Worker polymorphism in the arboricolous ant *Liometopum microcephalum* (Hymenoptera: Formicidae: Dolichoderinae): Is it related to territory size?

Lenka PETRÁKOVÁ & Jiří SCHLAGHAMERSKÝ

Abstract

Liometopum microcephalum (PANZER, 1798) is a rare arboricolous ant, which forms large colonies of high ecological importance and ranks at the top position in the hierarchy of ant assemblages. Many aspects of the species' biology remain unknown due to its scattered occurrence and bad nest accessibility. Published information is sometimes inconsistent, such as in the case of worker polymorphism. Our objectives were (1) to determine the level of polymorphism, (2) to ascertain if workers occupied by different tasks differ in size, and (3) to assess the effect of competitors, habitat type and territory size (as a proxy for colony size) on worker size. Fifteen colonies, with or without a competing ant species in their vicinity, were sampled in spring and summer 2011 in the south-eastern part of the Czech Republic. Head width, head length, hind femur and tibia lengths were measured as indices of worker size. Territory areas, assessed during each sampling, served as an indicator of the size and vitality of individual colonies. Worker size variability was continuous, with a broad size range for all measured characters within each studied colony. We found different levels of polymorphism for measured body parts in individual colonies: isometry and simple, diphasic and triphasic allometry; in most colonies, the level changed in the course of time. Generally, workers collected in spring were larger than those collected in summer (p < 0.0001). We did not find any differences between workers performing different tasks outside the nest. We found a positive correlation between territory size and body size, represented by mean femur length (p = 0.0068). Territory size was affected by the presence of behaviourally dominant ant species (p = 0.0036), in particular *Lasius fuliginosus* (LATREILLE, 1798). We conclude that in contrast to information in literature the species is not truly dimorphic and even colonies seemingly made of workers of one size class contain a wide range of worker sizes.

Key words: *Liometopum*, worker size, polymorphism, allometry, territory, competitors.

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Introduction

The existence of polymorphism is closely connected to labour division within a colony of social insects and helps to increase colony fitness through more efficient exploitation of available resources (OSTER & WILSON 1978, WILSON 1980). Polymorphism arose many times in the phylogenetic history of ants (WILSON 1953). At present, 15 - 20% of all described ant species are said to have polymorphic workers (HÖLLDOBLER & WILSON 1990). Striking differences between worker castes present within one colony are seen mainly in tropical representatives such as in army ants (*Eciton* spp.) or leaf-cutting ants (*Atta* spp.). In the temperate zone, *Camponotus* and *Messor* are examples of ant genera occurring in Europe that have distinct worker castes. In ants with worker polymorphism, morphologically distinct worker individuals, which often perform specialized functions, are produced within a single colony. Typically, the majors (or soldiers) defend the nest and territory, whereas minors ensure brood care (HIGASHI & PEETERS 1990, SCHWANDER & al. 2005, MERTL & TRANIELLO 2009). In some species, morphologically distinct castes are replaced by age groups: Young workers stay inside the nest,

whereas elder workers perform tasks in the open. This is a case of polyethism (= behavioural change during an individual's life). Polymorphism and polyethism do not exclude each other and can both occur in the same species (MADI & JAFFE 2006). Some studies indicate that at least in some ant species the ratio between minor workers and major workers or soldiers can shift based on environmental conditions, in particular competition with other ant colonies of the same or other species (PASSERA & al. 1996, MCGLYNN & OWEN 2002, MCGLYNN & al. 2012).

Worker polymorphism is characterized by allometric growth of body parts. Particular morphs can differ not only in size and shape of some body parts (mostly head and mandibles; WILSON 1953) but also in physiological features (production of different gland secretions or hind gut enzymes; ROBINSON 2009). They can even have different qualities, for instance in terms of longevity, running speed or tolerance to high or low temperatures (CERDÁ & RETANA 1997). Size variation is not always determined by genetic factors (SCHWANDER & al. 2005). It seems that the nutrition of larvae is crucial for their future appearance as

adults (WHEELER 1991). During metamorphosis, tissues of a developing individual interact and compete for limited nutrients; thereby some body parts grow faster than others (NIJHOUT & WHEELER 1996). This disproportionate growth results in allometry (TSCHINKEL & al. 2003). Generally, well-fed larvae develop into majors, whereas starving larvae become minors. The number of individuals belonging to a given caste can be modified at colony level through hormonal regulation (WHEELER & NIJHOUT 1984). The degree of polymorphism can change during a colony's life (TSCHINKEL 1988). At least one reason is the high energetic cost of the production of large workers, hardly affordable for a newly established colony.

According to WILSON (1953) several levels of polymorphism, which respond to the evolution of castes, are distinguished. At the bottom of that hierarchy is monomorphism, which is characterized by isometric growth of body parts, a narrow range of size variability and a unimodal frequency distribution of measured sizes. The following, polymorphic, levels are characterized by allometry. Allometric growth can be expressed as $y = b * x^k$, where x and y represent two body parts, b is the initial growth index and k is a growth constant obtained as the slope of the regression line fitted to log-transformed data in a bivariate plot of the two measured body parts. In the case of allometry the slope of the line always differs from one. The lowest level is called monophasic (or simple) allometry: The frequency distribution of measured values is unimodal, the size variability is small, but its lower and upper extremes can represent functional castes. In diphasic allometry, the regression line breaks into two segments with different slopes, corresponding to minor and major workers; the frequency distribution is bimodal. Similarly, in the case of triphasic allometry, three line segments with different slopes are present, often forming a curve of sigmoid shape; the outer segments represent relatively stable minor and major worker castes, whereas the middle segment, representing intermediate workers, is often unstable. Stabilizing selection leads to complete dimorphism, which is considered to be the highest degree of polymorphism: There are two segments of the regression line, corresponding to minor and major workers, that are separated by a gap.

