Jürgen HEINZE, Bert HÖLLDOBLER

Ants in the cold

Abstract. The life histories of boreal ants are examined for possible adaptations to long winters and severe climate. While comparing the life cycles of *Camponotus* s.str. and *Leptothorax* s.str., strategies are identified by which solitary colony founding is avoided or delayed from late summer to the beginning of the new season. Possible advantages of postponing colony founding are discussed.

INTRODUCTION

Life in extreme habitats requires unusual adaptations. In social insects, not only the behavior and physiology of individuals may be shaped by the environment, but the social organization of the colony as a whole may be changed by selective pressure. In insect societies, thousands of ants, bees, or termites cooperate to achieve bizarre adaptations which are impossible to a solitary insect. Termites, e.g., survive in extremely hot environments by air conditioning their nests (LÜSCHER 1961), army ants entwine their bodies to bridge small streams, fire ant colonies escape floods by forming live rafts (HÖLLDOBLER, WILSON 1990), and bees keep their hives at an almost constant temperature, regardless of external climate (MORITZ, SOUTHWICK 1992).

Considered to be generally thermophilous, ants have successfully conquered also cold or temperate biomes, including deciduous woodland, boreal and alpine coniferous forests, and subarctic forest-tundra. At high latitudes, however, the ant fauna is little diverse (HOLGERSEN 1942, KUSNEZOV 1957, PISARSKI 1978), and only about a dozen species from four or five genera reach the tree-line in northernmost Eurasia and North America (HEINZE 1993). Though the importance of ants in boreal ecosystems is well acknowledged (e.g. NIELSEN 1987), few studies have focused on how ants manage to thrive under the harsh climatic conditions in these subarctic environments.

Comparing certain aspects of the life cycles of boreal species of the two genera, *Camponotus* MAYR and *Leptothorax* MAYR, we attempt to demonstrate how both

adaptations of the individual's physiology and specialized colony founding strategies may facilitate life in habitats near the tree-line. For the life histories of other boreal ants see, e.g. BERMAN et al. 1987, KIPYATKOV 1988, ELMES, KELLER 1993, and references therein.

BOREAL ANTS: *CAMPONOTUS HERCULEANUS* (L.) AND *LEPTOTHORAX ACERVORUM* (FABR.)

Camponotus and *Leptothorax* are two extraordinarily large and complex ant genera which are known from most zoogeographical regions. In addition to several *Formica* L. and *Myrmica* LATR. species, *Camponotus herculeanus* (L.) and *Leptothorax acervorum* (FABR.) are the most widely distributed and best studied species of the few taxa occurring in the taiga and forest tundra. The two species differ widely in social organization, life history, and ecology, and they mark opposite ends of the scales of both individual and colony size. Whereas colonies of *L. acervorum* typically consist of 50 to 100 workers, SANDERS (1970) counted more than 13000 individuals in a single *C. herculeanus* nest. The total length of a *C. herculeanus* major worker can reach 10 to 12 mm, that of *L. acervorum* rarely exceeds 4.5 mm. *C. herculeanus* appears to be often associated with living trees, as it typically requires wood for nesting material (BROWN 1955, HÖLLDOBLER 1962a, BERMAN et al. 1980, FRANCOEUR 1983, GREGG 1972). *L. acervorum* and related species, on the other hand, which in coniferous forests live mainly in decaying twigs, have repeatedly been found well beyond the tree line in the tundra, where they nest under flat stones on south-facing slopes (BROWN 1955, BERMAN et al. 1980, 1982, FRANCOEUR 1983, NIELSEN 1987, HEINZE, ORTIUS 1991). The northernmost ant found in America is a *L. "muscorum"* worker (probably *L.* cf. *canadensis* PROVANCHER) taken at Kidluit Bay on Richards Island, about 75 km from any trees (BROWN 1955), and NIELSEN (1987) collected *L. acervorum* at Happy Valley Cut in interior Alaska, 150 km north of the tree line. Similarly, *L. acervorum* is the only ant species occurring in the Russian tundra (ARNOLDI 1968).

Whereas colonies of all boreal *Leptothorax* may contain several inseminated queens, *Camponotus* is monogynous, though occasionally several queens may co-exist in separate parts of a large colony (oligogyny, HÖLLDOBLER 1962b).

