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Standard metabolic rate of the fire ant, *Solenopsis invicta* Buren: effects of temperature, mass, and caste

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Abstract

Standard metabolic rates of *S. invicta* workers, males, female alates, larvae and pupae were determined using closed-system respirometry. $\dot{V}_{O_2}$ (ml h^{-1}) of all castes and life stages scaled with temperature and mass. Differences between castes and life stages are discussed in light of their different life histories and the different functions of these stages within the colony. Workers, female alates, male alates, larvae and pupae had mass-specific $\dot{V}_{O_2}$ (ml O_2 g wet weight^{-1} h^{-1}, corrected to 25°C) of 0.404±0.023, 0.316±0.010, 0.674±0.024, 0.291±0.020, and 0.227±0.015 (mean±SE), respectively. Measurement of CO_2 and O_2 made possible the examination of temperature and mass effects on respiratory quotient (RQ), as well as accurate transformation of O_2 consumption to metabolic rate (μW) for comparison with other ant species. Mass-specific metabolic rates of *S. invicta* females and workers compare favorably with data from 17 other ant species, but metabolic rates of males (177%) and pupae (42%) fall above and below predicted rates, respectively. Several equations relating temperature and mass to $\dot{V}_{O_2}$ are presented.

Keywords: Respiratory quotient; Mass scaling; Oxygen consumption; Respiration; Energetics

1. Introduction

The fire ant, *Solenopsis invicta* Buren, has been successful in colonizing large areas of the southeastern United States since its introduction in the 1930s (Buren, 1972; Vinson, 1994). Long recognized as a pest, *S. invicta* can also be important predators in agroecosystems (Reagan, 1986). Regardless of their status as pests or beneficials in any given situation, the fact that *S. invicta* is able to competitively displace native ants and can alter the composition of arthropod communities (Porter and Savignano, 1990) is indicative of their fundamental importance in ecosystems.

Energetics and respiratory physiology of *S. invicta* have received limited attention. Temperature effects on respiration, and mass scaling, or changes in physiological parameters as a function of body mass, are of comparative value both interspecifically and intraspecifically [for an overview of mass scaling phenomena, see Schmidt-Nielsen (1984) pp. 241]. Furthermore, reliable determination of these relationships is necessary for accurate estimation of energy budgets for the species. Since the pioneering work of Golley and Gentry (1964) energy budgets of ant species have received increased attention.

S. invicta colonies persist for several years, and are active throughout the year (Markin et al., 1971). *S. invicta* exhibits temperature optima for a number of functions including foraging (Markin et al., 1974; Porter and Tschinkel, 1987), nuptual flights (Markin et al., 1971), and colony growth (Porter, 1988; Porter and Tschinkel, 1993), with relatively wide temperature ranges for some activities. *S. invicta* appears to be restricted along the western front of infestation by high temperature and low rainfall (but see Phillips et al., 1996) and is restricted along the northern front by cold temperatures. Data on respiratory physiology of these animals in an area close to their introduction (Alabama) could be useful in future studies of their respiratory physiology in more extreme climates along the fronts of infestation.

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Elzen (1986) determined respiratory rates of *S. invicta* reproductives and workers at several temperatures and found significant differences, with male alates respiring at a greater rate than other castes. Porter and Tschinkel (1985) investigated relationships between worker size and respiratory rate, finding that respiratory rates increased with worker size, and mass-specific rates were lower in larger workers. Calabi and Porter (1989) investigated respiratory rates of three size classes of *S. invicta* workers at two temperatures, noting a 60% increase in respiration rate from 24 to 30°C, which corresponds to a typical Q_{10} value of 2. Their findings regarding mass effects were similar to those of Porter and Tschinkel (1985).

Given the importance of *S. invicta* in ecosystems in the Southeastern US, a more comprehensive work, investigating the effect of temperature, mass, and caste or life stage on respiration, is appropriate. We include measurement of respiratory quotient (RQ) and Q_{10}s for *S. invicta* castes and control for movement in the very active worker caste. Finally, mass scaling relationships are examined and compared with data for other ant species.

2. Materials and methods

2.1. Workers

Measurements of O_2 consumption and CO_2 production were obtained using *S. invicta* workers collected from a mature colony (containing workers, brood, and reproductives) located on the Auburn University campus in November and December of 1997. This colony, and the others referred to below, were assumed to be monogyne colonies as polygyny has not been reported in the Auburn, Lee County, AL area, and multiple dealate queens were not observed in colonies sampled. Ants were collected with a gardening trowel and placed in a small (19 cm wide×33 cm long×11 cm deep) plastic tray treated with a teflon emulsion to prevent ant escape. In the laboratory, colony fragments were provided with a test tube nest (20×150 mm test tube filled 2/3 to the top with water and plugged with cotton), a sugar solution, and insects (cockroaches and crickets). Colony fragments were maintained in the laboratory at room temperature (ca. 24°C) under an approximate 12:12 L:D photoperiod. Ants were used within 60 days of capture.

