



Pergamon

Journal of Insect Physiology 45 (1999) 559–564

Journal  
of  
Insect  
Physiology

www.elsevier.com/locate/ibmbjip

# Respiratory Q10 varies between populations of two species of *Myrmica* ants according to the latitude of their sites

M.G. Nielsen <sup>a</sup>, G.W. Elmes <sup>b,\*</sup>, V.E. Kipyatkov <sup>c</sup>

<sup>a</sup> Institute of Biological Sciences, Department of Zoology, University of Aarhus, Building 135, DK-8000, Aarhus C, Denmark

<sup>b</sup> Furzebrook Research Station, Institute of Terrestrial Ecology, Wareham, Dorset, BH20 5AS, UK

<sup>c</sup> Department of Entomology, Faculty of Biology, St. Petersburg State University 7/9 Universitetskaya emb., St. Petersburg 190034, Russia

Received 8 June 1998; accepted 3 September 1998

## Abstract

Metabolic respiration by groups of resting *Myrmica ruginodis* and *M. scabrinodis* worker ants from five sites representing a range of latitudes, have been compared by measuring rates of CO<sub>2</sub> production—standardised by fat-free weight—at 5 and 25°C. *M. ruginodis* which lives in cooler habitats than *M. scabrinodis* consistently produced more CO<sub>2</sub>. At 5°C ants of both species from southern latitudes were metabolically more active than those from more northerly latitudes, whereas at 25°C the situation was reversed. Estimates of Q10 were positively correlated with latitude indicating that the respiratory metabolism of northern populations increases relatively more in response to rising temperatures than southern populations. Values of Q10 at different latitudes were the same for both species. The results are discussed in terms of seasonal fluctuations of temperature at different latitudes. © 1999 Published by Elsevier Science Ltd. All rights reserved.

**Keywords:** Respiration-rate; Q10; Latitude; Formicidae; Myrmica

## 1. Introduction

Ants are social insects which live in family groups. Their abundance and impact upon most terrestrial ecosystems makes them true keystone species which have direct and indirect effects upon the biodiversity of terrestrial communities (Hölldobler and Wilson, 1990; Wilson, 1990). Most species nest in the soil where they can persist for many years, consequently the activity cycles of both individuals and colonies are highly temperature dependant (Peakin and Josens, 1978). Most respirometry studies on ants are concerned with energy flow through colonies or energy requirements of individuals performing different tasks (briefly reviewed by Nielsen, 1986). This trend has continued with studies of colony energetics (eg. Lighton, 1989; Martin, 1991; Porter and Tschinkel, 1985; Davidson, 1987), energetics of sexual production (eg. Peakin et al., 1989; Schmidt and Reuss,

1990; Boomsma and Isaaks, 1985; Boomsma et al., 1995) and foraging activity (eg. Fewell et al., 1996; Nielsen, 1987; Nielsen and Baroni Urbani, 1990). There have been a few studies on the direct effect of environmental variables upon the respiratory metabolism of individuals; for example the effect of temperature (Lighton and Wehner, 1993), the interaction between temperature and longevity (Calabi and Porter, 1989) and the effect of O<sub>2</sub> availability (Hebling et al., 1992), but since Nielsen (1986) there has been little further investigation of respiratory metabolism in response to altitude or latitude.

Published data giving direct comparisons over altitudinal or latitudinal gradients mostly show differences between species; in the case of ants there are differences between high and low altitude congeneric species (MacKay, 1985) and between groups of species from different latitudes (Nielsen, 1986). However we can find no published intra-specific comparisons for insects and only a few for plant species. These show that the respiratory metabolism of plants can vary over their geographical ranges in response to latitude or altitude (Anekonda et al., 1996; Mariko and Koizumi, 1993;

\* Corresponding author. Tel: +44-1929-551518; fax: +44-1929-551087.

