Eur. J. Entomol. **96**: 117–124, 1999
ISSN 1210-5759

Site latitude influences on respiration rate, fat content and the ability of worker ants to rear larvae: A comparison of *Myrmica rubra* (Hymenoptera: Formicidae) populations over their European range

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Key words. Formicidae, *Myrmica*, ants, latitude, longitude, respiration, edge-of-range, brood-rearing, fat-content

Abstract. *Myrmica rubra* is a northern, temperate Palaearctic ant species with a geographical range that extends from the Atlantic coast of Europe to central Asia. In Europe, its range covers > 25° of latitude where it lives under a variety of climates that vary from extreme oceanic in the west, to continental in the east. Colonies nest in the soil and their life cycles are known to be highly dependent on ambient temperature and soil moisture. We hypothesised that the brood-rearing behaviour of populations might be locally adapted to climate and that we might detect differences when the ants were reared under "common-garden" conditions. Brood-rearing behaviour was compared for 38 colonies of *M. rubra* drawn from 13 populations representing a range of 6 latitudes: all 6 were represented in eastern Europe and 2 in western Europe. A sample of ants from each colony was used to estimate respiration rate, body mass and fat content at the start of the experiment in spring (immediately post hibernation) and at the end of the experiment (mid summer). Respiration had a linear relationship with latitude, with northern populations having greater respiration rate in spring compared to southern populations. It is suggested that this is an adaptation to different seasonality over the species' range that results in the "more active" northern workers rearing fewer brood to maturity more quickly than southern workers. Fat content, a measure of worker "quality", had a parabolic relationship with latitude with mid latitude colonies having the fattest workers. Fatter workers appeared to rear heavier brood. This probably represented a functional response to environment with populations living at "edge of range" sites being physiologically more stressed and performing brood-rearing tasks less well than centre of range populations. We believe that this is the first demonstration of a consistent, intra-specific trend for variation in the social physiology of an ant species over its geographic range.

INTRODUCTION

Most ant species nest in the soil where they persist for many years: consequently the activity cycles of both individuals and colonies are highly temperature dependent (Peakin & Josens, 1978). *Myrmica* is a northern temperate genus that usually nests in soil, and inter-specific comparisons have shown that different species are adapted to the average temperatures of the sites where they live. For example, under laboratory conditions *Myrmica scabrinodis* Nylander colonies must be maintained at a 2–3°C warmer temperature than those of *Myrmica ruginodis* Nylander, for both species to produce new adults in the same period of time (Elmes & Wardlaw 1983). This correlated with the observation that in southern England, *M. ruginodis* normally live in soil which is 2–3°C cooler than that used by *M. scabrinodis* (Elmes, 1982). *Myrmica rubra* L. was intermediate to *M. ruginodis* and *M. scabrinodis* in both studies. Elmes & Wardlaw (1983) suggested that their results indicated intrinsic metabolic differences between species of *Myrmica*. Further support for this hypothesis was provided by the demonstration that *M. ruginodis* has a significantly higher maintenance respiratory requirement than *M. scabrinodis* (Nielsen et al., 1999). Furthermore, Nielsen and co-workers showed that individuals of both species, drawn from populations living at high latitudes, had higher respiration rates, and were more responsive to temperature change than those living at lower latitudes – the first demonstration of physiological differences between conspecific populations of ants related to geographical location.

We now hypothesise that populations might also show corresponding differences in social physiology, such as the ability of workers to rear larvae when reared under "common-garden" conditions, and test this by replicated experiments using colonies of *Myrmica rubra* L. This species was chosen for several reasons: (a) its social physiology has been well studied in the laboratory (reviewed by Elmes, 1991); (b) the design of cross replicated experiments is facilitated by its usually large colonies (> 800 workers which are abundant in damp habitats throughout the mid latitudinal zones of Europe); (c) brood can be "grafted" into cultures of other colonies to dissociate responses of brood from the effects of nurse workers; (d) collaboration enabled us to obtain sufficient stock colonies, in the same physiological condition, from sites over its European range.

Like all other *Myrmica* species studied, most *M. rubra* colonies have "split" brood cycles: eggs are laid in early summer and either develop rapidly to become new workers within six weeks or so, or grow more slowly, entering diapause before overwintering, and complete their growth in spring (see Elmes, 1991). On average, 50% of workers are reared in summer and 50% from overwintered larvae in spring, although the exact proportions vary over the species' range (Kipyatkov, 1993). Male larvae normally overwinter and cannot be separated from female larvae when small. New queens (gynes) can only develop from larvae that have diapaused. Therefore, the ability of workers to respond rapidly to early spring warmth and to begin rearing overwintered larvae is important for maintaining colony worker populations and producing the sexual castes.

