

The significance of latitudinal variation in body size in a holarctic ant, *Leptothorax acervorum*

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The mean body size of workers of the holarctic ant *Leptothorax acervorum* increases with latitude. Workers from populations near the Polar Circle were 10% larger than workers from central Europe. This gradient does not appear to be associated with variation in colony size. According to controlled rearing experiments with brood from populations in Cape Kartesh, Karelia (67°N) and Erlangen, Germany (49.7°N), larger adult body size in boreal populations is not an epiphenomenon of slow cell growth and larger cell size at lower temperatures. Larger workers survived longer without food both at room temperature and < 0°C, suggesting that selection for increased fasting endurance in boreal habitats might lead to this Bergmann's rule-like pattern in an ectothermic ant.

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Bergmann's rule states that, among related endothermic animals, body size increases with latitude (Bergmann 1847, Mayr 1956, Blackburn et al. 1999). This relationship, though far from being without exceptions, seems to be easily explained by a simple energetic consideration: larger animals have less total surface area per unit volume and therefore have a reduced cooling rate. However, it has repeatedly been argued that changes in insulating or heat-conserving structures might be better adaptations to climate than changes in body size (e.g., Scholander 1955, Geist 1987). Besides, a comparative analysis did not yield unambiguous support for large body size being a heat conservation mechanism in mammals (Ashton et al. 2000). Furthermore, this hypothesis cannot account for similar ecogeographic gradients in several ectotherms, such as fish or insects (Atkinson 1994, Atkinson and Sibly 1997). Consequently, a number of alternative explanations for the proximate mechanisms underlying Bergmann's rule, both adaptive and non-adaptive, have been suggested

(Blackburn et al. 1999). For example, size clines might result from a) larger animals dispersing more easily into high latitudes, b) larger animals being better protected against seasonal food shortage, c) competition being less intense in boreal habitats (David and Capy 1982), d) cells growing larger at lower temperatures (Van Voorhies 1996), or e) body size increasing due to bounded population growth rate at high latitudes (Demetrius 2000). Nevertheless, more empirical data, in particular common garden experiments, are needed to better understand the causes of Bergmann's rule (Partridge and Coyne 1997).

Several recent studies have examined whether Bergmann's rule holds in social insects. This is of particular interest as here, "body size" may mean both the size of individual ants, bees, or termites, or the size of the superorganism, i.e. the complete insect society. On the level of the superorganism, colony size was found to be significantly larger in ants from boreal and temperate areas than in the tropics (Kaspari and Vargo

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1995), but not so in termites (Porter and Hawkins 2001). On the level of the individual, Cushman et al. (1993) observed that the dominance of ant species with large-bodied workers increases with latitude in northern Europe and the British Isles.

Some authors (Mayr 1956) have questioned the validity of ecogeographic rules at an interspecific level and instead suggested to restrict it to an intraspecific context only ("neo-Bergmannian rule", James 1970, or "James's rule", Blackburn et al. 1999). The myrmicine ant *Leptothorax acervorum* (Fabricius, 1793) is a good candidate for such a study. It is probably the most widely distributed ant in Eurasia, ranging from central Spain and Italy (40°N) to the tundra/taiga-ecotone in northernmost Scandinavia and Siberia (ca 70°N; Radchenko et al. 1999). In preliminary studies we showed that *L. acervorum* workers from the Polar Circle are on average significantly larger than those from central Europe (Heinze et al. 1998, Heinze 1999). Here, we present data from almost the complete range of latitudes inhabited by this species. We also investigated the proximate causes of Bergmann's rule in *L. acervorum*. In particular, we examined whether larger body size at high latitudes is merely a plastic, non-adaptive response to cold temperatures alone, or adaptive and associated with increased fasting endurance.

Material and methods

Colonies of *Leptothorax acervorum* are small, with a few dozen to a few hundred workers and one to several queens. They nest in rotting branches, tree stumps, under bark etc. (e.g., Heinze et al. 1995, Seifert 1996). Nest densities may be very high and effective population sizes even in isolated forests may easily reach several ten thousands. Consequently, genetic differentiation between populations throughout Europe is low (Heinze et al. 1995). Our own observations do not give evidence of single colonies inhabiting several nest sites, e.g., colonies are presumably monodomous. Individual ants are comparatively small, with workers measuring ca 3 mm and queens being only 10% larger.