HIBERNATION AND COLD HARDINESS

It has long been known that ants hibernate in dense clusters, which in the case of *Leptothorax* consist of workers, queens, and larvae, and in *Camponotus* may also contain winged male and female sexuals. According to EIDMANN (1943) and HÖLLDOBLER (1961), the *Camponotus* queen, the larvae, and the nurses are positioned in the centre of the hibernation cluster and are surrounded by the foragers and nest guards. The guards are the last to join the hibernation cluster and also the first to resume their activity during a temperature increase. Similarly, in *Leptothorax* the

queen (or queens) and the brood are surrounded by workers, however, the structure of the hibernation clusters and the dynamics of their formation are not known.

In winter, the nest entrances are typically sealed with soil or wood particles, and the empty space of the nest chambers may be partially filled with ice crystals. Even under a protective snow cover, temperatures in nests near the tree-line may fall as low as $-30^{\circ}C$ (BERMAN et al. 1980), but as both adult ants and larvae accumulate large amounts of anti-freeze polyols, mainly glycerol, in the fall, they may survive temperatures of down to $-40^{\circ}C$. (LEIRIKH 1989). Other freeze-protecting agents, such as thermal hysteresis proteins, have as yet not been found in ants and other *Hymenoptera* (DUMAN et al. 1991).

COLONY FOUNDING IN BOREAL ANTS

Cold is not the only obstacle to be faced in the far north. The extremely long duration of winters and the shortness of the productive period in summer probably also pose severe problems to ants by prolonging the development of the brood and the growth of the colony. In many temperate *Leptothorax*, eggs may develop to adult workers within one summer, but in extremely boreal habitats all larvae hibernate at least once, some twice before pupation. In *Camponotus*, individuals may hibernate twice before reaching sexual maturity, independent from ambient temperature (Fig. 1).

Slow brood development also affects colony founding. Typically, sexuals of temperate ant species mate during a swarming flight in midsummer, seek shelter in a small cavity in wood or the soil, and start to lay eggs. The first workers may have eclosed by the onset of winter and the risky phase of solitary colony founding thus is completed within the first year of the queen's adult life. In extremely northern habitats, the first snow may fall shortly after the mating season and there is rarely time for the queens to produce their first brood before hibernation. Hence, a queen which mated in late summer would face one, probably two hibernations without adult workers and the colony founding phase would be extended to more than one year.

One way to counter the constraints of a short growing season is to develop a nest temperature household as was demonstrated in the mound building *Formica* L. wood ants. Metabolic heat production and the physical properties of the mound that enhance the collection of heat from sunlight raise the internal nest temperature rapidly in spring (e.g. KNEITZ 1970, DLUSSKY 1975, HORSTMANN, SCHMID 1986, ROSENGREN et al. 1986). This permits to rear male and female sexuals from eggs to adults in only 5 to 6 weeks. In this group of *Formica*, sexuals thus mate in early summer. Furthermore, the queens found new nests by temporary parasitism or colony budding after readoption into the maternal nest rather than solitary founding.

In *Leptothorax*, males and virgin queens eclose in midsummer and mate in August. Occasionally, sexuals are still present in the nest in early September. As in *Formica* and also *Myrmica* LATR., young queens may seek adoption into established colonies after mating. After hibernation, new colonies are founded both by solitarily emigrating queens or by budding of multiply-queened colonies. In some species, budding or

emigration is preceded by overtly aggressive or stereotyped dominance interactions among the queens (HEINZE, SMITH 1990, HEINZE, ORTIUS 1991). Observations show that during the first warm days of spring, some larvae are cannibalized by *Leptothorax* workers and queens. Before emigrating young queens thus probably replenish their fat reserves. Queen adoption, emigration and budding result in seasonal fluctuations of average queen number and colony size (Fig. 2, HEINZE 1989). Some *Leptothorax* queens disperse directly after mating rather then returning into their maternal nests, but laboratory studies indicate that the success of solitarily hibernating queens is low (HEINZE, BUSCHINGER 1988).
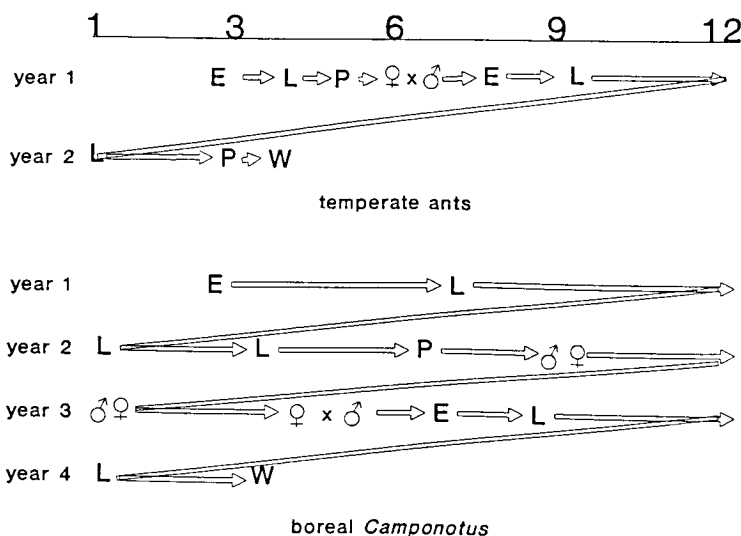