Liometopum microcephalum (PANZER, 1798) is a rare arboricolous ant of Pontomediterranean distribution in Europe and the Middle East. It forms large, sometimes polydomous, colonies of high ecological importance and behavioural dominance within ant communities (PETRÁKOVÁ & SCHLAGHAMERSKÝ 2011). Workers are aggressive and actively defend their territories. They are partly zoophagous, partly feed on honeydew and nectar (WIEST 1967, SCHLAGHAMERSKÝ & al. 2013). The species builds its nests within trunks or limbs of old and mighty trees, usually several metres above ground. Due to its limited distribution and bad nest accessibility, many aspects of the species' biology remain unknown. Published reports on the ant give a range of worker body length of 3 - 7 mm (EMERY 1916, STITZ 1939) and rather contradictory information on the level of polymorphism. According to EMERY (1912), *L. microcephalum* is monomorphic, whereas according to SHATTUCK (1992) the species is polymorphic, with minor workers lacking ocelli. However, according to AGOSTI & COLLINGWOOD (1987) all workers possess ocelli. According to SEIFERT (2007) the species is dimorphic, with only minors present in some colonies. Our observations on the large population in South Moravia (SCHLAGHAMERSKÝ & OMELKOVÁ 2007, PETRÁKOVÁ & SCHLAGHAMERSKÝ 2011, SCHLAGHAMERSKÝ & al. 2013) confirmed the occurrence of a wide range of worker sizes even within single colonies; moreover some colonies seemed to consist of substantially smaller workers than other colonies. The latter observation might be the consequence of the age and vitality of a colony: Presumably young (newly established) or very old (declining) colonies might produce mostly minors, the same could apply for mid-aged colonies barely surviving under adverse conditions.

Owing to the above-mentioned biology of the species it would be very difficult to measure the size, age and vitality of colonies. Thus we decided to study worker polymorphism in relation to territory area. Territory size should be correlated with colony size but may also reflect colony success in contests with competitors and food density in a given habitat. The shape and size of ant territories change in the course of time (e.g., AKINO & YAMAOKA 1999, TARTALLY 2006) as a consequence of resource preference and competition with neighbouring colonies (of the same as well as other species of similar requirements and competitive strength). We observed the same in *Liometopum microcephalum* during a preceding study (PETRÁKOVÁ & SCHLAGHAMERSKÝ 2011). Defending the territory can be costly and thus large and vital colonies are favoured. We hypothesized that vital and successful colonies, i.e., colonies with large territories, would produce workers of bigger size than colonies defending smaller territories.

In the present study we want to quantify worker size variability and to clarify the level of polymorphism in *Liometopum microcephalum*. Is it the same in all colonies within our study area? Does it change in the course of the annual activity period? Further we ask if worker size is connected to the different tasks performed by these individuals (defence, foraging) within a single colony. Finally, we investigate if worker size depends on the colony's territory size, the presence of major competitors or the type of habitat.

Methods

The study was carried out on 15 colonies of *Liometopum microcephalum* in South Moravia (south-eastern part of the Czech Republic). Five of the studied colonies neighboured with *Lasius fuliginosus* (LATREILLE, 1798) or *Formica rufa* LINNAEUS, 1761 colonies, another five were found close (less than 30 m) to another *L. microcephalum* colony (we first transferred several workers from one nest tree to the other and then observed the workers' reaction as to see if the workers belonged to the same or to two distinct colonies). The remaining five colonies had no nest of a strong competitor (in terms of behaviourally dominant ant species) in their vicinity. The study sites included three types of habitat, representing different conditions in terms of moisture and resource availability (nest sites, food resources): A landscape park with ancient oaks in meadows had the largest oaks of all compared habitats, with large interspaces partially filled by shrubs (site L – seven colonies), floodplain forests with oak as one of the dominant tree species had the highest density of trees, saplings and shrubs (sites: P – one colony, R – four colonies, Z – one colony) and a xerothermous forest (site M – two colo-

nies) that provided the least suitable conditions (lack of old trees of large diameter for nest building, lower vegetation density in comparison to the floodplain forests).

We sampled the colonies twice in 2011: In spring (from mid April to mid May) and in summer (from end of June to early August), except three colonies that were sampled only once due to their poor accessibility. At both times we collected the ants from the trunks of the nest trees. Furthermore, in spring we collected workers that were moving on trails in 5 - 10 metres distance from their nest trees. In the case of colonies neighbouring with competing colonies, we also sampled workers from their nest trees after induced enemy attacks (we transferred 20 - 30 workers of the competitor to the nest tree trunk and after 10 - 15 minutes we collected workers of the defending colony from this trunk segment) during the summer sampling. At each sampling date we drew maps of territories consisting of trails connecting nest trees with foraging trees and with patches on the ground where workers foraged, either individually or in foraging columns. Based on these maps we assessed the territory area for each colony and date separately.

The ants were sampled selectively, with the objective to capture workers of all sizes present and thus to record the entire size variability. From each group of workers (collected from nest trees, from trails and from nest trees after induced enemy attacks) we measured 50 individuals. Maximal head width (HW), head length (HL; from lower margin of clypeus to the end of vertex), hind femur length (FL), and hind tibia length (TL) were measured. Head width is the most variable character in polymorphic ant species (WILSON 1953, ARAUJO & TSCHINKEL 2010) whereas femur length rather correlates with total body size. As shown, for instance, in *Solenopsis invicta* BUREN, 1972, the relation between leg length and total body size is isometric (TSCHINKEL & al. 2003). Therefore femur length served as an index of worker body size in our study. We did not measure total worker size to avoid bias caused by variable gaster size – workers returning from foraging trees back to the nest may have a markedly larger gaster than others due to honeydew collection (SCHLAGHAMERSKÝ & al. 2013). Additionally, we analysed workers conserved in ethanol from the inner part of a nest. This sample had been collected by our colleague M. Omelková from an oak immediately after its uprooting in summer 2005 (also in South Moravia). Larvae and pupae prevailed in the sample. We measured all 119 workers in the sample to assess the body size of workers taking care of the brood.