METHODS

Sites and stock

Stock colonies were collected from seven regions in the autumn of 1997 and were overwintered in an incubator at 5°C. Four regions were selected to represent the northwest (NW), southwest (SW), northeast (NE) and southeast (SE) ranges of distribution of *M. rubra* in Europe: being the Isle of Coll, West Scotland (56.75°N, 6.75°W), South Dorset, UK (50.5°N, 2°W), Vyritsa, St. Petersburg region, Russia (59.25°N, 30.3°E) and Kiev, Ukraine (50.5°N, 30.5°E) respectively. Three colonies from two different isolated populations (sites) were collected from each of these regions. In addition, we collected 6 colonies (2 from one site and 4 from a second site) from the Carpathian region of Ukraine (48.5°N, 22.75°E), 3 colonies from Vladimir, Moscow region of Russia (56.25°N, 39.5°E), 3 colonies from the Black Sea region, Dnieper estuary, Ukraine (46.5°N, 32.5E) and 3 colonies from a third site in Dorset.

In NW and SW sites *M. rubra* were locally dominant, they nested under stones where they experienced a maritime climate with relatively cool wet summers and mild winters. In the NE, SE and Vladimir they lived mainly in moss in coniferous woodlands in competition with one or more congenerics, where they experienced a more continental climate, with colder winters and hotter summers. All sites except the Carpathian (c 800 m) were at low altitudes. The Carpathian sites had a wetter climate than lowland Ukraine, and superficially resembled the western ones with *M. rubra* nests living under flat stones in open grassland. The Black Sea site was atypical and probably represented the extreme southern edge of *M. rubra*'s eastern range. Here the ants nested in rotten wood in very heavily shaded wet deciduous woodland on the banks of the river Dnieper. All sites experienced different lengths of seasons and daylight regimes according to their latitude.

Worker quality and metabolism

In spring before the start of rearing experiments a sample of about 30 workers was taken from each of the stock nests. After a few days at 20°C to "warm-up" and become active, they were used to estimate respiration by measuring the rate of CO_2 production using a flowthrough analyser model LI-6251 connected to a data acquisition and analysis system (Sable System, Salt Lake, Utah using Datcan V software). We used 5°C and 25°C in our tests. Ants were then killed, dried in a vacuum oven at 60°C for 24 h and weighed. Their lipid contents were extracted using petroleum ether in a Soxhlet apparatus for 24 h, and fat content determined as the difference between the dry weight and the lipid-free dry weight. The details of these techniques are identical to those described by Nielsen et al. (1999). We calculated respiration rates at 5°C and 25°C as volume µl of CO_2 h^{-1} mg^{-1} fat-free weight. Similar measurements were subsequently made on a second sample of workers at the end of the rearing experiment after they had been active at 20°C for about 140 days. Due to technical problems results were not obtained for 2 colonies, one from each of the St. Petersburg sites.

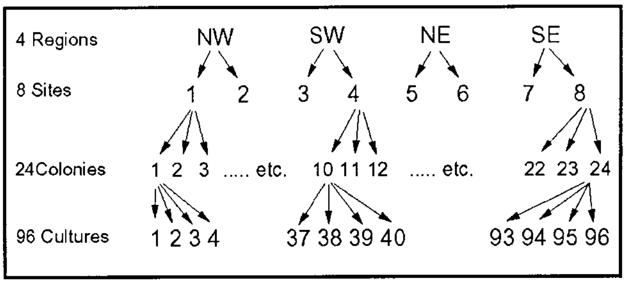

Fig. 1. Scheme for the design of the main experiment.

Brood rearing experiment

The main rearing experiment had a fully balanced design (Fig. 1), consisting of 96 cultures each containing 30 workers drawn at random from one of the stock colonies, and 15 overwintered larvae in the size range 0.3–0.4 mg live weight. The larvae were all "small" in the sense of Elmes & Wardlaw (1981) and were expected to develop mainly as workers, although some male larvae are normally present in this size class of larvae. Larvae were pooled because there were insufficient brood or workers to fully cross-replicate all permutations of workers and larvae. Groups of fifteen "standard larvae" from each region were obtained by first pooling all larvae of the correct weight class, from the three colonies in each of the two sites, and then selecting at random, 7 from one site and 8 from the other. Thus the four cultures from each nest (e.g. cultures 1–4 from nest 1 at NW site 1) reared larvae from a different region (e.g. in Fig. 1, cultures 1, 37, 93, cultures 2, 38, 94 cultures 3, 39, 95 and cultures 4, 40, 96 reared larvae from NW, SW, NE and SE regions respectively). A supplementary experiment was made at the same time. Workers were drawn from the remaining colonies at the other four eastern regions and the third SW site (in the same manner as previously), but they were given larvae from the NW, SW, NE and SE regions as described above rather than larvae from their own nests.

Once established, the cultures were maintained in Brian nests at 20°C, with ample food and water, and were handled as described by Wardlaw (1991). From day 6 to day 136, all cultures were examined every 2 or 3 days and the developmental stage of the larvae recorded; any pupae were removed and weighed. Worker mortality was not excessive (on average < 10% of the workers had died by day 60 which was not enough to affect either the survival or growth of brood) and was more or less random between the cultures following a Poisson distribution. Data were analysed by regression and ANOVA using the MINITAB® statistical package. Pupal weights were more or less normally distributed, log transformation improved normality but not sufficiently to make it worthwhile transforming the data for analyses. On the other hand, the time taken to reach pupation was very overdispersed with an indication of bimodality; consequently we used loglog transformations in statistical analyses.