Collecting sites and body size measurement

Complete colonies or colony fragments were collected with aspirators in 16 localities throughout Europe (Spain: Sra. de Albarracin, prov. Teruel, 40.5°N; Sra. de Ancares, prov. Lugo, 43°N. Germany: Aschaffenburg, 50°N; Nürnberg, 49.4°N; Erlangen, 49.7°N; Müritz, 53.5°N; Sylt, 55°N. United Kingdom: Dartmoor, Devon, 50.5°N; Santon Warren, Norfolk, 52.5°N; Aberfoyle, Central, 56.3°N. Sweden: Nyehusen, Kristianstad, 55.7°N. Russia: St. Petersburg, 60°N. Karelia: C. Kartesh, 66.5°N; Kindo, 67°N. Norway: Alta,

Finmark, 70°N) and Alaska (Denali N.P., 64°N) and stored in ethanol for subsequent analysis. Body size (head width and thorax length; Heinze and Buschinger 1987) were measured with the help of an ocular micrometer under a binocular microscope at 50 × magnification to the nearest 0.01 mm. Mean measurement errors, determined by measuring a subsample of 30 workers twice and estimated according to Sachs (1992), were 0.008 mm for thorax length and 0.007 mm for head width. Because thorax length and head width were found to be correlated (Spearman rank correlation; Erlangen, $n = 102$, $r_s = 0.705$, $p < 0.0001$; Karelia, $n = 82$, $r_s = 0.827$, $p < 0.0001$), only data for thorax length are given.

To determine the size of colonies (worker number), all workers were counted in a sample of colonies from Erlangen and Karelia.

Voucher specimens were deposited in the ant collection of the Staatl. Museum für Naturkunde, Görlitz, Germany.

Effects of cold rearing conditions on body size

To determine whether body size is affected by temperature, live colonies from Erlangen and Karelia (Cape Kartesh) were brought into the laboratory in collecting vials and transferred into microscope slide nests in three-chambered boxes using standard methods (Buschinger 1974, Heinze and Ortius 1991). A sample of approximately ten workers were taken from each colony and stored in ethanol for later analyses. The rest of the colonies were kept in a common garden experiment at artificial temperature and light rhythms in Rumed incubators for two complete breeding cycles. Colonies were either subjected to two cold cycles (26 weeks 14 h 0°C dark/8 h 10°C light; 10 weeks 12 h 10°C dark/12 h 20°C light) or two warm cycles (10 weeks 14 h 0°C dark/8 h 10°C light; 1 week 12 h 10°C dark/12 h 20°C light; 24 weeks 8 h 15°C dark/14 h 25°C light, 1 week 12 h 10°C dark/12 h 20°C light). Temperatures in these cycles were chosen in a way to be somewhat more extreme than average summer conditions in the natural habitat, i.e. somewhat warmer than in Erlangen and colder than in Karelia. The body size of workers found in the original colony was compared to that of workers eclosing from larvae reared under the respective conditions. At least ten colonies each from each population were subjected to either the cold or warm treatment. However, not all colonies produced sufficient quantities of brood under these extreme artificial conditions.

Assuming that, because of the constant anatomy of the insect eye, the diameter of ommatidia in the eyes of workers more or less reflects the size of retinula cells, we measured eye size, number of ommatidia and ommatidia size in workers from Erlangen and Karelia. Workers were fixed and their heads were sputtered with

gold and investigated by scanning electron microscopy at a magnification of 400–550 × .

Fasting endurance

Fasting endurance was investigated by isolating individual workers from both populations in Eppendorf caps at room temperature until they died (10 to 15 workers from each of eight colonies from Erlangen and eight colonies from Karelia). Workers were taken from colonies ready for hibernation, so that they should be prepared for winter and had a maximal fat content. Eppendorf caps were opened daily to allow gas exchange.