Statistical analysis: All statistical analyses were done in R 2.10.1. software (R DEVELOPMENT CORE TEAM 2011). The analyses script is available in the Appendix S1 (as digital supplementary material to this article, at the journal's web pages). For each colony and date we constructed bivariate plots of the measured body parts to determine the degree of polymorphism, with the femur length always depicted on the x-axis. We also plotted frequency distributions of the measured sizes to see if the variability of sizes was continuous or not. The workers were then divided into groups corresponding to the number of segments (clouds of points) using k-means cluster analysis (HARTIGAN & WONG 1979). That method allows partitioning the data points into k groups by finding the minimal sum of the within-groups sum of squares (BORCARD & al. 2011). We

fitted regression lines through each group of points in all bivariate plots and assessed their slopes (outliers were excluded from the analysis only when their Cook's distances were higher than 0.5). Differences between slopes of regression lines found in a given colony per sampling date were tested using analysis of covariance (e.g., HW = α + βFL + FL : group). If an interaction between continuous (FL) and categorical (group) variables was significant on a p-level lower than 0.1, the slopes of the fitted regression lines were considered different (p-levels under 0.05 indicated diphasic allometry, or dimorphism – when there was a gap between two segments, or triphasic allometry – when there were three segments; p-levels between 0.1 and 0.05 indicated slightly diphasic allometry). The approximate position of breakpoints was then assessed as the range between the maximal value measured in the group of "minor" workers and the minimal value in the group of "majors". If there were no differences between the slopes representing "minors" and "majors", a single slope was calculated for all data points representing given body parts measured for a single colony at a given date. Such colonies were considered to be simple allometric or isometric (if the slopes of the regression lines did not differ from 1). Allometric relations were tested also with ANCOVA as differences of the given slopes from a slope equal to 1.

To compare groups of workers collected from nest trees and from trails as well as from nest trees before and after induced competitor attack we used a Linear Mixed Model (lme function in nlme package; PINHEIRO & BATES 2000) with "colony" as random effect, which takes into account possible differences between individual colonies. Additionally, we tested the differences in head widths and femur lengths with the t-test, for each colony separately. The same approach was used in comparing sizes of workers collected in spring and summer.

To assess the dependence of worker size on territory size as well as the effect of season, competitor and type of habitat, we used marginal models with General Least Squares function (nlme package, PINHEIRO & BATES 2000). As almost all colonies were sampled two times, measurements were not independent, so we inserted correlation structure (compound symmetry correlation) into the models, taking colony identity into account. Two datasets were tested: The first included all measured workers, the second the average values calculated from the largest and the smallest worker sampled per colony and sampling date (i.e., one data point per colony and sampling date). The latter values were used to avoid bias caused by sampling – in some colonies a higher percentage of majors than in others could have been sampled accidentally.

Results

Worker size variability, degree of polymorphism: We found a broad range of measured sizes for all characters in every studied colony. Head width (HW) varied from 0.825 mm (± 0.044 mm SD; average of minimal values measured in each colony) to 1.634 mm (± 0.068 mm SD; average of maximal values), head length (HL) varied from 0.806 mm (± 0.06 mm SD) to 1.542 mm (± 0.109 mm SD). Femur length (FL) varied from 0.794 mm (± 0.076 mm SD) to 1.532 mm (± 0.052 mm SD) and tibia length (TL) varied from 0.731 mm (± 0.071 mm SD) to 1.460 mm (± 0.053 mm SD) on average. All measurements are avail-
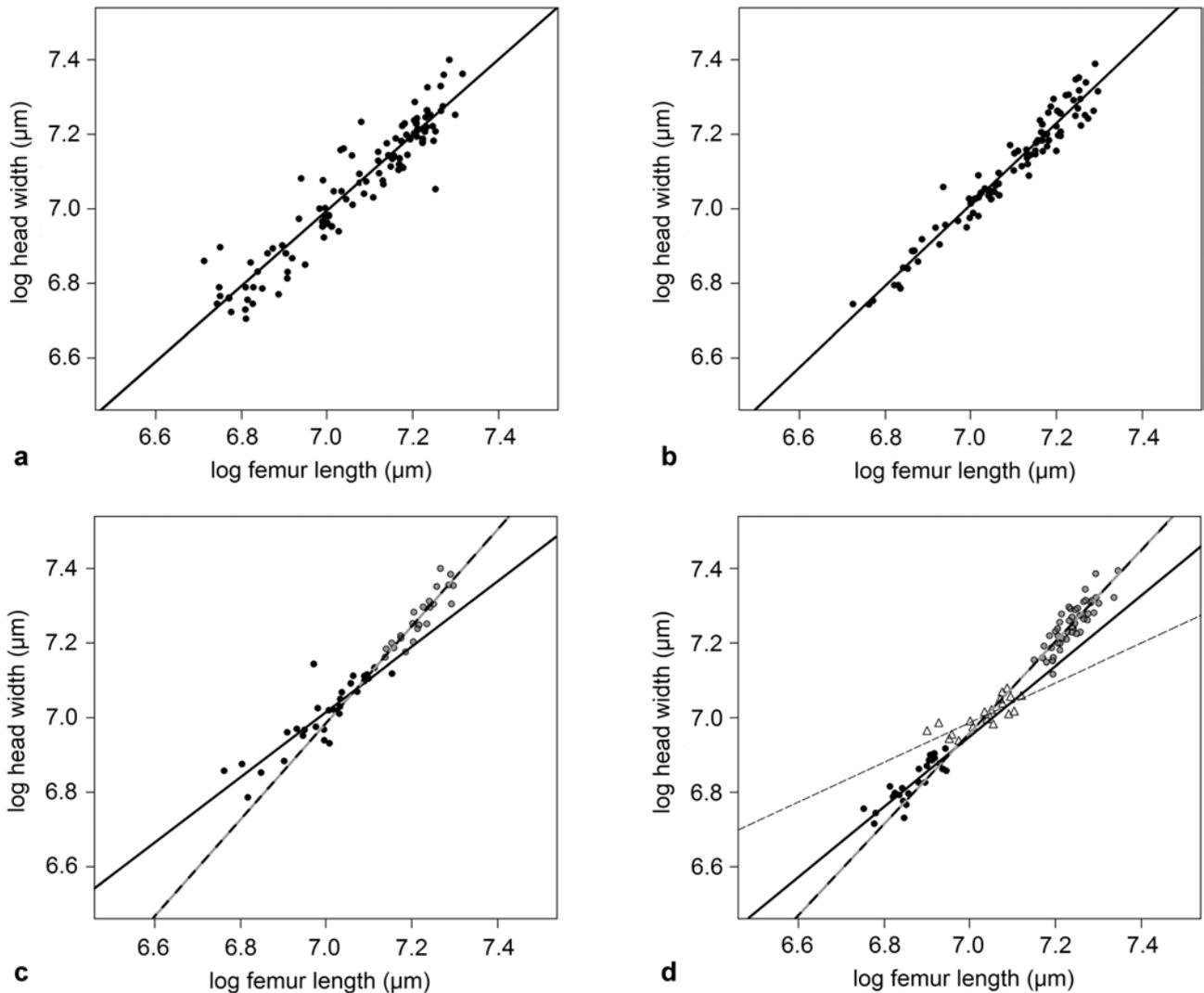
Fig. 1: Examples of different allometric relations between head width and femur length. Points show individual ant workers, lines show the fitted regressions with different slopes. a) Colony L3 (park landscape, close to another *Liometopum microcephalum* nest): isometry in summer; b) colony Z1 (floodplain forest, without competitor): simple allometry in spring; c) colony R3 (floodplain forest, close to another *L. microcephalum* nest): diphasic allometry in summer – minors = black, majors = grey; d) colony R2 (floodplain forest, close to *Lasius fuliginosus* and *Formica rufa* nests): triphasic allometry in summer – minors = black, majors = grey, intermediates = white triangles. See Table 1 for slope values.