E-mail address: g.elmes@ite.ac.uk (G.W. Elmes)

Criddle et al., 1994) and variations in characteristics appear to be heritable (Criddle et al., 1996). For example, dark respiration rates of needles of *Pinus sylvestris* trees grown in common gardens, varies according to the latitude of origin of the stock, with the rates of respiration of northerly stock being relatively greater than those of southerly stock (Reich et al., 1996).

Given that ant colonies are highly responsive to ambient temperatures, live in the soil, are relatively sedentary and in many respects have characteristics analogous to those of perennial flowering plants we hypothesised that ant populations might show climate mediated variations in respiratory metabolism. We have made a preliminary test of this for two common European red ant species, *Myrmica ruginodis* Nyl. and *Myrmica scabrinodis* Nyl. We have followed other studies by measuring changes in metabolic respiration of small groups of resting worker ants in response to two temperatures, and used this to calculate Q10 values (Nielsen, 1986).

## 2. Materials and methods

### 2.1. The ant colonies sampled

As part of an ongoing collaborative study of phenological variation in *Myrmica* ant populations over their European range, we were able to obtain samples of *M. ruginodis* and *M. scabrinodis* from 5 sites at 4 latitudes. The sites were: Chupa, White Sea region of Russia 66.25°N, 33°E; Vyritsa, St. Petersburg region, Russia 59.25°N, 30.3°E; Vladimer, Moscow region of Russia 56.25°N, 39.5°E; Kiev, Ukraine 50.5°N, 30.5°E; South Dorset, UK 50.5°N, 2°W. We aimed to test 3 colonies of each species from each site. Unfortunately, due to mortalities between collection and testing only one *M. scabrinodis* was available from Kiev and 2 *M. ruginodis* from Vladimer, but 6 *M. scabrinodis* were available from Dorset giving a total of 30 colonies. All colonies were sampled towards the end of summer and were maintained in laboratory culture with ample food (Wardlaw, 1991) prior to testing. Consequently all the ants should have been in the same pre-winter physiological state (eg. Kipyatkov, 1988).

### 2.2. The method of calculating respiration rate

Estimates of respiration rates were made by measuring CO<sub>2</sub> production using a flow-through analyser model LI-6251 connected to a data acquisition and analysis system (Sable System, Salt Lake, Utah using Datcan V software). The air flow was held constant at 150 ml min<sup>-1</sup>. This equipment is very sensitive and can measure concentrations to 50 ppb CO<sub>2</sub>. The respiratory chambers were cylindrical tubes (length 60 mm, diameter 13 mm with both ends stopped with rubber plugs) which were

placed in a temperature regulated water bath. We used 5°C and 25°C in our tests.

In order to eliminate individual variation about 20 workers were used in each run. The ants were counted at the finish of the test in order to reduce the effect of disturbance—they settle down to apparently normal resting behaviour in the test chamber if handling is reduced. After a minimum of 1 h acclimation at 5°C a minimum of two series of measurements were made; each series consisted of 516 readings of the CO<sub>2</sub> concentration over a 5.1 min period. The water bath was then raised to 25°C with the test ants left in place until the following day when a new series of measurements was made. The ants were then counted, weighed alive before killing and drying in a vacuum oven at 60°C for 24 h. The dried ants were reweighed and their lipid contents were extracted using petroleum ether in a Soxhlet apparatus for 24 h. Fat content was determined as the difference between the dry weight and the lipid-free dry weight.

The data analysis program converted the records of CO<sub>2</sub> concentrations to an estimate of the total CO<sub>2</sub> produced during each measuring period, and by averaging over the different periods between the 516 readings we could calculate a mean respiration rate as volume µl of CO<sub>2</sub> h<sup>-1</sup> mg<sup>-1</sup> fat-free weight. The average Q10 between 5 and 25°C was calculated as the square root of the ratio of the respiration rates at the two temperatures.

### 2.3. Statistical analysis

A simple test of the effect of latitude upon any variable recorded (for example respiration rate at 25°C) is confounded because the 30 colonies sampled were taken from only 5 sites at 4 different latitudes (Kiev and Dorset are about the same latitude); in other words there are far fewer than 29 ( $N-1$ ) degrees of freedom available to test the effects of latitude. Therefore, we have used a much more rigorous test based on estimating the proportion of the total between-site variation which can be explained by latitude (one attribute of the sites) and testing its statistical significance using the variance ratio ( $F$  test) based on this—see Table 1. All analyses were made using the MINITAB® statistical package.