Fig. 1. Schematic illustration of the life histories of a temperate ant and a boreal *Camponotus* species. E, L, P, and W stand for eggs, larvae, pupae, and adult workers respectively. In some temperate ants, larval development may be completed within several months and mating takes place in the first year of the young queen's life. In other species, sexual larvae hibernate once. Typically, foundresses begin to lay eggs shortly after mating (but see PLATEAUX 1970) and may occasionally have adult offspring before the onset of winter or early during the next summer. In boreal *Camponotus* and also in boreal *Leptothorax*, on the other hand, sexual larvae hibernate at least once, frequently twice. In *Camponotus*, rather than mating directly after eclosion in late summer, winged sexuals hibernate in the maternal colony and swarming takes place in early summer. *Camponotus* queens begin to lay eggs after mating, but first workers often eclose only during the following year. Nevertheless, by the shift of the mating season from late to early summer in *Camponotus*, hibernation without larvae is avoided.

Solitary colony founding does, however, occur in some ant species in the north. In boreal *Camponotus*, adult sexuals are produced in late summer and hibernate in the maternal nest before mating (e.g. HÖLLDOBLER 1962a, HANSEN, AKRE 1990). The resulting life history has been analyzed in detail in *C. herculeanus* (HÖLLDOBLER 1965) and will be summarized briefly. An "eclosion guild" of young workers and reproductive forms produced in late summer remains together until the nuptial flight in the following year. The young workers stay close to the males and virgin queens,

percentage colonies

winter

104 colonies

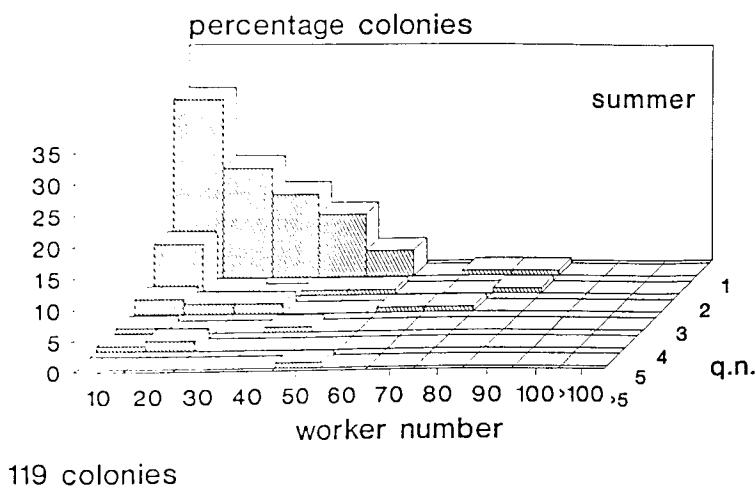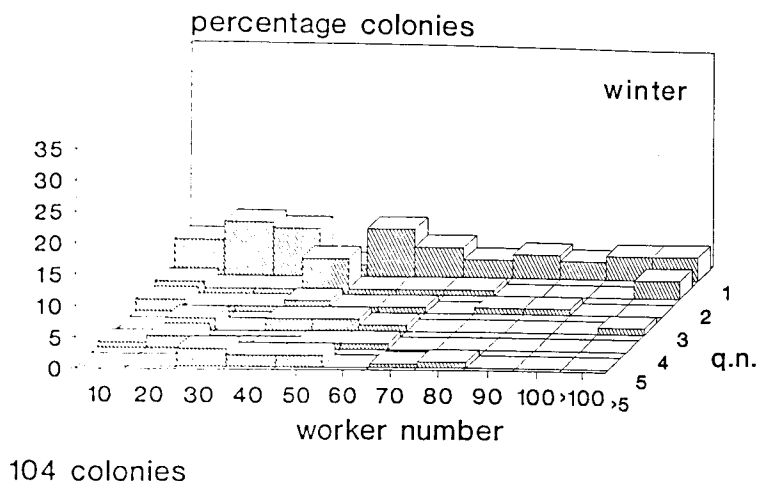percentage colonies

summer

119 colonies

Fig. 2. Seasonal fluctuations of colony composition in the nearctic ant *Leptothorax* sp. A from Québec. As in other boreal *Leptothorax*, colonies collected in winter contain on average more queens (q.n. stands for queen number) and more workers than summer colonies. In *Leptothorax* sp. A, the variation in colony structure is especially pronounced because of its habitat requirements, which promote queen adoption and budding rather than queen dispersal (e.g. HEINZE 1989).