In addition to fasting endurance at room temperature we investigated the survival rate of *L. acervorum* workers under cold temperatures. Ants for this experiment were collected in summer 2000 in Germany (Abensberg, 48.8°N), Russia (St. Petersburg area; 59.3°N) and England (Norleywood, Hampshire; 50.8°N). Colonies were subjected to standard winter conditions in incubators (0°C/8°C) for at least two weeks. Subsequently, four workers each from 12 German, 6 Russian colonies and 6 English colonies were individually placed into Eppendorf caps and either exposed to cold temperatures (two workers from each colony) or, as controls, to standard artificial hibernation conditions (0°C/8°C). In the cooling experiment, temperatures were kept at 0°C for two weeks and then decreased stepwise at –5°C per week to –35°C. Before each temperature change, all dead ants were removed. After the experiment we determined the thorax length of all ants to investigate the impact of body size on survival rate at cold temperatures.

Fat content

For the determination of fat content workers were killed by freezing, dried for at least 24 h and subsequently stored at 65°C over silica gel pearls. Ants were weighed individually using a Sartorius SC 2 microscale to the nearest 0.1 µg. Each individual was weighed four times on at least two different days. Subsequently, all fat was removed by soaking individual ants for 24 h in 1.25 ml petrol ether at room temperature. Workers were then weighed again four times. When the results from different measurements varied too strongly, weighing was repeated twice. We calculated the mean of the measurements per individual. Where six measurements were taken, two outliers were excluded. Fat content was estimated as mean dry weight after fat extraction subtracted from mean dry weight before fat extraction.

Data analysis

Statistical analyses were done with Statistica for Windows 4.5. Deviation of the data from a normal distribution was checked by Shapiro-Wilk's tests. Where parametric tests were not applicable, we used the respective non-parametric equivalents.

Results

Geographic variation of body size

Size measurements of workers from 16 populations in Europe and North America, ranging between 40.5°N and 70°N, clearly documented that thorax length was strongly correlated with latitude ($r_s = 0.798$, $p < 0.001$; Fig. 1). Workers from two populations with rough, alpine climate (Dartmoor and Sra. de Ancares) were much larger than expected from latitude, suggesting that altitude has a similar effect on body size. Excluding these two samples considerably improved the association between size and latitude ($r_s = 0.931$, $p < 0.001$).

Workers from the two best studied populations differed considerably in size. Workers from Karelia (Cape Kartesh) were on average 10% larger than workers from Erlangen (Mann-Whitney U-test; Erlangen, $n = 169$, $x = 1.08 \pm \text{SD } 0.05$ mm; Karelia, $n = 220$, $x = 1.15 \pm 0.07$ mm; $U = 8732.5$, $p < 0.001$). The sizes of workers from a single colony might not be independent data points. Therefore, we repeated the statistic analysis using the median sizes of five to 11 workers from ten colonies from Karelia and 11 colonies from Erlangen. Again, worker size was significantly larger in the Karelian population ($U = 8.5$, $p = 0.001$). A similar difference was observed in queens (two-tailed t-test, Erlangen, $n = 24$, $x = 1.29 \text{ mm} \pm 0.02$; Karelia, $n = 26$,

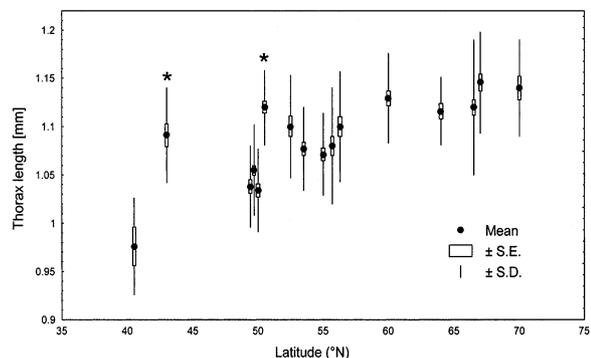


Fig. 1. Average body size (thorax length) of workers of the ant, *Leptothorax acervorum* from different latitudes in Eurasia and North America (for details see methods). Asterisks indicate two high elevation populations with considerably harsher climate than expected from latitude.