## 3. Results

### 3.1. Estimates of individual weights of ants

There was considerable variation for the average individual dry weights of the ants used in the respirometer runs; this mainly reflects real differences between the source colonies because 15–25 workers are usually sufficient to give a reasonable estimate of individual dry weights within colonies. The mean of the average dry

Table 1  
Analyses of variance used to estimate the effect of latitude upon the variables measured<sup>a</sup>

Source	df	Sum Squares	Mean squares	F	dfF
Species	1	SS <sub>species</sub>	MS <sub>species</sub>	$F_{\text{species}} = \text{MS}_{\text{species}} / \text{MS}_W$	1,24
Latitude	1	SS <sub>Lat</sub>	MS <sub>Lat</sub>	$F_{\text{Lat}} = \text{MS}_{\text{Lat}} / \text{MS}_R$	1,3
Residual	3	SS <sub>R</sub>	MS <sub>R</sub> = SS <sub>R</sub> /3	–	–
Total Between-sites	4	SS <sub>B</sub> = SS <sub>Lat</sub> + SS <sub>R</sub>	MS <sub>B</sub> = SS <sub>B</sub> /4	$F_B = \text{MS}_B / \text{MS}_W$	4,24
Within site (residual)	24	SS <sub>W</sub>	MS <sub>W</sub> = SS <sub>W</sub> /24	–	–
Total	29	SS <sub>T</sub> = SS <sub>species</sub> + SS <sub>Lat</sub> + SS <sub>R</sub> + SS <sub>W</sub>			

<sup>a</sup> Thirty nests of two species were sampled from 5 sites. The proportion of the within site variation which can be explained by latitude = SS<sub>Lat</sub>/SS<sub>B</sub> and its statistical significance can be estimated from F<sub>Lat</sub> with 1,3 degrees of freedom.

weight estimates from the 14 colonies of *M. ruginodis* was significantly greater than that for the 16 colonies of *M. scabrinodis* (0.96±0.22 mg v 0.79±0.16 mg;  $F_{1,24}=7.8$ ,  $P=0.01$ ). We used fat free dry weights used to standardise the estimates of rate of production of CO<sub>2</sub> and these also varied significantly between the species (0.81±0.17 mg v 0.65±0.08 mg;  $F_{1,24}=10.6$ ,  $P<0.01$ ) but within species, variation was due to differences between individual colonies with no indication of significant variation due to sites ( $F_{4,24}=0.4$ ,  $P>0.7$ ). On the other hand, the average fat reserves of workers did not vary between the two species either in absolute weight (0.15±0.10 mg v 0.13±0.12 mg;  $F_{1,24}=0.8$ ,  $P>0.3$ ) or as a percentage of dry weight (16±9% v 15±10%;  $F_{1,24}=0.1$ ,  $P>0.7$ ). However, there was an indication that percentage fat varied between sites ( $F_{4,24}=3.1$ ,  $P=0.03$ ), with workers from high latitudes tending to have less fat than workers from lower latitudes.

### 3.2. Estimates of respiration rates

At 5°C, the weight specific (fat-free weight) rate of CO<sub>2</sub> production varied significantly between the species ( $F_{1,24}=14.8$ ,  $P<0.01$ ) with an indication of variation between the sites ( $F_{4,24}=2.0$ ,  $P<0.15$ ) of which latitude explains 56% ( $F_{1,4}=3.8$ ,  $P<0.15$ ; Fig. 1(a)). However at 25°C, weight specific CO<sub>2</sub> production not only varied significantly between the species ( $F_{1,24}=34.2$ ,  $P<0.001$ ) but it also varied significantly between the sites ( $F_{4,24}=6.9$ ,  $P<0.001$ ) with latitude explaining 66% of this ( $F_{1,3}=5.7$ ,  $P<0.10$ ; Fig. 1(b)). When we analysed the data for Q10 which are independent of individual weights, we detected no evidence for a difference between the two species ( $F_{1,24}=0.2$ ,  $P>0.70$ ) but a relatively strong difference between the five sites ( $F_{4,24}=6.6$ ,  $P<0.001$ ) of which the latitude explained a statistically significant 80% of the variation ( $F_{1,3}=12.2$ ,  $P<0.04$ ; Fig. 1(c)).

