changed life histories. Some *Leptothorax* (s.str.) queens emigrate from their nests directly after hibernation and probably attempt solitary founding in spring rather than budding. Similarly, due to the unusual rearing time of winged sexuals in *Camponotus*, new colonies are founded by solitary queens in spring. Due to the delay of colony founding from late summer and fall to spring, solitary hibernation is avoided and the period during which a young queen can rear her first brood is extended. In preliminary laboratory studies with *Leptothorax cf. canadensis*, solitarily hibernating ant workers and ants whose winter clusters were experimentally scattered suffered distinctly increased mortality (Heinze, unpubl. data). Herbers (1986) reported that polygynous colonies of *Leptothorax (Myrafant) longispinosus* survived winter better than

monogynous nests. A positive effect of group size on winter mortality, probably caused by a higher resistance of clustered ants against both desiccation (Sigal and Arlian, 1982; but see Copp, 1983) and excessive moisture, might thus favor hibernation of young queens in established nests.

Further studies on hibernation strategies and colony and population structures of boreal *Leptothorax* (s.str.) are planned to substantiate these ideas. Data on the social organization of sub-Antarctic ants, which belong to other subfamilies (Ponerinae: *Acanthoponera*; Dolichoderinae: *Dorymyrmex*, *Tapinoma*) and thus have adapted convergently to cold climates, will be of special interest.

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