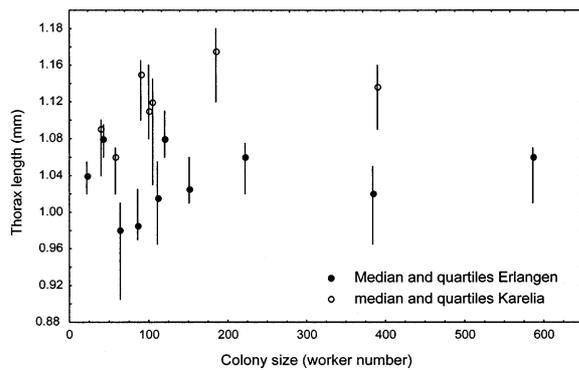


Fig. 2. Median thorax length of *Leptothorax acervorum* workers from colonies of different size from populations near Erlangen (49.7°N) and Karelia (67°N).

$x = 1.35 \pm 0.05$ mm, $t = -4.947$, $p < 0.001$; using medians of queens per colony from seven colonies from Karelia and ten colonies from Erlangen; $U = 13.0$, $p = 0.030$).

Colony size

The difference in body size between the two populations did not appear to be due to differences in colony size. Within populations, body size differed with colony of origin, i.e., some colonies contained on average larger workers than others (Kruskal-Wallis H-test: Erlangen, 96 workers from ten colonies, $H = 24.84$, $p < 0.004$; Karelia, 87 workers from seven colonies: $H = 25.31$, $p < 0.001$). However, the number of workers per colony had only a very weak effect on body size, if at all (Gamma correlation was used because of the many tied observations; Erlangen: $\text{Gamma} = 0.049$, $p > 0.5$; Karelia: $\text{Gamma} = 0.340$, $p < 0.001$) (Fig. 2). Furthermore, colonies from Karelia were on average not larger than colonies from Erlangen (Mann-Whitney U-test, $U = 32.0$, $p = 0.770$).

Queen number did not have a clear effect on worker body size (Erlangen: $\text{Gamma} = 0.039$, $p = 0.616$; because of several queenless colonies this analysis was not possible in the sample from Karelia).

Effects of cold rearing conditions on body size

As shown before in a carpenter ant (Klotz et al. 1992), eye diameter increased with increasing body size. This was due to an increase in the number of ommatidia, whereas ommatidium diameter did not differ between Karelian and Erlangen workers (median of three ommatidia from ten workers each, one worker per colony, from each population, median, 25 and 75% quartiles: Erlangen 14 μm , 12 μm , 14 μm ; Karelia 14 μm , 12.5 μm , 14 μm ; $U = 45.0$, $p = 0.705$).

In addition, we investigated whether rearing colonies under similar conditions has an effect on the size of workers eclosing from the brood. Based on Van Voorhies (1996) we expected workers eclosing from brood reared under relatively cold conditions to be larger and workers eclosing from brood reared under relatively warm conditions to be smaller than workers that had eclosed under natural conditions. However, at least in the Erlangen population the opposite was the case. In six of nine Erlangen colonies, workers that eclosed after two years of warm treatment were on average 6% larger than workers that had eclosed under natural conditions (with p -values < 0.05 ; Fisher's combined probability for all nine colonies: $-2\sum \ln p = 86.36$, $p < 0.001$). No effect was observed in the four Karelian colonies that reared sufficient numbers of workers under these conditions (with p -values > 0.3 in all cases; Fisher's combined probability: $-2\sum \ln p = 6.04$, $p > 0.1$; Fig. 3). Individuals from Erlangen and Karelia did no longer significantly differ in size after warm treatment (93 workers from Erlangen, 48 workers from Karelia, $U = 1943.5$, $p > 0.2$).