Ants were weighed individually on an electronic balance to the nearest 0.01 mg. Following weighing, each individual ant was placed in a 3 ml syringe (Becton, Dickinson and Company, Rutherford, NJ, USA) modified to serve as a closed-system respirometer. Each syringe was fitted with a two-way stopcock. A small (3 mm) hole was drilled in the wall of each syringe above the last gradation. Syringes were attached to a manifold through which dry, CO_2-free air was forced at the rate of ca. 230 ml/min/port. Air was allowed to flow through the syringes via the small hole by positioning the syringe plungers just above the edge of the hole, allowing enough room for air to flow but not allowing escape of the ants. After flushing with dry, CO_2-free air for 5 min, the volume of each syringe was adjusted to 1.5 ml, stopcocks were closed and syringes were placed in a temperature-controlled cabinet set at one of five experimental temperatures (15, 20, 25, 30, and 35°C). Temperature in the cabinet was checked with a calibrated mercury thermometer traceable to the US Bureau of Standards.

Incubation (1 to 3 h depending on temperature) took place under light from a 4 W red light bulb positioned approximately 50 cm above the experimental animals. The low level and color of light in the chamber facilitated filming of ants during incubation and had no apparent effect on ant activity. Activity was documented on videotape using a Panasonic GR-AX70u Compact VHS camera mounted on a tripod directly above the syringes containing ants. The distance (mm) traveled by each ant in a syringe during incubation was recorded. Using this method, we account for locomotory activity on the part of the experimental animals, and use only data from inactive to minimally active ants for analysis (see below).

We used a Sable Systems TR-3 respirometry system (Sable Systems, Henderson, NV, USA) to determine O_2 depletion and CO_2 enrichment in the syringe respirometers. Briefly, outside air was scrubbed of CO_2 and H_2O, drawn through a computer-controlled baselining system, a Li-Cor CO_2 and H_2O analyzer (LI-6262), a Sable Systems FC-1 Oxygen Analyzer, and a Sierra Instruments Side-Track flowmeter which was set to allow air to flow through the system at a rate of 150 ml/min at STP. A 1 ml sample of air from each syringe was injected into a syringe barrel installed anterior to the CO_2-H_2O analyzer, and passed through the system for analysis. Exact time of incubation (from sealing of the syringe to injection of the sample) was noted for each ant. Details on calculations involved and additional information on closed-system respirometry can be found in Lighton (1991).

2.2. Reproductives

In July 1997, alate male and female *S. invicta* were collected from mature colonies in Tuskeegee National Forest approximately 16 km from the Auburn University campus by breaking the tumulus of several mounds and aspirating the alates. Groups of alates were placed in small (9 cm×2 cm) petri dishes, each containing a 20 ml vial filled with ca. 2/3 water and plugged with cotton. Alates were held in the laboratory overnight Measurements proceeded as described for the workers, with the

exception of chamber volume (4 ml) and filming (see Section 4).

2.3. Immatures

Respiratory rates were determined at 10, 20, 30, 35, and 40°C for larvae and pupae of varying mass and undetermined age. A mass range was obtained for immatures by estimating the actual range in mounds from which collections were made, and choosing individuals representing the range of masses observed. Sampling, therefore, was not random but was undertaken so that we might duplicate the situation in in situ colonies. The majority of larvae collected were likely 3rd or 4th instar larvae, as larvae were generally >1 mm in length [length of larval instars of *S. invicta* were reported by O'Neal and Markin (1975)]. Larvae and pupae were collected in October 1997 from mounds near Auburn University with a gardening trowel. Brood, workers, and soil were placed in plastic shoeboxes treated with a teflon emulsion to prevent ant escape. The resulting colony fragments were provided with test tube nests, water, and crickets. Respirometry proceeded as described above for workers, within two days of capture. Since larvae and pupae are nonmotile, filming was unnecessary. Both larvae and pupae were incubated individually in syringe respirometers (1.5 ml volume).