able in the Appendix S2. Frequency distribution plots as well as bivariate plots showed that the worker size variability was continuous without any conspicuous gap between minors and majors.

Different body parts had often different degrees of allometry, even within the same colony. We detected both positive ($k > 1$) and negative ($k < 1$) allometries and also isometry ($k = 1$). The TL / FL relationship was in most cases isometric whereas the HW / FL relationship was mostly simply allometric or diphasic (see Tab. 1). Colonies varied in allometries also in the course of the season. One colony (R2) that had been diphasic in spring was triphasic in summer (Fig. 1).

In spring, slopes of regression lines varied from 0.808 to 1.233 for the HW / FL relationship, from 0.859 to 1.113 for HL / FL and from 0.695 to 1.103 for TL / FL. In summer, they varied from 0.532 to 1.300 for the HW / FL relationship, from 0.594 to 0.994 for HL / FL and from 0.777

to 1.168 for TL / FL. In those cases in which R^2 values were low and SE values high in the regression models (Tab. 1) this was the consequence of low numbers of individuals within the corresponding groups or of a small range of worker sizes within the groups. In colonies with diphasic allometries, the breakpoints of the regression lines were situated approximately between 1.10 mm and 1.30 mm of femur length (variation between colonies). Workers with femur lengths above these values had ocelli, whereas minor workers lacked them. In the case of triphasic allometry two breakpoints were present (at 0.99 - 1.04 mm and 1.16 - 1.24 mm of FL). Intermediate workers did not have true ocelli but instead only three small dark and raised planes could be recognized in their place.

In spring 2011, we found in one colony (L3, neighbouring with two other *Liometopum microcephalum* colonies) two individuals distinctly different from the rest of the measured workers. These had conspicuously large, rounded

Tab. 1: Slopes of the regression lines fitted into bivariate plots. The p-values show the significance of differences between the slopes of the regression lines. In cases of simple allometry the values resulting from testing the difference between groups obtained by k-means cluster analysis are presented in brackets. Where two values are given in one row, the top values correspond to the group of minor workers and the bottom ones to that of majors. R^2 (coefficient of determination) indicates the quality of the fitted regression model. Abbreviations: BP = breakpoint, HW = head width, HL = head length, TL = tibia length, FL = femur length.

Colony	Ratio	Spring							Summer						
		Allometry	BP (µm)	p	Slope	SE	R^2	Df	Allometry	BP (µm)	p	Slope	SE	R^2	Df
Z1	HW / FL	simple	–	(0.6739)	1.094	0.03	0.95	98	simple	–	(0.11)	1.073	0.03	0.96	47
	HL / FL	isometry	–	(0.8883)	0.969	0.03	0.90	98	simple	–	(0.919)	0.920	0.03	0.94	47
	TL / FL	isometry	–	(0.5612)	0.998	0.03	0.92	98	isometry	–	(0.8778)	1.007	0.04	0.94	48
L1	HW / FL	slightly diphasic	1141-1265	0.0612	1.030 0.809	0.05 0.10	0.91 0.50	34 60	simple	–	(0.4438)	1.085	0.03	0.92	97
	HL / FL	simple	–	(0.2063)	0.913	0.04	0.82	98	simple	–	(0.7553)	0.932	0.03	0.89	97
	TL / FL	simple	–	(0.2451)	0.920	0.03	0.89	98	isometry	–	(0.4000)	1.021	0.03	0.94	96
L2	HW / FL	isometry	–	(0.8621)	1.045	0.04	0.88	98	simple	–	(0.1492)	1.115	0.03	0.95	97
	HL / FL	isometry	–	(0.5364)	0.953	0.04	0.85	98	isometry	–	(0.3029)	0.953	0.03	0.93	97
	TL / FL	isometry	–	(0.9577)	0.973	0.03	0.91	98	isometry	–	(0.4671)	0.960	0.03	0.93	97
L3	HW / FL	diphasic	1248-1257	0.0409	0.808 1.076	0.08 0.10	0.77 0.64	30 66	isometry	–	(0.4407)	1.017	0.04	0.88	98
	HL / FL	isometry	–	(0.1530)	0.962	0.04	0.84	98	simple	–	(0.1468)	0.917	0.03	0.88	98
	TL / FL	isometry	–	0.1033	0.998	0.03	0.93	98	simple	–	(0.8135)	0.958	0.02	0.94	98
L4	HW / FL	simple	–	(0.1716)	1.097	0.03	0.93	96	simple	–	(0.9639)	1.242	0.05	0.94	46
	HL / FL	isometry	–	(0.4632)	0.962	0.04	0.87	97	isometry	–	(0.4782)	0.985	0.04	0.91	46
	TL / FL	slightly diphasic	1210-1236	0.0728	1.103 0.900	0.08 0.08	0.83 0.71	39 57	diphasic	1237-1279	0.0237*	0.777 1.168	0.18 0.18	0.49 0.64	31 10
L5	HW / FL	simple	–	(0.3864)	1.069	0.04	0.88	98	simple	–	(0.6448)	1.098	0.02	0.98	95
	HL / FL	isometry	–	(0.8589)	0.978	0.04	0.89	98	diphasic	1150-1173	0.0026*	0.629 0.886	0.07 0.05	0.75 0.80	28 68
	TL / FL	isometry	–	(0.5868)	1.008	0.03	0.91	98	isometry	–	(0.8161)	0.994	0.02	0.94	97
L6	HW / FL	simple	–	(0.9011)	1.070	0.03	0.92	98	simple	–	(0.5274)	1.146	0.05	0.93	47
	HL / FL	diphasic	1221-1261	0.0193*	0.982 0.860	0.05 0.08	0.92 0.64	27 68	isometry	–	0.9122	0.982	0.05	0.90	47
	TL / FL	isometry	–	(0.5897)	0.965	0.03	0.94	98	isometry	–	(0.4457)	1.052	0.03	0.95	48
L7	HW / FL	diphasic	1243-1268	0.049*	1.020 1.233	0.06 0.09	0.90 0.77	30 62	slightly diphasic	1163-1184	0.0689	0.950 1.028	0.08 0.08	0.92 0.83	12 33
	HL / FL	diphasic	1243-1268	0.0561	0.859 1.113	0.08 0.11	0.80 0.64	30 62	simple	–	(0.5102)	0.949	0.03	0.97	47
	TL / FL	isometry	–	(0.2929)	0.998	0.02	0.95	98	isometry	–	(0.6819)	1.013	0.03	0.95	47