feeding them food that they themselves have received from returning foragers. It is remarkable that the males during their "social phase" not only receive food but also donate liquid food to their nestmates (HÖLLDOBLER 1966). All of the members of the guild accumulate fat reserves before hibernation begins. During late summer, the

mother queen lays a clutch of eggs which hatch and develop to second instar larvae before the entire colony shuts down for the winter. Colony inactivity is based on a true physiological diapause, because it continues even if the colony is transferred to the laboratory and kept at 22–25°C (HÖLLDOBLER 1961). If the nest temperature is maintained below 18°C the colony will remain relatively inactive and the virgin queens and males than stay within the nest for an entire additional year. But if the temperature is sustained above 22°C, a common event in the field in April, the hibernation phase ends. The males become "socially emancipated" in the sense that they now participate much less in food exchange and other social activities. They start to use up their fat bodies. With their bodies light in weight and their sperm poised for ejaculation, they are primed for the nuptial flight. The workers continue to fatten the virgin queens as well as the overwintered larvae, which are destined to mature during the late spring and summer.

By May or June, the stage is at last set for the *C. herculeanus* nuptial flights. In the afternoon the queens and males start to move to the nest entrance to sun themselves. Their excursions become more and more extended, until finally, aided by a synchronization pheromone from the mandibular glands of the males (HÖLLDOBLER, MASCHWITZ 1965), a mass flight occurs. The newly mated queens then start new colonies by sealing themselves into old beetle burrows or other preformed cavities in wood. They live on their body reserves until the first brood of workers is reared. Some individuals, which had a relatively early nuptial flight, might raise the first workers before the second hibernation starts. Often, these nanitic workers do not survive, however, the winter period. Other queens hibernate with second instar resting larvae, some of which will be eaten after hibernation, while other larvae develop into workers which eclose in late spring (Fig. 1).

The complex life cycle of *C. herculeanus* represents a "storage economy" of reproductives, maintaining males and virgin queens inside the colony for many months. The social economic burden caused by this system is probably alleviated by the fact that males participate in food distribution during their social phase. One of the advantages of hibernation of sexuals is that at least one generation of males and virgin queens is available for the nuptial flight whenever the environmental conditions are suitable. Overwintering of mature forms in the colony before mating is a rather uncommon strategy in ants, though winged males or females have been sporadically found in winter nests of other species (e.g. EIDMANN 1943). It might be intriguing that adult sexuals hibernate and mate in late spring or early summer in most, probably all boreal *Camponotus* species, whereas in several temperate and tropical species mating flights occur in midsummer (e.g. BASALINGAPPA et al. 1989, WHEELER, KRUTZSCH 1992) and alates are present in the colony only for a short period of time (SATOH 1989, HASEGAWA 1992). However, sexuals stay in the maternal nest for a longer period also in some *Camponotus* from warm-temperate or tropical areas [e.g. *C. floridanus* (BUCKL.) (HÖLLDOBLER, unpubl.), *C. yamaokai* TERAYAMA et SATOH (SATOH 1989), *C. kiusiuensis* SANTSCHI (ITO et al. 1988) and in *Paratrechina flavipes* (F. SMITH) (ICHINOSE 1987).

THE BENEFITS FROM DELAYING COLONY FOUNDING

It appears that by hibernation of adult sexuals and queen readoption colony founding is similarly postponed from the end of summer to the beginning of a new growing period and hibernation without adult workers or larvae is avoided. The advantages of budding or temporary parasitism to a founding queen are evident, however, the benefit from delaying solitary founding to spring is less clear.

Camponotus queens, which had the whole summer to produce larvae with which they then hibernate, clearly have a headstart during the next spring. They regularly cannibalize some of their larvae to raise new brood to adulthood more quickly. The resting larvae might serve in part as food reserves which can be recycled after hibernation, in order to speed up the development of the other larvae.