2.4. Statistical analysis

Data were subjected to analysis of covariance (ANCOVA) (SAS Institute, 1985) to estimate the overall effects of temperature (main effect) and mass (covariate) on respiratory rate. Individual r^2, partial r^2, and β-coefficients were calculated for each factor in these analyses. Effects of temperature and mass on RQ were examined using analysis of variance (ANOVA). Caste or life stage effects on metabolic rate were investigated using ANOVA and mean separation was carried out with LSD tests. Specific comparisons were made with orthogonal contrasts. Linear regressions were performed where appropriate.

Units are as follows, except where otherwise indicated: mass in grams (g), volumes in ml, metabolic rate in microwatts (μW). Rate of oxygen consumption ($\dot{V}_{O_2}$) is expressed in ml per hour (ml h^{-1}) or ml per gram hour (ml g^{-1} h^{-1}), as noted. Means are reported with standard errors, except where otherwise noted.

3. Results

3.1. Workers: respiratory rates

Activity rates, expressed as distance traveled (mm h^{-1}), ranged from 0 to 2950 (one major worker at 35°C). To control for the confounding effect of activity on metabolic rate, we defined as inactive only those individuals moving at a rate of less than 75 mm h^{-1} (n=76, or ca. 19% of all workers) for the purposes of our investigation. We compared respiration rates of ants which exhibited zero movement during incubation (n=36, median=0.000922 ml h^{-1}) with those moving between zero and 75 mm h^{-1} (n=40, median=0.00111 ml h^{-1}) with a Mann-Whitney Rank Sum Test and found no significant difference between the median $\dot{V}_{O_2}$ of the groups (P=0.19). Examination of the residuals for the regression of mass-corrected $\dot{V}_{O_2}$ (ml $O_2 g^{-1}$ h^{-1}) on temperature revealed one outlier which was not included in our analysis.

Analysis of covariance yielded the following equation relating worker respiration to temperature and mass:

$$\log_{10}\dot{V}_{O_2} = -6.58(\pm 1.47) + 0.155(\pm 0.064)\text{Temperature} - 1.15(\pm 0.576)\log_{10}\text{Mass} + 0.050(\pm 0.025)\text{Temperature} \times \log_{10}\text{Mass}$$

(F=32, df=3, 72, $P<0.0001$, r^2=0.5712). Coefficients for temperature, mass and the interaction term were all significant (P=0.017, 0.049, and 0.047, respectively). The r^2 values for individual factors, partial r^2, and β-coefficients are presented in Table 1 to assist the reader in evaluating the contribution of each factor to the overall model; however, caution should be exercised in using partial r^2 as low partial r^2 does not necessarily indicate lack of statistical significance. To examine the effect of either independent variable alone on $\dot{V}_{O_2}$ we adjusted each data point, removing the mean effect of the unwanted variable and interaction term. In the original ANCOVA, the P-value for mass effect borders on insignificance (see above). Removing the mean effect of temperature resulted in a regression line with slightly negative slope of −0.096 (log-log regression), indicating very little effect of mass on $\dot{V}_{O_2}$ in our data (probably due in part to low mass range; see Table 2). Adjusting for the mean effect of mass resulted in the following equation relating mean $\dot{V}_{O_2}$ (ml h^{-1}) to temperature:

$$\log_{10}\dot{V}_{O_2} = -6.84 + 0.154\ \text{Temperature}$$

(r^2=0.9762). Oxygen consumption is often reported on a mass-specific basis. We calculated $\dot{V}_{O_2}$ in ml g^{-1} h^{-1} for comparability with other studies and for calculation of Q_{10} (see below). The regression of mean, mass-specific $\dot{V}_{O_2}$ on temperature yielded the equation:

$$\log_{10}\dot{V}_{O_2}(\text{ml g}^{-1}\text{ h}^{-1}) = -0.887(\pm 0.082) + 0.020(\pm 0.003)\text{Temperature}$$

(F=43.1, df=1, 3, P=0.007, r^2=0.9350) (Fig. 1).

Table 1
Individual r^2, partial r^2, and β coefficients for factors in ANCOVAs for all castes/life stages of *S. invicta*

Caste	Factor	r^2	Partial r^2	β-coefficient
Worker	Temperature	0.5469	0.0353	4.25
	$\log_{10}$ Mass	0.0031	0.0237	−0.62
	Interaction	0.5234	0.0241	3.51
Female alate	Temperature	0.9552	0.0106	3.64
	$\log_{10}$ Mass	0.0001	0.0040	−0.18
	Interaction	0.9419	0.0057	2.68
Male alate	Temperature	0.9167	0.0034	−2.36
	$\log_{10}$ Mass	0.00005	0.0143	0.35
	Interaction	0.9002	0.0067	−3.37
Larvae	Temperature	0.8300	0.8393	0.92
	$\log_{10}$ Mass	0.0379	0.0472	0.22
Pupae	Temperature	0.7689	0.7875	0.89
	$\log_{10}$ Mass	0.1104	0.1290	0.36