RESULTS

Worker quality and metabolism

Respiration rates (CO_2 production per unit fat-free dry-weight) for the 38 colonies tested, showed significant Pearson correlations (*r*) between the estimates made at 5°C and 25°C at both the start and end of the rearing ex-

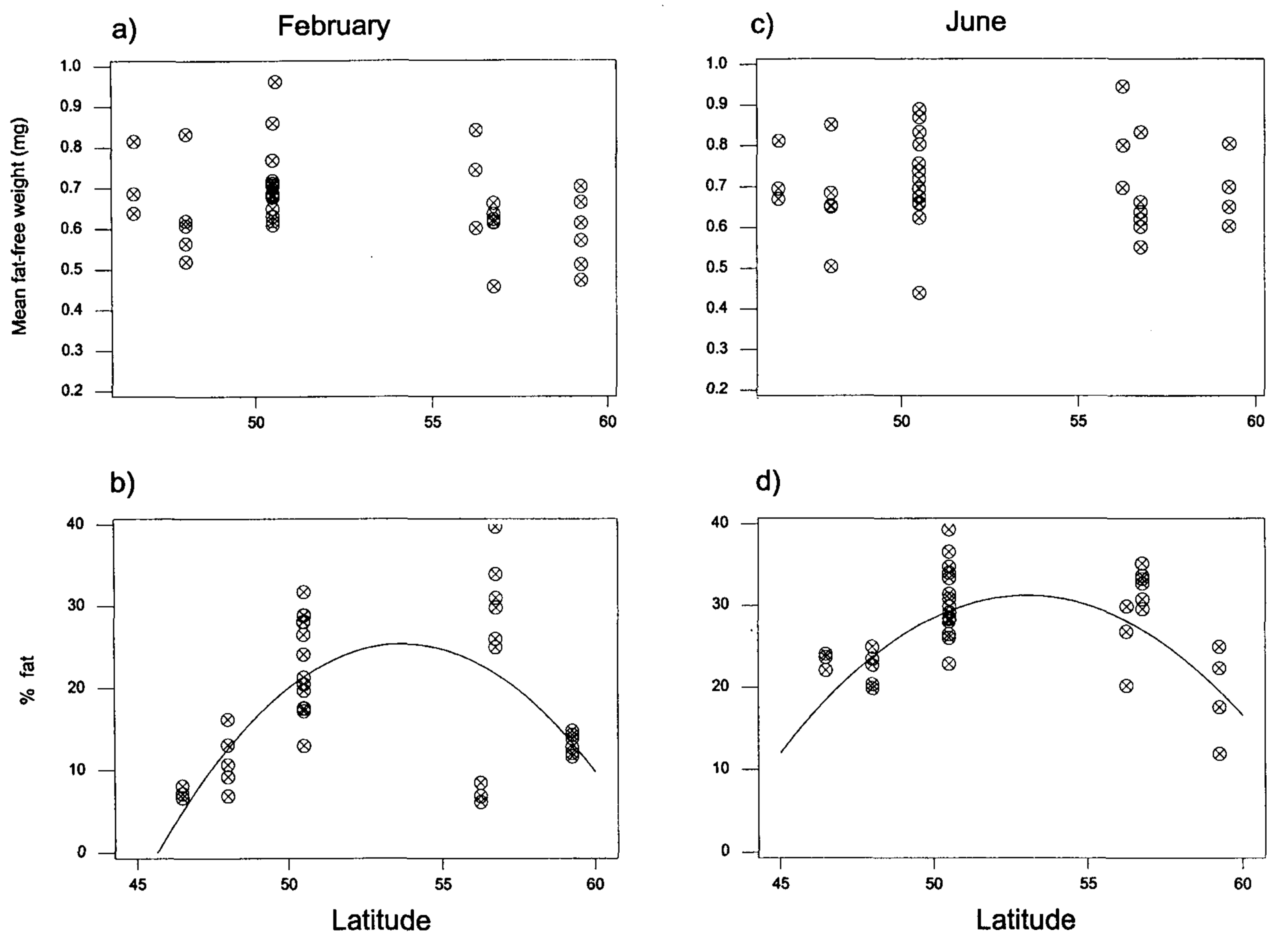

Fig. 2. The mean estimates of fat-free weight and percentage of fat in workers from 38 colonies of *M. rubra* collected from 13 sites at 6 latitudes in Europe, plotted against latitude of the collection site. The estimates were made immediately following hibernation (a & b) and in June after ca. 140 days activity (c & d).

periment ($r = 0.62$, $n = 38$, $p < 0.001$ and $r = 0.38$, $n = 36$, $p = 0.02$ in February and June respectively). However there was no correlation between the February and June estimates ($r = 0.18$, $n = 36$, $p = 0.31$ and $r = 0.08$, $n = 36$, $p = 0.69$ at 5°C and 25°C respectively). To simplify the subsequent analyses we used a simple average of respiration at the two temperatures to give a mean value for "colony respiration". This has less biological meaning than a geometric average (which is related to Q10), but has the advantage here, in that it places slightly more weight on responses at 25°C which might be more relevant to the 20°C laboratory temperature used for the rearing experiment.