We conclude that latitude has an effect upon the respiratory response (Q10) of ants drawn from different populations. *M. ruginodis* consistently recorded a higher

weight specific production of CO<sub>2</sub> than *M. scabrinodis* but the relationship for change in Q10 with latitude was the same for both species (best least squares fit  $Q10=0.057*\text{Latitude}-0.653$ ,  $P<0.01$ ; Fig. 1(c)).

## 4. Discussion

The relationship between Q10 and latitude is important. It means that ants at high latitudes respond relatively more to increased temperature than others of the same species originating from lower latitudes. This is consistent with other studies of sub-arctic invertebrates which shows northern species to be more responsive than southerly species (eg. Block et al., 1994). We believe that this is the first demonstration of such a response between different populations of the same species of insect and is consistent with results for plants (Reich et al., 1996). Furthermore, the relationship between Q10 and latitude is statistically the same for both of the *Myrmica* species investigated, despite these belonging to quite different species-complexes (Radchenko, 1994).

Although Q10 is a useful parameter, the temperature response curves from which it derives are not normally linear so that in most biological reactions Q10 itself varies with temperature, generally decreasing as temperatures increase. This holds for worker ants. For example, Nielsen (1986) calculated Q10 values for a number of different species over the 5°C and 35°C range of temperatures and showed that although most had Q10 values of about 3.0 over the 5–25°C range, values in the 5–15°C range were generally greater than those at higher temperatures. There were considerable variations between species: temperate ant species from Arizona had lower values of Q10 over the 5–15°C range than ants from Alaska, but desert ants from Arizona had similar values to Alaskan ants, although they can survive at 35°C, a temperature which is lethal to temperate species. Ideally such populations should be compared using the shapes of their temperature response curves.