Solitary hibernation is nevertheless costly even for large *Camponotus* queens which are packed with fat reserves. According to field data (HEINZE, unpubl.) and laboratory studies (G. GRÄF, pers. comm.) 50 to 75% of all solitarily nesting *Camponotus* queens, which survived until the beginning of hibernation, died during the winter. Smaller, less endowed *Leptothorax* queens might rarely survive solitary hibernation in extremely northern habitats.
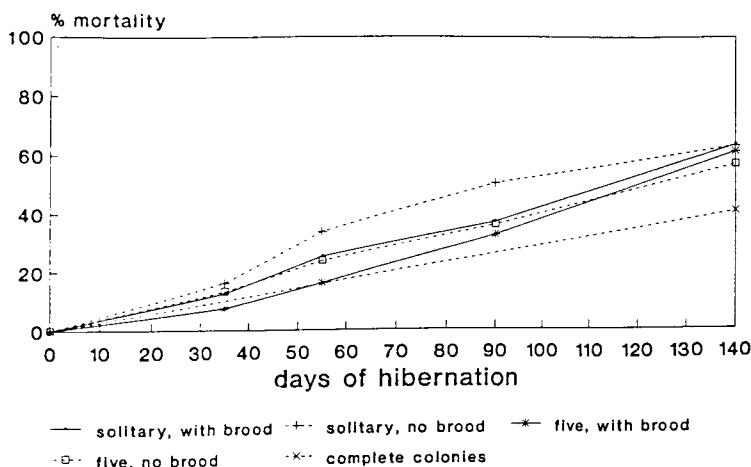

Fig. 3. Winter mortality of *Leptothorax* cf. *canadensis*. Workers from various populations in Québec and the White Mountains in New Hampshire were isolated in 1.5 ml plastic vials with perforated lids either solitarily or in groups of five, with and without brood (appr. three to five larvae). The ants were then subjected to temperatures of between $-5°C$ and $5°C$ at 90% humidity in an incubator. Mortality rates were checked every month. Compared to complete hibernating colonies, the mortality rate of solitarily hibernating ants was significantly increased (for details see text).

Survival experiments suggest that clustering by itself increases the winter survival of *Leptothorax* workers. Workers of *L.* cf. *canadensis* from New England and Québec, which hibernated in isolation, had a significantly higher mortality than workers, which hibernated in groups of 15 to 250 (2×2 test of independence with William's correction, $G_{adj.} = 87.1$; $p \ll 0.001$). Workers clustered in groups of five, however, did not show increased survival rates ($G = 0.92$; $p > 0.1$; Fig. 3). Though

queens of social insects are probably less sensitive to cold than are the workers (e.g. STRASSMANN et al. 1984 and own observations) it might nevertheless be advantageous for *Leptothorax* queens to seek adoption into established colonies just for the sake of higher winter survival. The relatively high relatedness among nestmate queens suggests that queens typically return into their maternal nests (e.g. STILLE et al. 1991, LIPSKI et al. 1992, HEINZE et al. 1992), hence, this strategy will also be favored by resident workers and queens.

The proximate factors which increase winter survival of clustered individuals are currently unclear. Whereas clusters of honeybees are capable of thermoregulation (e.g. SOUTHWICK 1983, HEINRICH 1985, MORITZ, SOUTHWICK 1992) and temperatures may be somewhat increased over ambient temperatures in large *Formica* nests (DLUSSKY 1975, ROSENGREN et al. 1986) this is not the case in the winter clusters of *Leptothorax*. Clustering, however, might protect the ants in the centre of the cluster, especially the queens and larvae, from desiccation, exceeding moisture, inoculative freezing, or mechanical damage by ice crystals. Workers surrounding the core of the cluster might thus have a similar function as the winter cocoons found in hibernating solitary insects (SAKAGAMI et al. 1985, DANKS 1991). Furthermore, the observation that ants in the outer layers of the clusters of *C. herculeanus* are predominantly outside foragers (EIDMANN 1942, HÖLLDOBLER 1961), which are typically the oldest workers (HÖLLDOBLER 1965), might suggest that to hibernate deeply within the cluster may be less costly than overwintering in the periphery.

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Theodor-Boveri-Institut
LS Verhaltensphysiologie
und Soziobiologie
Am Hubland, D 97074
Würzburg, FR Germany

STRESZCZENIE

Mrówki a zimno

Na przykładach gatunków z podrodzajów *Camponotus* s.str. i *Leptothorax* s.str. (różniących się bardzo tak wielkością osobników, jak i liczebnością i strukturą społeczeństw) przeanalizowano bionomię mrówek żyjących w strefie borealnej pod kątem ich przystosowań do długich zim i surowego klimatu. Wykazano, że wyrazem strategii życiowych w takich warunkach jest unikanie zakładania gniazd przez samotne królowe lub przesunięcie terminu zakładania mrowisk z późnego lata na początek następnego sezonu. Przedyskutowane są domniemane płynące z tego korzyści.