Table 2
Mass data (live weights) of various castes and life stages of *S. invicta* used in respirometry experiments

Caste	*n*	Mass (g) $\bar{X}$±SE	Minimum	Maximum
Workers	76	0.00296±0.0001	0.0001	0.00436
Female alates	55	0.01460±0.0019	0.00971	0.0177
Male alates	56	0.00730±0.0013	0.00598	0.00902
Larvae	56	0.00256±0.0002	0.00065	0.00557
Pupae	50	0.00289±0.0002	0.00063	0.00547

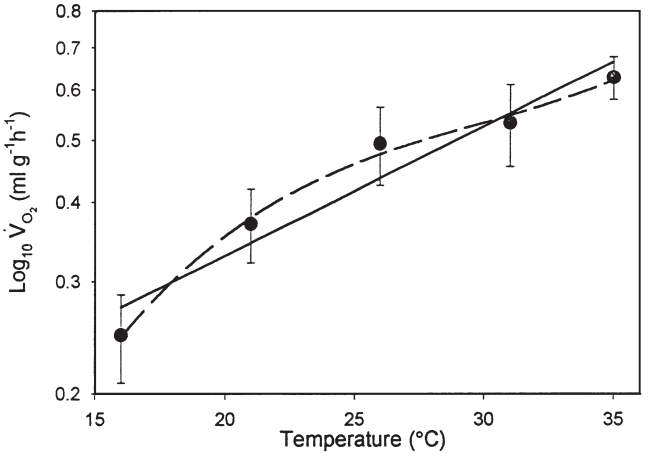

Fig. 1. Rate of oxygen consumption of *S. invicta* workers at several temperatures. Solid line represents the first-order regression of log-transformed oxygen consumption (ml g^{-1} h^{-1}) on temperature, broken line represents the third-order regression. See text for equations.

3.2. Respiratory quotient and Q_{10}

Respiratory quotient (RQ) of workers was not influenced by temperature (ANOVA, P=0.71) or by mass (ANOVA, P=0.067). Mean RQ of inactive individuals across all temperatures was 0.714±0.016 (n=76), which is statistically indistinguishable from mean RQ considering all individuals (0.706±0.007) (n=392) (t-test, P=0.06).

Mean Q_{10} can be calculated by taking the antilogarithm of the slope of the first order log-linear regression of $\dot{V}_{O_2}$ (ml g^{-1} h^{-1}) on temperature multiplied by 10, yielding a mean Q_{10} of 1.75 through our experimental temperature range. Information about changing Q_{10}s with respect to temperature can be useful, however, so we fitted a cubic equation to the temperature means to quantify changes in Q_{10} by differentiation of the polynomial (Lighton, 1989). The equation for the polynomial regression was:

$$\log_{10}\dot{V}_{O_2}(\text{ml g}^{-1}\text{ h}^{-1}) = -2.41(\pm 0.84) + 0.192(\pm 0.107)\ \text{Temperature} - 0.0061(\pm 0.0043)\ \text{Temperature}^2 + 0.00007(\pm 0.00006)\ \text{Temperature}^3$$

(r^2=0.9948) and is illustrated as the broken line in Fig. 1. While the model for the polynomial was not significant (P=0.09), a high F-value (64) and high r^2 indicated good fit. The fitted curve is rather typical of temperature effects on metabolic processes and is useful for illustrating changes in temperature sensitivity. The Q_{10} curve resulting from differentiation of the cubic equation is illustrated in Fig. 2.

3.3. Alates: respiratory rates

Both female and male alate respiratory rates were dependent on temperature and mass. For females, the

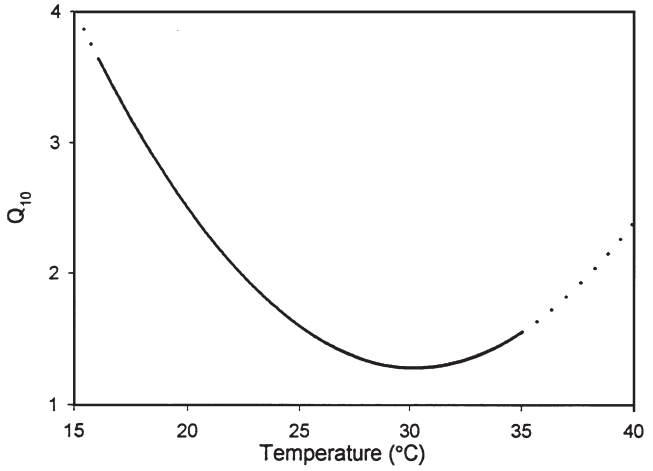

Fig. 2. Relationship between temperature and Q_{10} in *S. invicta* workers.