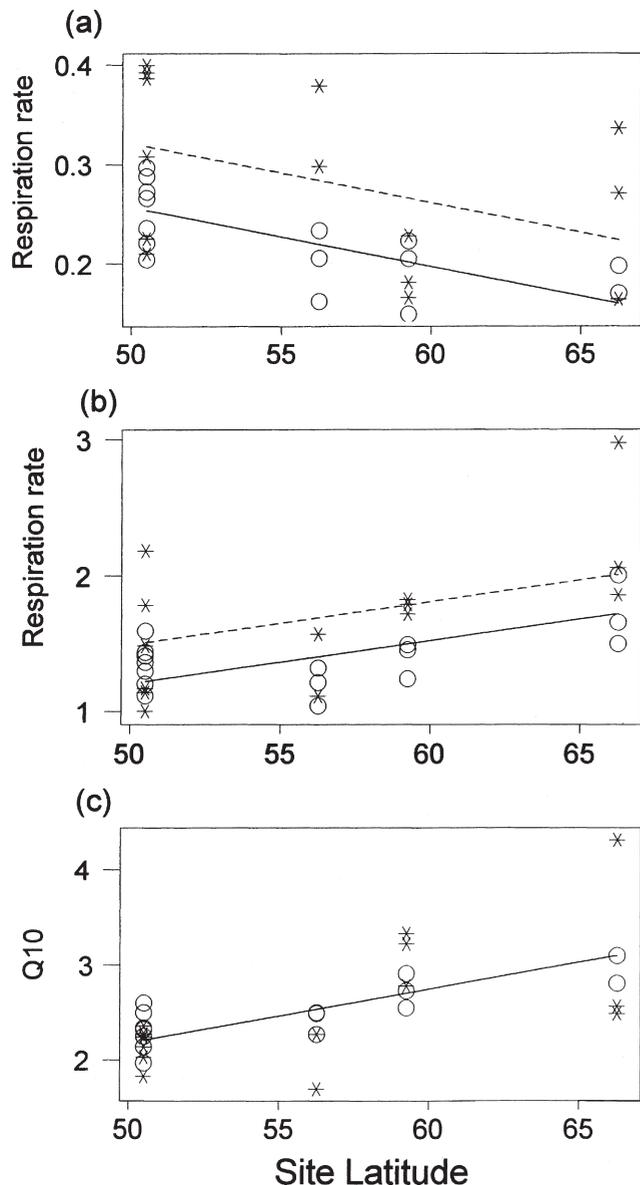


Fig. 1. Data for respiration rates ( $\mu\text{l CO}_2 \text{ h}^{-1} \text{ mg}^{-1}$  fat-free weight) of 30 samples of c. 20 workers from a series of *Myrmica scabrinodis* (circles and solid line) and *M. ruginodis* (star and dashed line) colonies sampled from sites at 4 different latitudes. (a) relationship between  $\text{CO}_2$  production and latitude at 5°C; (b) relationship at 25°C; (c) relationship between Q10 over range 5–25°C and latitude, the line is the best least squares fit for both species.

Our data also provided only two points on each curve sufficient to estimate a Q10 for each population, because in this preliminary study there was a trade off between the number of colony samples studied and the range of temperatures used. However, we suggest that this is sufficient to indicate the probable shape of the response curves. The observed relationship between Q10 and latitude (Fig. 1(c)) is due equally to the respiratory rates at both temperatures (Figs. 1(a), 1(b)). Bearing in mind that we used a rigorous estimate of the degrees of freedom (see methods), we suggest that these probably reflect a

real effect of latitude despite the relatively high probability that in both cases the proportions of between-site variation in respiration attributable to latitude, could be due to chance ( $P=0.14$  and  $0.09$  at 5 and 25°C respectively). We suggest that temperature response curves probably follow the scheme indicated in Fig. 2 where the curves are relatively steeper (higher Q10s) at high latitudes pivoting around a mid temperature of about 14°C, the temperature at which most *Myrmica* colonies become socially active. This would produce the observed result whereby ants drawn from colonies at high latitudes (both species) produced relatively less  $\text{CO}_2$  at 5°C, than ants from colonies sampled from lower latitudes (negative relationship—Fig. 1(a)), while at 25°C the situation was reversed, with ants from high latitudes producing relatively more than ones from low latitudes. The lack of statistical difference in the relationship between Q10 and latitude for the two species (Fig. 1(c)) indicates that the scheme suggested (Fig. 2) might be the same for all *Myrmica* species.

A “steeper” response curve for populations living at high latitudes compared to conspecifics from lower latitudes, is consistent with the thermally reduced summer seasons in northern habitats. Approximate estimates from climate tables indicate that on average the White Sea, Moscow and Dorset populations experience about 100, 150 and 180 days per annum when mean air temperatures exceed 10°C giving estimates 1400, 2000 and 2400 total degree-days during those periods. Obviously ants experience different temperatures in their soil nests and have the ability to modify the temperature regimes to some extent according to nest construction, but we suspect that precise estimates would follow the same overall pattern. Consequently northern individuals need to be able to respond quickly to rising temperatures and be physiologically more active during the short warm season to achieve the same colony growth as more southerly individuals. Furthermore, they must hibernate