heads (HW: 1.71 and 1.72 mm) disproportionate to their rather small bodies (FL: 1.42 and 1.35 mm) and, in particular, to their small gasters.

We found differences in worker size between the two sampling dates: In most colonies workers were bigger in spring than in summer (Fig. 2). These differences were significant in five colonies (Welch Two Sample t-test; R2 – FL: t = 2.57, df = 190, p = 0.0109; R3 – HW t = 3.99, df = 89, p = 0.0001, FL: t = 4.23, df = 88, p < 0.0001; R4 – HW: t = 5.55, df = 197, p < 0.0001, FL: t = 4.73, df = 198, p < 0.0001; L3 – HW: t = 2.82, df = 198, p = 0.0053, FL: t = 2.34, df = 197, p = 0.0202; L6 – FL: t = 2.55, df = 101, p = 0.0122). Only in one case were workers significantly smaller in spring than in summer (Welch Two Sample t-test, HW: t = -2.68, df = 104, p = 0.0086; FL: t = -2.51, df = 113, p = 0.0133): That colony (L4) was situated in a landscape park and neighboured two independent *Liometopum microcephalum* colonies. When all colonies were tested together, the difference between spring and summer was also significant (LME; FL: F = 39.45, df = 2533, p < 0.0001; HW: F = 32.81, df = 2533, p < 0.0001).

Worker size versus task partitioning: Workers collected on nest trees had a similar size as the workers collected on trails (LME; HW: F = 0.705, df = 1484, p =
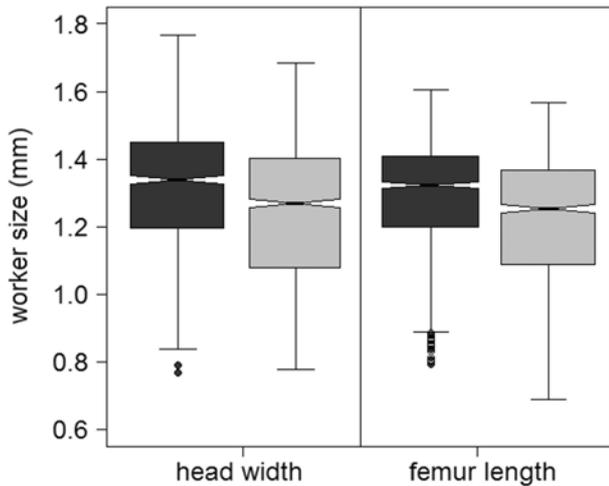
Fig. 2: Measured sizes (head width and femur length range) of workers collected in spring (shown in dark grey) and in summer (in light grey). Measured values: medians (bars) with 95% confidence limits (notches), 25 - 75% quantiles (boxes), 1.5 interquartile ranges (whiskers) and outliers (dots); sample sizes: 1300 workers were measured in spring, 1249 workers in summer.
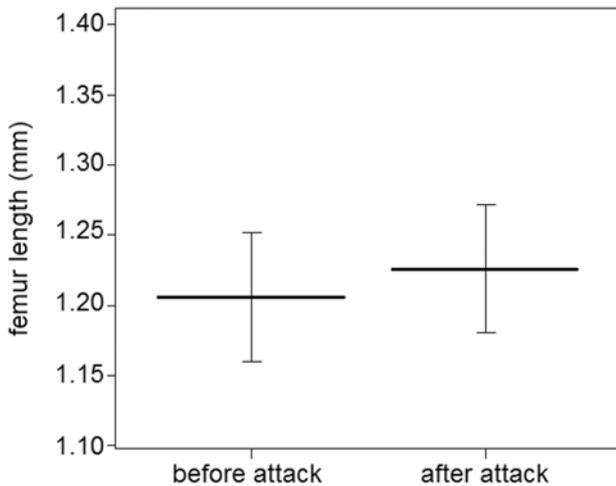

Fig. 3: Size of workers (femur lengths) collected before and after simulated attacks in spring 2011. Values predicted using Linear Mixed Models (LME): femur length mean values with 95% confidence intervals; sample size: 900 workers (450 workers measured before and 450 workers after the attacks).

0.4013; FL: F = 0.027, df = 1484, p = 0.8695). Testing individual colonies, none showed significant differences in this respect.