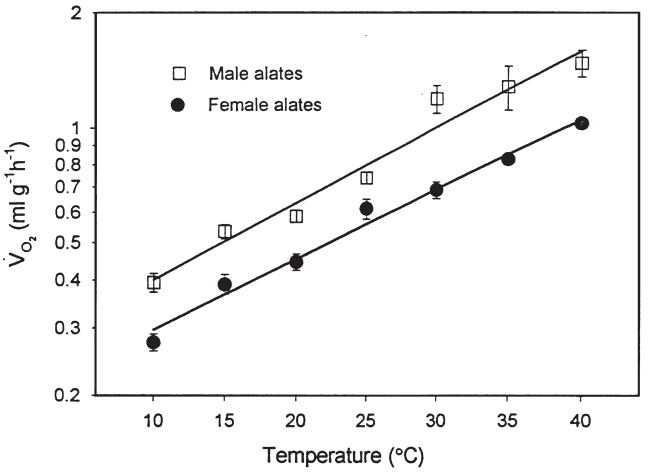

Fig. 3. Rate of oxygen consumption (ml g^{-1} h^{-1}) of male and female *S. invicta* alates at several temperatures. See text for equations.

equation relating oxygen consumption (ml h^{-1}) to temperature and mass was:

$$\log_{10}\dot{V}_{O_2} = -5.89(\pm 1.06) + 0.159(\pm 0.042)\ \text{Temperature} - 1.35(\pm 0.577)\ \log_{10}\text{Mass} + 0.063(\pm 0.023)\ \text{Temperature} \times \log_{10}\text{Mass}$$

(F=430, df=3, 52, $P<0.0001$, r^2=0.9613). For males, the equation was:

$$\log_{10}\dot{V}_{O_2} = 1.947(\pm 1.70) - 0.062(\pm 0.063)\ \text{Temperature} + 2.50(\pm 0.796)\ \log_{10}\text{Mass} - 0.049(\pm 0.030)\ \text{Temperature} \times \log_{10}\text{Mass}$$

(F=266, df=3, 52, $P<0.0001$, r^2=0.9388).

Temperature effects were examined as with workers, by regressing mass-specific $\dot{V}_{O_2}$ (ml g^{-1} h^{-1}) over temperature. For females:

$$\log_{10}\dot{V}_{O_2} = -1.58(\pm 0.038) + 0.043(\pm 0.001)\ \text{Temperature}$$

(F=899, df=1, 54, $P<0.0001$, r^2=0.9434). For males, the relationship was:

$$\log_{10}\dot{V}_{O_2} = -1.26(\pm 0.042) + 0.043(\pm 0.002)\ \text{Temperature}$$

(F=755, df=1, 54, $P<0.0001$, r^2=0.9333). The effect of temperature on oxygen consumption of male and female alates is illustrated in Fig. 3.

Adjusting each data point for mean temperature effect allowed for examination of mass effects on respiration of males and females. For males, regression of temperature-adjusted $\dot{V}_{O_2}$ (ml h^{-1}) on mass resulted in the equation:

$$\log_{10}\dot{V}_{O_2} = -0.078 + 1.05\ \log_{10}\text{Mass}$$

(r^2=0.2157) (Fig. 4). Regression of temperature-adjusted data for female alates results in an equation with r^2=0.0263; mass is obviously of little importance by itself as a predictor of $\dot{V}_{O_2}$ in female alates.

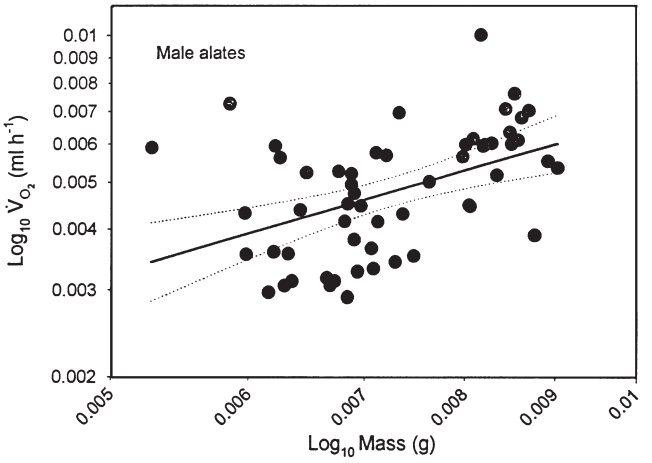

Fig. 4. Mass scaling of rate of oxygen consumption (ml h^{-1} adjusted to 25°C) of male *S. invicta* alates. The dotted lines enclose the 95% confidence interval for the regression.