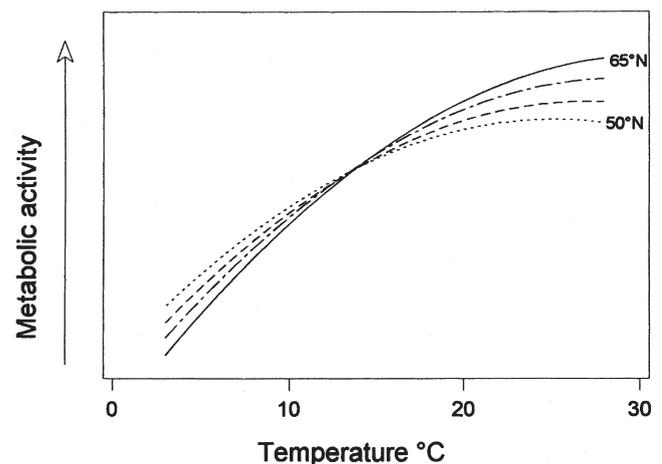


Fig. 2. Suggested shapes for the change in metabolic activity of *Myrmica* ants at four latitudes, in response to temperature.

for longer and perhaps this selects for a lower winter metabolism while at low latitudes, populations experience short winters with variable temperatures during which it might be disadvantageous to be very torpid.

It is significant that *M. ruginodis* metabolises about 25% more oxygen per gram of body tissue than *M. scabrinodis*, assuming that inert cuticle forms a constant proportion of the fat-free dry weights. Elmes and Wardlaw (1983) showed that *M. scabrinodis* workers are less efficient at rearing brood, taking about 30–40% longer at any temperature, than *M. ruginodis*; but on average, *M. scabrinodis* live in sites that are 1°C warmer enabling them to complete their brood-rearing at the same time as *M. ruginodis*. If the same relationship holds within a species we would expect that populations might to some extent adapt to cooler habitats (lower cumulated degree-days) by evolving greater metabolic activity as indicated by our results.

This study suggests therefore, that the respiratory metabolism of conspecific *Myrmica* ant populations is locally adapted to environmental conditions, and is probably an inheritable characteristic. Much more detailed study is required before the full consequences of such adaptation becomes clear; for example apart from obtaining full temperature response curves from a range of latitudes, ants should be tested at different times in their active season. We tested ants only at the end of the season and it might be that differences between populations are more exaggerated in spring after hibernation when insects might be most sensitive to rising soil temperatures (Block et al., 1994). If our conclusion is valid then it has important implications for the spread of these keystone species into new habitats in the event of global climate change. For example, should boreal habitats suddenly become much warmer the existing ant populations might not expand as rapidly as might be expected; colonisation of new sites might either require selection to operate on the existing populations, a process which might take a number of generations, or await immigration from more southerly populations.

## Acknowledgements

This collaborative work was done as part of the INTAS 94-2072 programme supported by a grant from INTAS and the basic research programmes of our Institutes. We thank R.T. Clarke for statistical advice and N.R. Webb for comments.

## References

Anekonda, T.S., Hansen, L.D., Bacca, M., Criddle, R.S., 1996. Selection for biomass production based on respiration parameters in Eucalypts—effects of origin and growth climates on growth rates. Canadian Journal of Forest Research 26, 1556–1568.