Workers collected after simulated attacks were somewhat larger than workers collected before these attacks, however, only in one of nine colonies this difference was statistically significant (R1, situated in a wet forest and neighbouring with a *Lasius fuliginosus* colony; Welch Two Sample t-test; HW: t = -2.88, df = 98, p = 0.0049; FL: t = -2.9, df = 98, p = 0.0046). When workers from all colonies were tested together the difference between the size of workers collected before and after an attack was not statistically significant (LME; HW: F = 2.121, df = 889, p = 0.1456; FL: F = 2.877, df = 889, p = 0.0902; Fig. 3). We
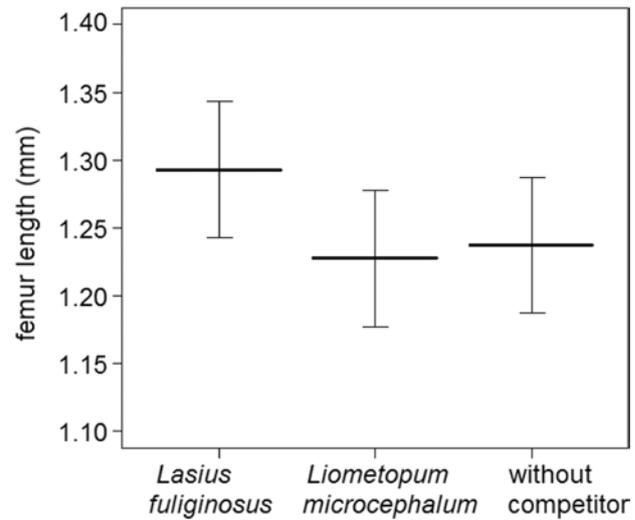

Fig. 4: Differences in femur lengths of *Liometopum microcephalum* workers depending on the presence of a competitor (either *Lasius fuliginosus* or another colony of *L. microcephalum*). Values predicted using marginal models with General Least Squares function and correlation structure: femur length mean values with 95% confidence intervals; sample size: 2550 workers (900 workers collected from colonies neighbouring *L. fuliginosus* colonies, 900 workers from colonies adjacent to other, hostile *L. microcephalum* colonies and 750 workers from colonies not adjacent to colonies of any strong competitor).

repeated the experiment with simulated attacks in spring 2012 using five of the previously studied colonies. However, neither differences in head width nor in femur length were significant. We did not find any additional workers with conspicuously big heads.

We compared worker sizes of individuals collected from the inside of a nest (including also numerous brood; collecting site: Lednické rybníky, summer 2005 – exact sampling date unknown, leg. M. Omelková) with those of every colony sampled by us in 2011. The workers from most of our colonies (n = 11) were significantly smaller than the workers found inside the nest (Welch Two Sample t-test; FL: M1 - t = -4.067, df = 260, p < 0.0001, M2 - t = -7.141, df = 242, p < 0.0001; Z1: t = -6.455, df = 256, p < 0.0001; L1: t = -4.518, df = 228, p < 0.0001; L3: t = -5.676, df = 269, p < 0.0001; L4: t = -3.449, df = 238, p = 0.0007; L5: t = -3.848, df = 257, p = 0.0002; L7: t = -2.666, df = 265, p = 0.0081; R2: t = -4.402, df = 286, p < 0.0001; R3: t = -2.003, df = 251, p = 0.0463; R4: t = -10.68, df = 246, p < 0.0001). Only one colony (P1, situated in a floodplain forest and neighbouring with a *Lasius fuliginosus* colony) consisted of workers that were larger than those sampled inside the nest (Welch Two Sample t-test; FL: t = 3.263, df = 210, p = 0.0013). We found diphasic allometry in the workers collected from the nest (slopes of regression lines in HW: k1 = 0.884, k2 = 1.112, slopes significantly different: p = 0.0096).

Factors potentially affecting worker size: When we used all measured femur lengths for modelling of the relationship between worker size and all explanatory variables, we found that the sampling date had a crucial effect on the worker size (femur length). Workers collected in spring were bigger than workers collected in summer (GLS:
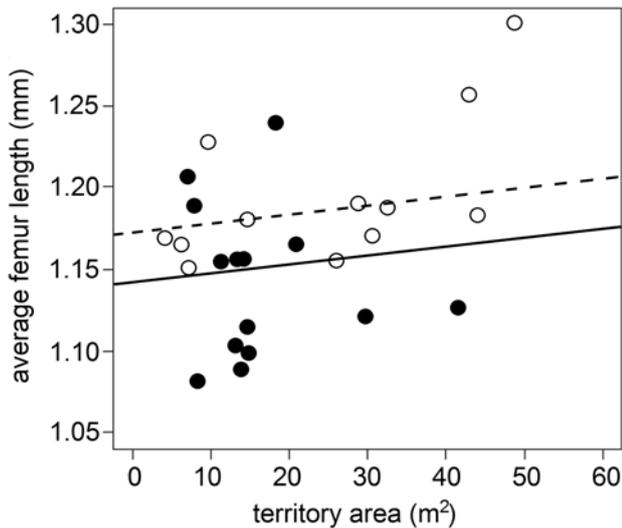
Fig. 5: Differences in femur lengths of *Liometopum microcephalum* workers depending on territory area and sampling date. Measured values: white circles = mean femur lengths in spring, black circles = mean femur lengths in summer; values predicted using marginal models with General Least Squares function and correlation structure: dashed line = correlation between territory area and mean femur length in spring, solid line = correlation between territory area and mean femur length in summer.
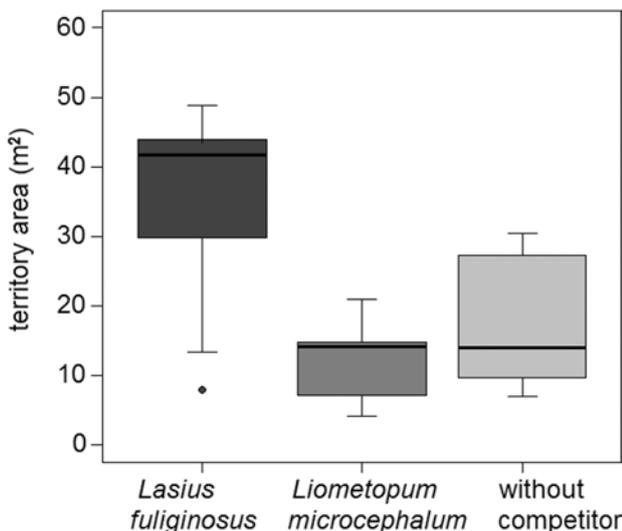

Fig. 6: Differences in territory area depending on the presence of competitors. Measured values: medians (bars), 25 - 75% quantiles (boxes), 1.5 interquartile ranges (whiskers) and outliers (circles); sample size: 27 territories of 15 *Liometopum microcephalum* colonies were measured, 13 in spring, 14 in summer.