There was no significant correlation between estimates of fat-free dry weight of workers and the estimates of percentage of body fat ($r < 0.17$, $n > 36$, $p > 0.30$ in both February and June). There was no statistically significant relationship between fat-free weight and latitude of the site (Fig. 2a, c). However, the percentage fat had a parabolic relationship with latitude in both measuring periods (Fig. 2b, d); the curves illustrate the statistically significant quadratic regressions with latitude ($F_{2,37} = 10.0$, $p < 0.001$ in fat content, in February and $F_{2,35} = 13.1$, $p < 0.001$ explaining 40% of the variation in June, all coefficients being significantly greater than zero in both periods, $T_{df>35} > 4.0$, $p < 0.001$). This shows that worker ants of *M. rubra* living at mid latitudes (ca. 53°N) contained more fat than those collected from more northerly or southerly latitudes.

Estimates for weight specific (fat-free weight) respiration varied negatively with the fat-free weight in February (Pearson $r = -0.59$, $n = 38$, $p < 0.001$) but in June, the relationship was not statistically significant ($r = -0.13$, $n = 36$, $p = 0.45$). The percentage fat had no statistically significant relationship with respiration in either period ($r < 0.10$, $p > 0.50$ in both cases). There was a significant linear regression between site latitude and the residual variation in the February mean respiration once the effect of size was removed (Fig. 3a: $F_{1,37} = 7.9$, $p = 0.008$, both coefficients being significantly greater than zero) but by June, the relationship disappeared (Fig. 3b).

Brood-rearing differences

The main experiment

Most larvae developed into worker pupae and a smaller number were males (Table 1). A small number of gynes (28) were produced in a proportion of the cultures but these were insufficient to make meaningful comparisons and are not considered here. On average males developed faster and were heavier than workers (47 vs 58 days and 3.1 vs 4.5 mg). Analysis of variance on the time taken for

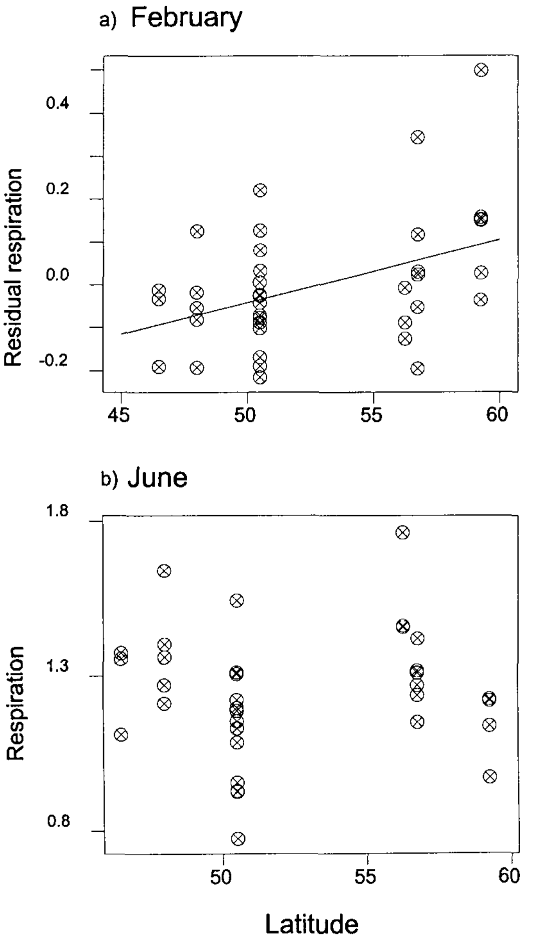

Fig. 3. Mean respiration (µl of CO_2 h^{-1} mg^{-1} fat-free weight) of workers from 38 colonies of *M. rubra* collected from 13 sites at 6 latitudes in Europe, plotted against latitude of the collection site. (a) Residuals of the estimate in February immediately post hibernation once the significant relationship between respiration and fat-free weight has been removed. (b) Estimate in June after ca. 140 days activity.

pupation by workers, showed significant variation attributable to both the region of origin of the workers ($F_{3,618}$ = 28.8, P < 0.001) and the origin of the brood ($F_{3,618}$ = 8.7, P < 0.001); there was no significant interaction. A similar result was obtained for male pupae ($F_{3,195}$ = 3.6, $p < 0.02$ and $F_{3,195}$ = 6.7, $p < 0.001$). Differences between the treatments could be gauged by comparison of row and column totals (Table 1). This analysis showed that regardless of which workers reared them, (i) brood of eastern origins tended to grow faster than brood of western origin, (ii) southern brood pupated more quickly than northern brood, (iii) northern workers reared brood to pupation more quickly than southern workers, regardless of the origin of the brood, and (iv) there were significant differences in the time to pupation by worker brood, between the two sites within the SW and SE regions ($F_{1,157}$ = 7.9, p = 0.006 and $F_{1,153}$ = 5.8, p = 0.017 respectively) but not between sites within the NW and NE regions. The effect of worker origin on male development time was less clear.