3.4. Respiratory quotient and Q_{10}

There was no temperature by mass interaction for males or females, so analysis of the main effects on RQs were carried out separately using ANOVA. There was no mass effect on female alate RQs (P=0.47), but analysis of RQ of male alates yielded a significant relationship:

$$\text{RQ} = 0.884(\pm 0.067) - 39.15(\pm 9.13)\ \text{Mass}$$

(F=18.4, df=1, 54, $P<0.0001$, r^2=0.2541) (Fig. 5). Temperature had a significant effect on RQ for both sexes. For males, mean RQ values at each temperature ranged from 0.54 (±0.02) at 10°C to 0.65 (±0.02) at 40°C. The relationship between temperature and RQ for males, however, is not linear. RQs at 20 and 30°C are given in Table 3. Female RQ ranged from 0.53(±0.03) at 10°C to 0.72(±0.06) at 35°C, dropping thereafter. The equation relating RQ to temperature in female alates is:

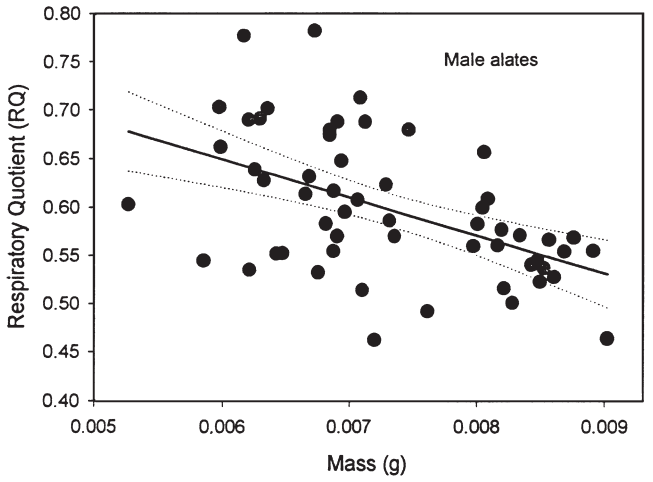

Fig. 5. Influence of body mass on respiratory quotient (RQ) in male *S. invicta* alates. The dotted lines enclose the 95% confidence interval for the regression. See text for equation.

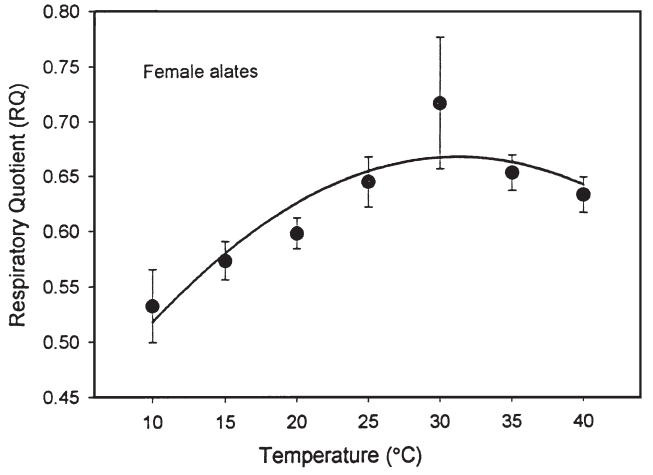

Fig. 6. Relationship between temperature and respiratory quotient (RQ) for female *S. invicta* alates. Error bars represent standard errors of the means. See text for equation.

$$RQ = 0.346(\pm 0.077) + 0.021(\pm 0.007)\ \text{Temperature} - 0.0003(\pm 0.0001)\text{Temperature}^2$$

(F=9.2, df=2, 4, P=0.03, r^2=0.8214) (Fig. 6).

The slopes of the lines relating $\dot{V}_{O_2}$ to temperature are identical for males and females, thus they share identical Q_{10}s. Calculating Q_{10} over our temperature range as above yields a mean Q_{10} of 2.69.