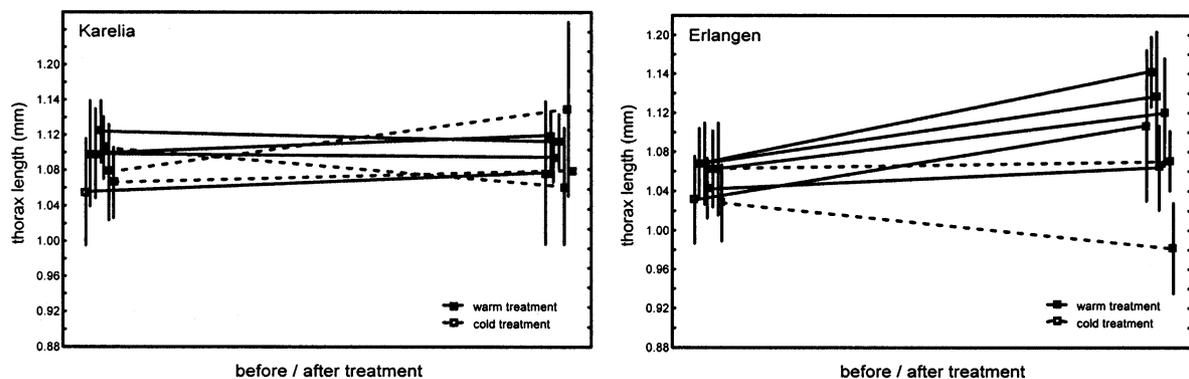


Fig. 3. Thorax length (median \pm quartiles) of *Leptothorax acervorum* workers from Karelia (67°N) and Erlangen (49.7°N) that eclosed under field conditions (left side of each figure) and, in the same colonies, from brood that eclosed after two artificial breeding cycles with warm or low temperatures (right side of each figure).

Cold treatment resulted in a considerable loss of brood and high colony mortality and the data basis therefore is probably too small to draw definite conclusions. Thorax length was ca 5% smaller in one of the two colonies from Erlangen that produced sufficient numbers of young workers under these conditions (10 field workers, 1.069 ± 0.04 mm vs 9 lab workers, 1.02 ± 0.05 mm, $U = 9.0$, $p = 0.023$) but remained unchanged in the other Erlangen colony ($U = 15$, $p = 0.81$) and the three Karelian colonies (with p -values > 0.2 ; Fisher's combined probability: $-2\sum \ln p = 5.46$, $p > 0.1$). When eclosing under cold conditions, workers from Erlangen were significantly smaller than workers from Karelia (10 workers each from Erlangen and Karelia, $U = 16.5$, $p = 0.011$).

Fasting endurance

Workers from Karelia survived starvation significantly longer at room temperature than workers from Erlangen (199 individuals, Gehan's Wilcoxon test, -2.894 , $p < 0.002$). Survival time was correlated with thorax length in the Erlangen colonies (Gamma = 0.253, $p < 0.005$), but not in the colonies from Karelia (Gamma = 0.058, $p = 0.417$). The results remained unchanged when individuals that died during the first five days of the experiment were excluded from the analysis to minimize the effect of handling on mortality (Erlangen, $n = 96$, Gamma = 0.277, $p < 0.001$; Karelia, $n = 86$, Gamma = 0.001, $p = 0.987$; Fig. 4). Because several individuals per colony were analyzed and colony of origin had an impact on both body size and survival time (Erlangen, survival time; $H = 39.85$, $p < 0.001$, body size: $H = 22.92$, $p < 0.002$; Karelia, survival time; $H = 31.69$, $p < 0.001$, body size: $H = 29.80$, $p < 0.001$), we investigated how body size and starvation resistance were correlated within individual colonies. Rank correlation coefficients (r_s) were > 0.1 in seven of eight Erlangen colonies and four of eight Karelian colonies,

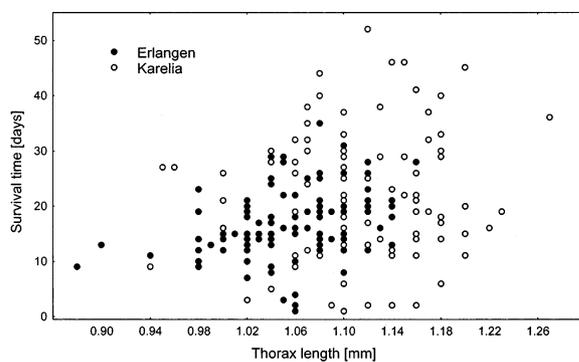


Fig. 4. Survival time of *Leptothorax acervorum* workers of different body size (thorax length) under starvation. Survival time was significantly associated with body size in the Erlangen population.

but none of these values was statistically significant after Bonferroni correction.