The effects of origins of brood and workers on pupal-weight were examined by analyses of variance. The time to pupation was included as a covariate because it might be expected that larvae which grow more slowly and pupate later might achieve a greater pupal weight. This proved to be the case for workers with time to pupation being statistically significant ($F_{1,617}$ = 26.6, $p < 0.001$). The region of origin of the brood had a big effect ($F_{3,617}$ = 25.5, $p < 0.001$) and region of origin of the workers had a smaller effect ($F_{3,617}$ = 3.4, p = 0.018) the overall relationship being:

$$\text{Worker pupal weight} = 1.53 + 1.23 \cdot \text{loglog(time to pupation)} \qquad (1)$$

However the reverse held true for males with the largest being produced first ($F_{1,194}$ = 13.6, $p < 0.001$) although there were still significant effects for the regions of origin of the brood and workers ($F_{3,194}$ = 2.8, p = 0.041; $F_{3,194}$ = 5.2, p = 0.002 respectively):

$$\text{Male pupal weight} = 7.06 - 1.86 \cdot \text{loglog(time to pupation)} \qquad (2)$$

This was best illustrated by the means adjusted for the effect of time to pupation (Fig. 4). Workers which developed from "small" brood originating in the west of Europe, were larger than those from eastern Europe, with a trend for southern workers to be heavier than their northern counterparts (Fig. 4a). Similarly workers from southern Europe tended to rear larger larvae than the northern stock but in contrast there were no east-west differences (Fig. 4b). There was no clear trend in the results for male pupae, except for males reared from larvae collected in Scotland being distinctly heavier than the rest (Fig. 4c), and workers from southern England reared heavier males than the other regions (Fig. 4d). This probably resulted from most males originating from SW brood (Table 1) and is an indication that workers might give their own male brood preferential treatment.

Supplementary experiment

Similar results emerged from the supplementary experiment where workers from four additional regions reared brood from the same sources as in the main experiment. Analysis of variance showed that weights of worker pupae were affected positively by the time taken to pupation ($F_{1,418}$ = 38.9, $p < 0.001$) whereas male weights were negatively affected ($F_{1,85}$ = 5.0, $p < 0.03$). The actual relationships were close to those obtained in the main experiment:

$$\text{Worker pupal weight} = 0.63 + 1.90 \cdot \text{loglog(time to pupation)} \qquad (3)$$

$$\text{Male pupal weight} = 7.33 - 1.99 \cdot \text{loglog(time to pupation)} \qquad (4)$$

As in the main experiment, there were significant differences in weights of both worker and male pupae, due to the origin of brood ($F_{3,418}$ = 30.0, $p < 0.001$) and ($F_{3,85}$ = 9.5, $p < 0.001$) respectively. However, although the origin of the nurse workers had a significant effect on worker pupal size ($F_{3,418}$ = 14.9, $p < 0.001$) it did not affect male pupal size ($F_{3,85}$ = 2.1, p = 0.1). The mean weights of the pupae, standardised for the effect of pupation time, are given as Table 2; these can be compared directly with those in Fig. 4. As before, worker brood from western Europe grew larger than that from eastern Europe regard-

TABLE 1. Brood reared in the main experiment. The numbers of worker (♀) and male (♂) pupae together with their mean live weights (mg) and mean time taken to become a pupa (days) reared by the six cultures (drawn from 3 colonies from 2 different sites) in each region being Scotland (NW), S. England (SW), St. Petersburg (NE) and Kiev (SE). Each colony was replicated with brood drawn from each of these four regions (see methods).

		Workers									
Brood		NW		SW		NE		SE		Total	
		♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
	number	41	7	34	5	26	7	35	4	136	23
NW	weight	3.30	4.56	3.72	5.02	3.13	5.40	3.69	4.56	3.47	4.92
	time	66	47	78	55	73	73	81	37	74	55
	number	8	30	17	30	9	19	14	28	48	107
SW	weight	3.23	4.29	3.67	4.65	3.42	4.32	3.61	4.56	3.53	4.67
	time	66	44	73	61	54	41	65	51	66	51
	number	45	16	42	18	47	15	40	14	174	63
NE	weight	2.94	4.62	2.97	4.52	2.86	4.36	2.96	4.03	2.93	4.40
	time	55	36	60	47	49	35	56	44	55	40
	number	72	2	69	2	57	4	69	1	267	9
SE	weight	2.99	5.07	3.08	4.39	3.03	4.70	3.07	4.28	3.04	4.67
	time	50	33	57	39	49	44	50	35	52	40
	number	166	55	162	55	139	45	158	47	625	202
Total	weight	3.07	4.44	3.25	4.63	3.02	4.54	3.23	4.39	3.14	4.50
	time	56	42	64	55	54	44	60	47	58	47

less of which ants reared them: however, there was no support for the suggestion in Fig. 4a that southern brood might produce larger workers than northern brood. The pattern for male pupal weights was similar to that in Fig. 4b. The workers from a third site in southern England produced heavy worker and male pupae whereas the *M. rubra* from the Black Sea region produced light males and workers.