- Block, W.C., Webb, N.R., Coulson, S., Hodkinson, I.D., Worland, M.R., 1994. Thermal adaptation in the Arctic Collembolan *Onychiurus arcticus* (Tullberg). Journal of Insect Physiology 40, 715–722.
- Boomsma, J.J., Isaaks, J.A., 1985. Energy investment and respiration in queens and males of *Lasius niger* (Hymenoptera Formicidae). Behavioral Ecology and Sociobiology 18, 19–27.
- Boomsma, J.J., Keller, L., Nielsen, M.G., 1995. A comparative analysis of sex ratio parameters in ants. Functional Ecology 9, 743–753.
- Calabi, P., Porter, S.D., 1989. Worker longevity in the fire ant *Solenopsis invicta*: ergonomic considerations of correlations between temperature, size and metabolic rates. Journal of Insect Physiology 35, 643–649.
- Criddle, R.S., Hopkin, M.S., McArthur, E.D., Hansen, L.D., 1994. Plant-distribution and the temperature-coefficient of metabolism. Plant Cell and Environment 17, 233–243.
- Criddle, R.S., Breidenbach, R.W., Fontana, A.J., Henry, J.M., Smith, B.N., Hansen, L.D., 1996. Plant respiration responses to climate determine geographic-distribution. Russ. Journal of Plant Physiology 43, 698–704.
- Davidson, E.A., 1987. Respiration and energy flow in two Australian species of desert harvester ants, *Chelalaner rothsteini* and *Chelalaner whithei*. Journal of Arid Environments 12, 61–82.
- 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 sociaux 30, 106–118.
- Fewell, J.H., Harrison, J.F., Lighton, J.R.B., Breed, M.D., 1996. Foraging energetics of the ant *Paraponera clavata*. Oecologia 105, 419–427.
- Hebling, M.J.A., Pentead, C.H.S., Mendes, E.G., 1992. Respiratory regulation in workers of the leaf cutting ant *Atta sexdens rubropilosa* Forel, 1908. Comparative Biochemistry and Physiology A. Comparative Physiology 101, 319–322.
- Hölldobler B., Wilson E.O., 1990. The Ants, Springer Verlag, Berlin.
- Kipyatkov, V.E., 1988. *Myrmica* prepares for winter. Science USSR 1, 76–83.
- Lighton, J.R., 1989. Individual and whole-colony respiration in an African formicine ant. Functional Ecology 3, 523–530.
- Lighton, J.R.B., Wehner, R., 1993. Ventilation and respiratory metabolism in the thermophilic desert ant, *Cataglyphis bicolor* (Hymenoptera, Formicidae). Journal of Comparative Physiology B-Biochemical, Systemic and Environmental Physiology 163, 11–17.
- MacKay, W.P., 1985. A comparison of the energy budgets of three species of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae). Oecologia 66, 484–494.
- Mariko, S., Koizumi, H., 1993. Respiration for maintenance and growth in *Reynouria japonica* ecotypes from different altitudes on Mt. Fuji. Ecological Research 8, 241–246.
- Martin, P.J., 1991. Respiration of the ant *Leptothorax unifasciatus* (Hymenoptera, Formicidae) at individual and society levels. Journal of Insect Physiology 37, 311–318.
- Nielsen, M.G., 1986. Respiratory rates of ants from different climatic areas. Journal of Insect Physiology 32, 125–131.
- Nielsen, M.G., 1987. Energetic cost of foraging. In: Eder, J., Rembold, H. (Eds.), Chemistry and Biology of Social Insects. Peperny, Munich, pp. 505–506.
- Nielsen, M.G., Baroni Urbani, C., 1990. Effect of load carriage on the respiratory metabolism of running worker ants of *Camponotus herculeanus* (Formicidae). Oikos 39, 137–142.
- 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.
- Peakin, G.J., Nielsen, M.G., Skyberg, N., 1989. Respiration during metamorphosis of sexuals in *Lasius flavus* (Hymenoptera Formicidae). Physiological Entomology 14, 203–210.
- Porter, S.D., Tschinkel, W.R., 1985. Fire ant polymorphism: the ergo-

- nomics of brood production. Behavioral Ecology and Sociobiology 16, 323–326.
- Radchenko, A.G., 1994. Taxonomic structure of the genus *Myrmica* (Hymenoptera, Formicidae) of Eurasia. (Original in Russian, English translation). Entomological Revue 74, 91–106.
- Reich, P.B., Oleksyn, J., Tjoelker, M.G., 1996. Needle respiration and nitrogen concentration in Scots Pine populations from a broad latitudinal range. Functional Ecology 10, 768–776.
- Schmidt, G.H., Reuss, H., 1990. Respiration and distribution of the mitochondria in the fat body cells during the caste differentiation of *Formica polyctena* (Foerster). Insectes sociaux 37, 294–314.
- Wardlaw, J.C., 1991. Techniques for rearing *Myrmica* ants (Hym.) and *Maculinea rebeli* Hir. caterpillars (Lep. Lycaenidae). Entomologist's Monthly Magazine 127, 233–241.
- Wilson, E.O., 1990. Success and Dominance in Ecosystems: The Case of Social Insects, Ecology Institute, Nordlünke.