F = 39.2, df = 2549, p < 0.0001). The second most important, albeit only marginally significant, explanatory variable was the territory size (GLS: F = 3.51, df = 2549, p = 0.0612). Colonies neighbouring with *Lasius fuliginosus* nests consisted of the biggest workers (Fig. 4). However, taking into account colony identity, the differences were not statistically significant (GLS: F = 1.95, df = 2549, p =

0.1426). Differences between colonies neighbouring with *L. fuliginosus* and those neighbouring with other *Liometopum microcephalum* colonies were marginally significant (t = -1.82, df = 2549, p = 0.068). Furthermore, we found a positive correlation between territory size and mean femur length (i.e., mean of the smallest and the largest worker collected in a given colony; GLS: F = 8.78, df = 27, p = 0.0068; regression coefficient = 0.5433; Fig. 5). Also the sampling date had a significant effect in this model (GLS: F = 4.42, df = 27, p = 0.0462). Territory size was affected by the presence of competitors (GLS: F = 3.81, df = 27, p = 0.0366). Colonies neighbouring with *L. fuliginosus* had the largest territories of all studied colonies (Fig. 6), differing in size from colonies neighbouring with other *L. microcephalum* colonies (t = -2.58, df = 27, p = 0.0163). We did not find any relationship between territory size and type of habitat. Neither territory area nor average worker size affected the level of polymorphism.

Discussion

Based on our results we consider *Liometopum microcephalum* a polymorphic species – in all studied colonies always at least one measured body part showed an allometric relationship with femur length. Worker size variability was in all colonies continuous on a broad size range for all measured characters, i.e., worker size changed gradually and no distinct morphs were detected. The range of femur lengths was a bit smaller than the head width range.

Bivariate plots are often used to visualize physical variability of ant workers (e.g., WILSON 1953, ESPADALER & al. 1990, WHEELER 1991, FERNÁNDEZ & al. 1994, FRASER & al. 2000, TSCHINKEL & al. 2003). Our results showed that different body parts had sometimes different degrees of allometry, even within the same colony. We found variability in slopes among colonies, however no correlation (not even a trend) with the presence of competitors, territory size or type of habitat was observed. We consider the colonies to be simply allometric only when the difference of their slopes was above p = 0.1, because even some colonies differing, e.g., at p = 0.08 seemed markedly diphasic in the bivariate plots. As the worker size changed in the course of time, so did the slopes of regression lines in the bivariate plots. Caste structure is not a fixed characteristic – it can change with colony age and size (TSCHINKEL 1988). However, we did not observe any pattern in these changes. In summer, the regression lines were "broken" and in a few cases the number of workers decreased near these breakpoints.

The bivariate plots showed that workers with femur lengths exceeding 1.2 mm prevailed in most colonies. This could have been caused by unintentional selective sampling in the field. However, the breakpoints in the bivariate plots were situated near this value. Workers with a femur longer than 1.2 mm usually possessed ocelli. This was in agreement with SHATTUCK (1992), who pointed out the presence of ocelli in majors only. Intermediate workers had only rudiments of ocelli and we did not find any traces of ocelli in minor workers. However, this was also true in colonies with simple allometry and even isometry. We did not find any case of a distinctly dimorphic colony. Dimorphism is characterized by the absence of intermediates, whereas in partial dimorphism at least one measured character forms a continuous chain of points in the bivariate

plot and the frequency distribution is bimodal (WILSON 1953). The low number of intermediate workers can be interpreted as a consequence of stabilizing selection, which leads to the existence of distinct morphs. We observed a similar pattern in two diphasic colonies (L7, R1), which can be interpreted as a tendency to partial dimorphism in summer. In another three simply allometric colonies (L3, L4 and L5) we also noted lower numbers of individuals with femur lengths approaching 1.2 mm.

Workers collected from the trails were approximately the same size as workers collected from nest trees. The nest of this species is in most cases situated high up in the trunk or in large limbs and thus trails are also present on the tree trunk. The nest trees were occupied exclusively by *Liometopum microcephalum* workers, and we had assumed that the proportion of larger workers would increase with the distance from the nest trees and thus with an increasing probability of enemy attacks. Majors should be better adapted to move far from the nest – e.g., they have longer legs than minors and their bodies lose water more slowly than minors (LIGHTON & al. 1994). However, also the opposite distribution of majors and minors in space can be found, for instance in the driver ant *Dorylus molestus* (GERSTÄCKER, 1859), in which soldiers were found to be more abundant in the vicinity of nests containing brood than in outer parts of its territory (BRAENDLE & al. 2003). We did neither find larger *L. microcephalum* workers to be more frequent in greater distance from their nest trees than on its trunk, nor the opposite. Also minor workers moved far away from their nest trees or even close to enemies during attacks. PFEIFFER & LINSENMAIR (2001) had observed the same in *Camponotus gigas* (LATREILLE, 1802). A broad range of worker sizes participating in foraging allows better exploitation of various food items and prey of a broader size range (DAVIDSON 1978).

Of the almost 3000 workers measured, only two individuals were conspicuously different from the others. Originally, we assumed that they were representing a distinct soldier caste, because soldiers are often big-headed. Soldiers of *Pheidole obtusospinosa*, for example, plug the nest entrance with their heads and thus prevent enemies to intrude into the nest (HUANG & WHEELER 2011); the same adaptation occurs in *Camponotus truncatus* (SPINOLA, 1808) (SEIFERT 2007) and in the genus *Cephalotes* – according to POWELL (2009) this is a morphological adaptation having direct consequences for colony reproduction. That was the reason why we tried to induce defensive reaction through simulated enemy attacks on the nest trees and thus to provoke the appearance of these soldiers. We did not find any additional individuals of that appearance during these trials. We undertook another attempt to get hold of additional specimens of this assumed soldier caste in April 2012, when we sampled five colonies at the same site where the two aberrant specimens had been collected before (we supposed that more soldiers could be produced in spring, when colonies establish their territory borders). Despite this effort we did not succeed in finding any similar individuals. We cannot confirm the existence of a distinct soldiers caste just based on the two individuals found. A more probable explanation could be that they presented an aberration. For instance, we cannot exclude a possible effect of parasites, which can induce morphological changes in ants, such as differences in shape and size of the head, mesonotum and

petiolus or missing ocelli (WHEELER 1928, TRABALON & al. 2000, CSŐSZ 2012).