Brood-rearing, worker condition and metabolism

We used as dependent variables the mean fresh weight and the number of worker pupae reared by the 4 cultures from the 38 colonies from the 8 regions. We assumed the time taken to pupate, the various measures of colony condition (fat content, respiration etc.) and the latitude of the region where the colony was collected, to be the independent variables. Any effect on mean larval growth could be attributed to the effect of the nurse workers from the tested colonies rather than the larvae, because each colony reared equivalent larvae (60 larvae, 15 from each region – see methods). There was considerable correlation between the independent variables so we combined them in multiple regression dropping in turn those that contributed least to the overall R^2.

TABLE 2. Mean weights of worker and male pupae (± standard error) according to the region of origin of the brood and workers (see methods), standardised for effect of time to pupation.

	Worker pupae		Male pupae	
	Mean	(± SE)	Mean	(± SE)
Brood source				
NW	3.54	0.049	5.09	0.168
SW	3.43	0.079	4.64	0.100
NE	2.93	0.049	3.90	0.153
SE	3.07	0.040	4.63	0.293
Worker source				
Carpathian	3.06	0.051	4.62	0.127
S. England	3.34	0.053	4.86	0.185
Vladimir	3.47	0.053	4.52	0.166
Black Sea	3.09	0.050	4.26	0.185

The best description, which accounted for about 33% of the variation in pupal weight, was a parabolic function of latitude ($F_{2,35} = 8.9, p = 0.001$, Fig. 5a):

$$\text{Mean weight of worker pupae} = -13.38 + 0.63 \cdot \text{Latitude} - 0.0060 \cdot (\text{Latitude})^2 \quad (5)$$

The number of larvae reared to pupation had a negative relationship with both latitude ($F_{1,35} = 6.7, p < 0.02$) and the time taken to pupate ($F_{1,35} = 9.6, p < 0.01$). The time taken to pupate also had a negative relationship with latitude ($F_{1,36} = 4.7, p < 0.04$). There was a strong correlation between the coefficient of variation of mean pupal weight in colonies and the average time taken to rear them but there was no relationship between the coefficient of variation and latitude. When the number of larvae reared was standardised for the mean time taken for them to reach pupation (Fig. 5b), the results suggested that colonies at the most southerly latitudes produced ca. 25% more workers from the same number of small overwintered larvae compared workers from the most northerly latitudes.

DISCUSSION

The results for production of worker pupae can be interpreted directly in terms of the physiological conditions of the *M. rubra* worker ants, but the results for male production are less clear-cut. This is probably because the

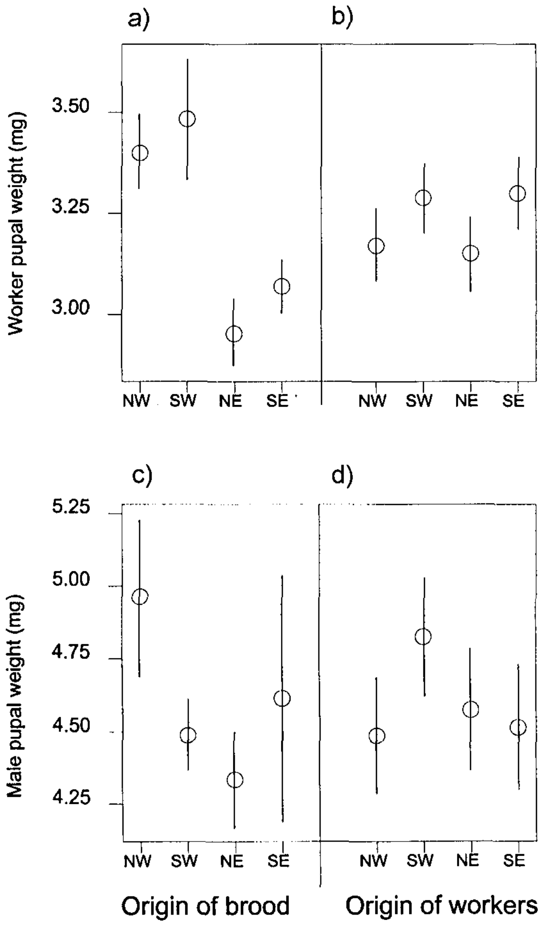

Fig. 4. The mean pupal fresh weights (mg) and 95% confidence bars, for worker pupae (a & b) and male pupae (c & d) reared in the main experiment, according to origins of brood (a & c) and the origins of the nurse workers (b & d).

size and development rates of sexual ants are influenced more by external factors than is the case for workers. For example, the trade off between numbers and size of males, in response to local factors such as the average distances flown and time needed to survive and mate, might outweigh any more general constraints related to environment and nurse worker condition. We therefore restrict this discussion to consideration of worker development.