3.5. Immatures: respiratory rates

ANCOVA revealed no significant interaction between temperature and mass for larvae (P>0.5), so we removed the interaction term from the analysis. The equation relating rate of oxygen consumption (ml h^{-1}) to temperature and mass for larvae was:

$$\log_{10}\dot{V}_{O_2} = -2.89(\pm 0.353) + 0.0456(\pm 0.00263)\ \text{Temperature} + 0.549(\pm 0.134)\log_{10}\text{Mass}$$

(F=157, df=2, 43, P<0.0001, r^2=0.8771). Similarly, for pupae, the interaction term was non-significant (P>0.7). The relationship between rate of oxygen consumption (ml h^{-1}), temperature, and mass for pupae was:

$$\log_{10}\dot{V}_{O_2} = -2.78(\pm 0.215) + 0.0420(\pm 0.00223)\ \text{Temperature} + 0.600(\pm 0.0787)\ \log_{10}\text{Mass}$$

(F=202, df=2, 46, P<0.0001, r^2=0.8978).

In considering the effect of temperature alone on mass-specific $\dot{V}_{O_2}$ (ml g^{-1} h^{-1}) we fitted a polynomial line to the data. For larvae, the relationship was:

$$\log_{10}\dot{V}_{O_2} = -0.104(\pm 0.408) - 0.229(\pm 0.0621)\ \text{Temperature} + 0.0131(\pm 0.00272)\ \text{Temperature}^2 - 0.000184(\pm 0.0000362)\ \text{Temperature}^3$$

(F=146, df=3, 43, P<0.0001, r^2=0.9104). Pupal $\dot{V}_{O_2}$ (ml g^{-1} h^{-1}) scaled similarly with respect to temperature:

$$\log_{10}\dot{V}_{O_2} = -0.837(\pm 0.350) - 0.132(\pm 0.0519)\ \text{Temperature} + 0.00906(\pm 0.00223)\ \text{Temperature}^2 - 0.000135(\pm 0.0000295)\ \text{Temperature}^3$$

Table 3
Respiratory variables for different castes and life stages of *S. invicta*[a]

Caste	Respiratory Quotient $\bar{X}$±SE		$\dot{V}_{O_2}$ $\bar{X}$±SE
	20°C	30°C	ml g^{-1} h^{-1} at 25°C
Worker	0.741(±0.040)a	0.716(±0.031)a	0.404(±0.023)b
Female alate	0.597(±0.014)b	0.715(±0.060)a	0.316(±0.010)c
Male alate	0.612(±0.015)b	0.565(±0.012)b	0.674(±0.024)a
Larva	0.616(±0.0.34)b	0.621(±0.040)ab	0.291(±0.020)c
Pupa	0.557(±0.027)b	0.596(±0.030)b	0.227(±0.015)d

[a] Means within the same column that are followed by the same letter are not significantly different (LSD test, P>0.05).

(F=164, df=3, 45, $P<0.0001$, r^2=0.9161). Temperature effect on oxygen consumption of immatures is illustrated in Fig. 7.

We adjusted data to 25°C to examine the effect of mass alone. The resulting relationship between larval $\dot{V}_{O_2}$ (ml h^{-1}) and mass is:

$$\log_{10}\dot{V}_{O_2} = -1.76 + 0.549 \log_{10}\text{Mass}$$

(r^2=0.5585) and for pupae:

$$\log_{10}\dot{V}_{O_2} = -1.74 + 0.600 \log_{10}\text{Mass}$$

(r^2=0.2778) (Fig. 8).

3.6. Respiratory quotient and Q_{10}

Respiratory quotient was not affected by larval or pupal mass, or by temperature. Larvae had a mean RQ of 0.63±0.014. Mean RQ of pupae was 0.56±0.013.

To examine Q_{10} of immature stages, it may be most useful to consider that part of the curve prior to reduction in oxygen consumption (see Section 4). Performing a first-order regression of $\dot{V}_{O_2}$ (ml g^{-1} h^{-1}) over the temperature range 10 to 35°C, we obtained a slope for both immature stages which yielded Q_{10} of 3.44 and 3.31 for larvae and pupae, respectively.

3.7. Caste and life stage effects

The effect of caste and life stage on mass-specific oxygen consumption (ml O_2 g^{-1} h^{-1}) was investigated. Analysis of covariance (caste/life stage as the main effect and temperature as the covariate) indicated that temperature and caste/life stage had a significant effect on mass-specific $\dot{V}_{O_2}$ (F=165.5, df=9, 274, $P<0.0001$). There was a significant interaction between caste/life stage and temperature (F=9.94, df=4, 274, $P<0.0001$) indicating that the respiratory rates of different castes scale differently with temperature. Visual examination of the data provides a better understanding of the effect of caste/life stage. Worker respiration remains relatively consistent through our temperature range and respiration of males is higher than the other castes and life stages, whereas larvae, pupae, and queens respire at similar rates (Fig. 9).