Survival time at cold temperatures was significantly correlated with thorax length in two workers each from 12 German, 6 Russian and 6 English colonies (Spearman rank correlation, $r_s = 0.493$, $p = 0.014$).

Absolute fat content increased with body size (Spearman rank correlation, Erlangen, $n = 96$, $r_s = 0.436$, $p < 0.001$; Karelia, $n = 89$, $r_s = 0.471$, $p < 0.001$; Fig. 5). However, the relative fat content remained constant (Erlangen: $r_s = -0.120$, $p = 0.2442$; Karelia; $r_s = -0.038$, $p = 0.723$).

Discussion

The body size of workers of the holarctic ant, *Leptothorax acervorum*, increases with latitude, a pattern previously observed in general in an interspecific comparison with European ants (Cushman et al. 1993). Body size variation in ectothermic animals might be adaptive or a non-selected consequence of the dynamics of cell growth. Our study suggests that larger body size in *L. acervorum* from boreal habitats might result from selection for increased fasting endurance.

We reared brood from two different populations, Erlangen in southern Germany and Cape Kartesh in Karelia, in common garden experiments under warm or cold conditions, respectively. Body size did not change in the direction expected from Van Voorhies' (1996) assumption that slow cell growth in cold climate leads to increased cell and body size. Ommatidium diameter did not differ between workers from the two populations. Assuming that because of the fixed architecture of insect eyes, ommatidia size reliably reflects the cell size of the photoreceptors, this could also be interpreted as evidence against larger cell size being exclusively responsible for larger body size.

Workers from both populations eclosing from brood reared under the same warm conditions did not differ

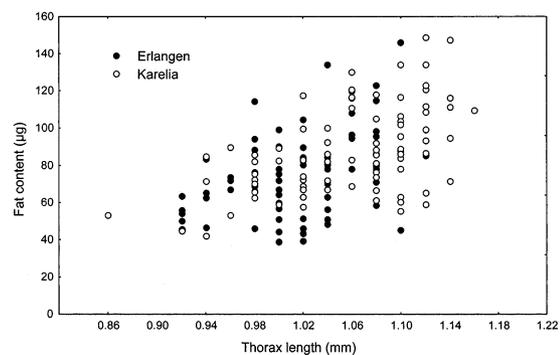


Fig. 5. Fat content in relation to body size (thorax length) in *Leptothorax acervorum* workers from Karelia and Erlangen.

in size, but the size differences observed in nature persisted under cold conditions. This suggests that body size is to some extent genetically determined though in the different populations it might follow different reaction norms. Larger worker size in Northern populations might therefore be adaptive.

Of the various hypotheses suggesting an adaptive cause for ectotherm animals following Bergmann's rule, most are not easily applicable to *Leptothorax* ants. For example, ants stay in their nests year-round and do not migrate to avoid cold climate. It is also unlikely that only the largest *L. acervorum* managed to re-immigrate into northern habitat after the end of glaciation. Though little is known on dispersal distance in ants, the low genetic differentiation among European populations does not suggest the occurrence of strong founder effects or bottlenecks (Heinze et al. 1995).