However, any conclusions from the brood rearing experiment must be interpreted with two provisos. First, the ontogeny of *M. rubra* workers is determined by a complicated behavioural interaction with their nurse workers (e.g. Brian, 1955). As soon as larvae have achieved a certain amount of development, nurses can either precipitate early metamorphosis or permit larvae to develop further with the possibility of becoming new queens (reviewed Brian, 1974). Apart from social factors, the behaviours that control caste determination can be affected directly by environmental factors such as temperature and food supply. Therefore variations in the social parameters measured here (the size of pupae and time to pupation), might be some combination of direct consequences of ergonomic factors affecting larvae (e.g. the rate of feeding) or an indirect consequence of nurse worker condition, that affects their behaviour towards larvae. Secondly, we assumed that all the populations respond to temperature in the same way: for example, NW workers do not rear brood optimally at a different temperature to SW workers. Preliminary (unpublished) experiments suggests that this assumption is valid and it is supported by the observation that within the SW region, four different *Myrmica* species responded to temperature in the same way (Elmes & Wardlaw, 1983).

At the start of the experiment, workers from mid latitudes (50–55°N) appeared to be in "better" condition than those from further north or south, containing a greater percentage of body fat (Fig. 2b). The average fat content of the workers in a colony might depend upon a huge variety of local factors operating at both individual nest-site and habitat levels, and it was rather unexpected that geographical position could explain as much as 35% of the variation between colonies. There was an indication for a similar trend (but explaining much less of the overall variation) in fat-free body weight (Fig. 2a), but many more nest samples would be required to confirm this. Under the "common garden" conditions of our laboratory (with ample food) all ants gained fat by June, but the parabolic relationship with latitude still remained intact (Fig. 2d) although it became flattened (ants with less fat in February gaining relatively more). We suggest that if we had maintained the experiment until August (six months after the start of the experiment when the ants enter dormancy), the relationship would probably have flattened further, perhaps disappearing. Thus variation in worker fat content is probably a response to environment and food availability in the previous year, rather than innate condition. Conversely, the relationship between respiration and latitude (Fig. 3a) which was lost in June (Fig. 3b) might be restored by the time all colonies become dormant. We hypothesise that while the average respiration rate of workers might change (decline) by the same amount over the course of active period, the duration of the active period probably differs between populations, with northern populations being adapted to short summer seasons. Thus when measured in June, southern colonies were probably physiologically "mid-season" and northern ones were "end-of-season". This hypothesis should be investigated further.

The observed variation in fat content probably is an "edge-of-range" effect with *M. rubra* colonies living at the margins being on average less viable (fewer energetic reserves) than those central to the range. In addition to variation in habitat quality and food supply expected at the edge of range, northern populations bear an additional metabolic cost. Respiration varied (Fig. 3a) with workers living at 60°N spent about 5–10% more metabolic energy than those living at 45°N, this result mirrored that for the *M. scabrinodis* and *M. ruginodis* (Nielsen et al., 1999). Northern workers reared larvae to pupation more quickly – workers from 60°N are expected to produce half their pupae in 52 days compared with 64 days for workers from 45°N – which might be a direct consequence of the increased metabolic activity of the workers. This was due

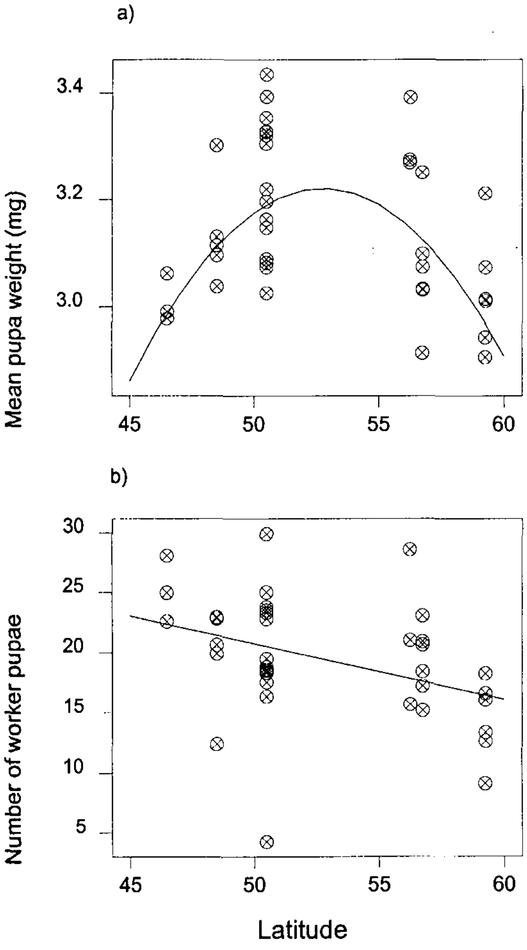

Fig. 5. The mean weights and numbers of worker pupae reared by from 38 colonies of *M. rubra* collected from 13 sites at 6 latitudes in Europe, plotted against latitude of the collection site. Each estimate is the average of four cultures each rearing larvae from colonies collected in NW, SW, NE and SE regions. (a) Average fresh weight has a significant parabolic relationship with latitude. (b) The number of workers reared is negatively related to latitude.