We expected a higher percentage of minors inside the nest – smaller workers should be more vulnerable and slower than larger workers. Based on the comparison of workers found inside of a nest (the only sample from inside a nest available to us, collected in 2005) with all workers collected in 2011, the opposite seems to be true. However, the nest sample had been taken at a different site (although in the same area) from a downed tree (the colony therefore later ceased to exist) and no corresponding sample of ants collected outside the nest (and under undisturbed conditions) had been taken. On the other hand, we can hardly imagine that workers of this colony moving outside the nest could have been larger than those found within the nest, which were of extraordinary size.

Colonies were sampled two times per year: In spring, when workers were searching for new food resources and often moved in foraging columns on the ground, and in summer, when workers ran mainly along trunk trails leading to foraging trees or other permanent food resources. That was the reason why the assessed territory areas were larger in spring than in summer. Workers collected in spring were obviously individuals that had overwintered. Large workers are more resistant to suboptimal conditions and live longer than minors (PORTER & TSCHINKEL 1985b). When a colony is starving or the queen dies or ceases oviposition for long periods of time, the majors : minors ratio rises. For instance, in the genus *Solenopsis*, majors are much more numerous than minors in early spring because of a seasonally high rate of brood production (MARKIN & DILLIER 1971, MARKIN & al. 1974). Thus one explanation of the difference in worker body size between spring and summer may be that the workers were representatives of different, albeit overlapping, generations.

All studied colonies were at least five years old (i.e., had been observed in other studies before, e.g., SCHLAGHAMERSKÝ & OMELKOVÁ 2007, PETRÁKOVÁ & SCHLAGHAMERSKÝ 2011), thus potential effects of colony age were likely negligible. According to GORDON (1995), territory size in *Pogonomyrmex barbatus* (SMITH, 1858) (Myrmicinae) changes rapidly until five years after colony foundation, and then colonies become fully mature. Territory size changes over time as a consequence of resource preferences and interactions with competitors. Costs of territory defence are closely connected to costs of the production of majors or soldiers. Immediately after colony founding, all workers are very small as production of major workers is quite costly and the colony invests energy into the increasing of the worker number instead. In the course of time increasingly larger workers are produced and once a colony reaches sufficient size a new worker caste can arise (HÖLLDOBLER & WILSON 1990). Worker size polymorphism should be positively correlated with colony age (WOOD & TSCHINKEL 1981) and negatively correlated with the intensity of competition (DAVIDSON 1978). Our results do not support the latter hypothesis.

The biggest workers were noted in colonies neighbouring with *Lasius fuliginosus* nests. These colonies also occupied the largest territories. *Lasius fuliginosus* is an important competitor of *Liometopum microcephalum*. Both exploit to a large extent the same resources in terms of food and habitat (*L. fuliginosus* is also preferably arboricolous).

Lasius fuliginosus is able to combat *L. microcephalum* very successfully, using effective chemical weapons, whereas the strength of *L. microcephalum* is based on the quantitative preponderance of workers biting with their sharp mandibles (PETRÁKOVÁ & SCHLAGHAMERSKÝ 2011). If a colony of *L. microcephalum* can survive close to a *L. fuliginosus* nest, it must be strong enough to withstand its competition as well as direct confrontation. We propose that selective pressure in that case could lead to increased production of workers with big body size. According to MCGLYNN & OWEN (2002) the presentation of clumped food baits, which had been shown to attract more competitors, leads to an increased production of soldiers in the dimorphic, tropical *Pheidole flavens*. They assumed that both inter- and intraspecific competition were probable factors. On the other hand, we hypothesize that *L. microcephalum* colonies neighbouring with conspecific colonies (thus having the very same niche) limit each other in terms of colony growth and therefore small-bodied workers prevail. However, we have to say that PASSERA & al. (1996) found a higher percentage of soldiers in colonies of the tropical *Pheidole pallidula* (NYLANDER, 1849) experimentally exposed to intraspecific competition compared to colonies without contact with conspecific competitors.

Positive correlation between worker size and colony size was noted in many ant genera (GRAY 1971, PORTER & TSCHINKEL 1985a), the same holds for colony size and territory area (TSCHINKEL & al. 1995). Younger colonies, which have usually lower competitive strength, are generally only able to defend small territories. We considered the territory size as an indicator of the colony's vitality and success in competition. In accordance with this assumption, we observed a positive correlation of worker body size with territory area. If a colony reaches a stable size (in terms of worker number) and has optimal conditions for further growth, it begins to produce sexuals and major workers. If the colony is successful, it can consist of larger workers than a colony living under suboptimal conditions. Moreover, the level of polymorphism could be affected by the availability of food resources because the nutrition of larvae is important for worker development. Colonies consisting of workers with smaller body size have lower resource-holding potential in comparison with colonies of the same species that have larger workers (BATCHELOR & BRIFFA 2010). Another aspect that we did not consider in our study is the genetic structure of colonies. As shown for the ant genus *Pheidole*, the number of matings of the queen with different males correlates positively with the diversity in worker body size within a colony (HUANG & al. 2013).

We summarize that worker size variability in *Liometopum microcephalum* was high both within colonies and among colonies. Colonies having four different levels of polymorphism were found within a small part of the species' distribution area. Small workers did not possess ocelli, in somewhat larger workers only rudimentary ocelli were present, whereas the ocelli of larger workers were well developed. Worker size within a colony was positively correlated with territory size and marginally with the presence of a strong competitor. Workers collected in summer were smaller than those collected in spring. We found no effect of the type of habitat on worker size (but we had only a small sample from dry oak-hornbeam forests due to the rare occurrence of the species in this habitat in our study area). Not a single distinctly dimorphic colony was found within the South Moravian population of *L. microcephalum*.

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