Relaxation of competition might lead to increased body size in areas with lower diversity (David and Capy 1982). In general, diversity and structure of ant communities differ strongly with latitude. For example, the number of ant species decreases from temperate to boreal areas (Kusnezov 1957), while the density of nests of some dominant taxa, such as wood ants (*Formica rufa* group) increases, *Leptothorax acervorum* is typically a subordinate ant with little interference with *Formica*, but wood ants might indirectly influence *L. acervorum* through effects on competitive relations with other taxa, such as *Lasius* and *Myrmica* (Savolainen and Vepsäläinen 1989). However, with a few exceptions (e.g., Aschaffenburg, Denali N.P.), the studied populations of *L. acervorum* were from dry coniferous forests with similar species number and composition of the ant community. The presence or absence of other *Leptothorax* species in a certain ant community might be more important. *Leptothorax* species that live syntopically differ more in size than expected from the size distribution of all species, and it was suggested that competition for food or, more likely, nesting sites has led to this character displacement (Foitzik and Heinze 1999). Larger size in the populations from the British Isles and northern Scandinavia might reflect a relaxation of competition, as other *Leptothorax* species, especially *L. muscorum*, do not occur in these areas. However, *L. muscorum* is widely distributed in Russia including our Karelian study sites (in contrast to Radchenko et al. 1999, Kipyatkov unpubl.). The increased body size of Russian *L. acervorum* therefore is unlikely to be a consequence of decreased competition between related *Leptothorax* species. The slave-making ant *Harpagoxenus sublaevis* and the workerless social parasite *Leptothorax kutteri*, which occasionally exploit colonies of *L. acervorum*, occur in both study populations, though perhaps in different abundance (Kipyatkov unpubl.), but are absent from the British Islands (Collingwood 1971, D'Etorre and Heinze 2001). Differences in the distribution of socially parasitic ants therefore also do

not explain the observed size differences in *L. acervorum*.

In several species of ants, worker size is positively associated with colony size, especially because small, founding colonies produce nanitic workers. In *L. acervorum*, average colony size differs considerably between populations. For example, colonies collected in Alaska lived in small cavities under sun-exposed pebbles and contained only a few dozen individuals (Heinze and Ortius 1991). In contrast, colonies from the Alps may live in extended nests under the bark of fallen trees or tree stumps and often contain thousands of ants (Bernard 1968). Average colony size did not differ strongly between the two best studied populations, and though there was a tendency for worker size to slightly rise with colony size in the Karelian population, the magnitude of the increase was not large enough to completely explain the observed body size difference between the populations. It has been suggested that large colony size might act as a buffer against food shortage in boreal habitat, leading to an increase of colony size with latitude among species (Kaspary and Vargo 1995). Our data do not support this hypothesis for *L. acervorum*, however, additional data are needed to uncover the proximate determinants of plasticity in colony size in this species.

Colony organization might similarly affect the body size of workers. Previous studies documented that colony structure, in particular the average number of queens per colony, differs between populations (Heinze et al. 1995). In the present study we did not find evidence for variation in body size being associated with variation in queen number.

Larger workers had absolutely more fat than small workers and in a fasting endurance experiment at room temperature, larger workers at least from the Erlangen population survived on average longer than smaller workers. Similarly, larger workers survived significantly longer than smaller workers when kept in isolation under cold temperatures. The observed cline in body size might therefore be associated with variation in starvation resistance. Laboratory studies with hibernating *Leptothorax* have shown that especially at the beginning of hibernation, the ants are active to some extent even at low temperatures, when foraging is not possible (Heinze et al. 1998). Dissection of individuals that died during hibernation revealed that their crops were empty, suggesting that some individuals starved during winter. *Leptothorax acervorum* might extend their survival time in areas with long winters and unpredictable climate just before and after hibernation by storing more reserves. It is not yet known whether fat content alone is responsible for the observed better survival of large workers at temperatures below freezing or whether additional size-related factors are involved. Previous work has shown that *L. acervorum* from boreal populations survive temperatures of

< -25°C due to the accumulation of antifreeze polyols in the hemolymph (Leirikh 1989), but whether polyol content depends on size has never been studied.

Finally, it cannot be ruled out that large worker size in boreal habitats might be a by-product of selection for larger body size in female and/or male sexuals. Queens from Karelia were significantly larger than queens from Erlangen. Though in both populations, queens may return into their maternal nests after mating and become fertile there, a certain percentage of queens might attempt to found their new societies solitarily. It is likely that variation in queen size is associated with variation in absolute fat content and that large queens have an advantage in independent colony founding. Increased worker size could therefore be a pleiotropic response to selection on starvation resistance of founding queens. Furthermore, forest succession and the availability of nest sites differ between boreal and temperate habitats (Seppä et al. 1995). Dry, pine-dominated forests remain much longer uninhabitable for *L. acervorum* than spruce-dominated forests in the boreal zone. Habitat longevity might affect the founding tactics and presumably also the body size of queens and – in the case of pleiotropic effects – also that of workers.

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