to differences in the workers not the brood; although on average, east European brood pupated earlier than west European brood, northern brood pupated at about the same time as southern brood from the same longitude. However, in contrast northern workers reared fewer larvae to maturity than southern workers (Fig. 5b).

Generally, workers from mid latitudes reared heavier pupae than those at the extremes (Fig. 5a) mirroring the relationship between condition (% fat) and latitude (Fig. 2b). We did not measure the fat content of the pupae so we do not know whether this represents a real difference in mass (fat-free dry weight) or simply the amount of body fat. We suspect that it is probably a combination of both. Workers in good condition might spend less energy on processing food and laying down fat in their own bodies and thus make more available to the brood. This implies that colonies at the edge of range will produce new workers with less fat that thereby, are less able to survive stressful conditions than core populations.

We conclude that there are real differences between populations of *M. rubra* in different parts of its range. Some, such as respiration rate, might be heritable and locally adapted to climate. Key factors are probably the length of summer (number of degree days available for growth – see Nielsen et al., 1999), the length of winter and the rate of change between winter and summer climate. Such factors vary progressively from north to south, with colonies living in southern habitats experiencing relatively short mild winters and long summers. The general condition of the workers however, might simply be a consequence of local nest site conditions and food supply, which over a large geographical range will be affected by average summer climate. At the southern edge of range, summers might frequently be too hot and in the north too cold for optimum production of brood. *M. rubra* also requires relatively humid conditions for foraging: workers will not forage when the soil surface is hot and dry (at mid-day or during periods of drought). Consequently, we predict that at most latitudes, conditions should be more suitable for *M. rubra* in the humid west of Europe and become less suitable in the east as continentality (hot dry summers) increases. Our data, suggesting that western larvae grow larger, is consistent with a west-east decline in habitat suitability. Ignoring the effects of mountains, we also predict that *M. rubra* populations will be restricted to a narrower band of latitudes in its drier eastern range.

ACKNOWLEDGEMENTS. Our collaboration was made possible by INTAS (grant 94-2072) which provided travel funds enabling us to collect experimental material from geographically dispersed sites. We thank Z. Randlel for assistance with laboratory experiments.

REFERENCES

Brian M.V. 1955: Studies of caste differentiation in Myrmica rubra L. 2. The growth of workers and intercastes. *Insectes Soc.* **2**: 1–34.

Brian M.V. 1974: Kastendetermination bei Myrmica rubra L. In Schmidt G.H. (ed.): *Soziale Insekten, Kastenbildung – Polymorphismus.* Ernst Kieser KG, Augsburg, pp. 565–589.

Elmes G.W. 1982: The phenology of five species of Myrmica (Hym. Formicidae) from South Dorset, England. *Insectes Soc.* **29**: 548–559.

Elmes G.W. 1991: The social biology of Myrmica ants. *Actes Coll. Insectes Soc.* **7**: 17–34.

Elmes G.W. & Wardlaw J.C. 1981: The quantity and quality of overwintered larvae in five species of Myrmica (Hymenoptera: Formicidae). *J. Zool. (London)* **193**: 429–446.

Elmes G.W. & Wardlaw J.C. 1983: A comparison of the effect of temperature on the development of large hibernated larvae of four species of Myrmica (Hym. Formicidae). *Insectes Soc.* **30**: 106–118.

Kipyatkov V.E. 1993: Annual cycles of development in ants: diversity, evolution and regulation. In Kipyatkov V.E. (ed.): *Proceedings of the Colloquia on Social Insects. Vol. 2.* Socium, St. Petersburg, pp. 25–48.

Nielsen M.G., Elmes G.W. & Kipyatkov V.E. 1999: Respiratory Q10 varies between populations of two species of Myrmica ants according to the latitude of their sites. *J. Insect Physiol.* **28** (in press).

PEAKIN G.J. & JOSENS G. 1978: Respiration and energy flow. In Brian M.V. (ed.): *Production Ecology of Ants and Termites.* Cambridge University Press, London, pp. 111–164.

WARDLAW J.C. 1991: Techniques for rearing Myrmica ants (Hym.) and Maculinea rebeli Hir. caterpillars (Lep., Lycaenidae). *Entomol. Mon. Mag.* **127**: 233–241.

Received September 29, 1998; accepted January 25, 1999