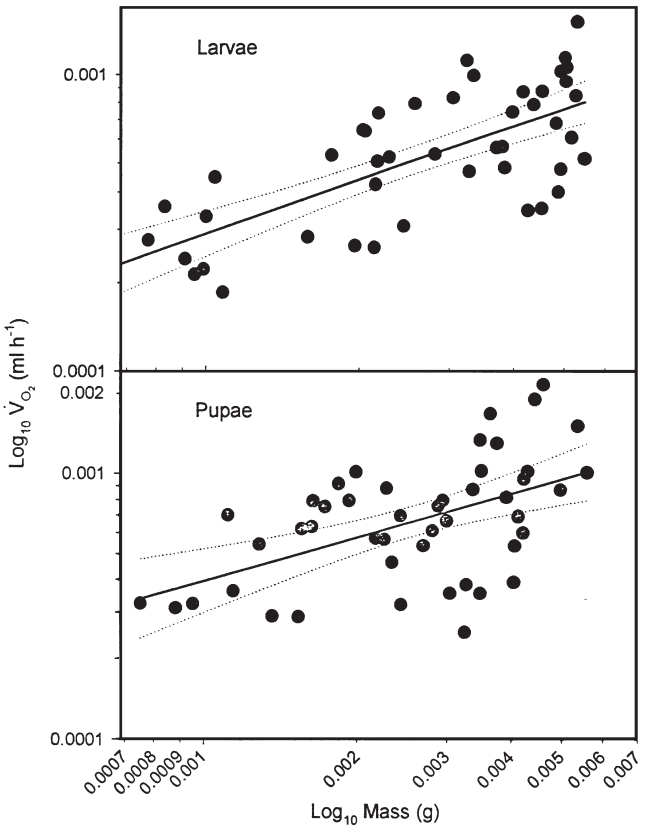

Fig. 8. Mass scaling of rate of oxygen consumption (ml h^{-1}) in *S. invicta* larvae and pupae. The dotted lines enclose the 95% confidence intervals for the regressions. See text for equations.

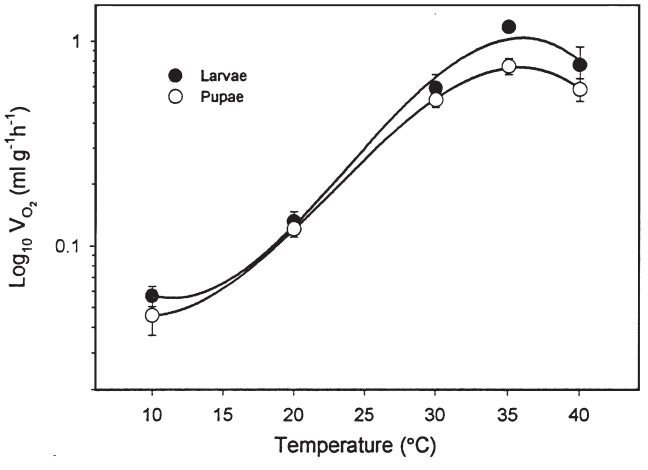

Fig. 7. Relationship between temperature and rate of oxygen consumption (ml g^{-1} h^{-1}) in *S. invicta* larvae and pupae. Error bars represent standard errors of the means. See text for equations.

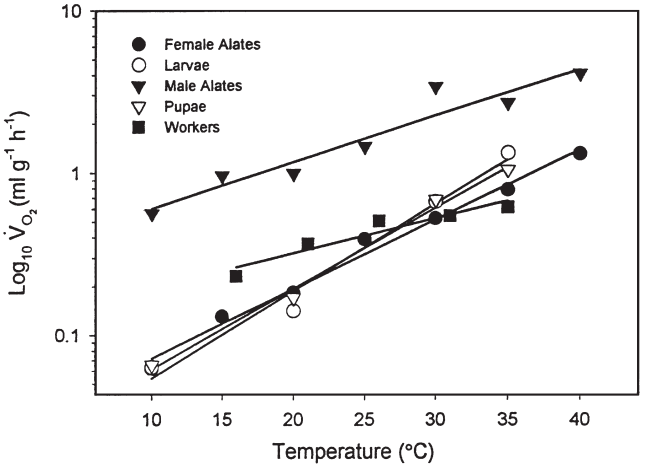

Fig. 9. Comparison of temperature effects on rate of oxygen consumption (ml g^{-1} h^{-1}) in *S. invicta* castes.

The effect of caste/life stage on $\dot{V}_{O_2}$ was also examined by using temperature-corrected, mass-specific $\dot{V}_{O_2}$ (ml g^{-1} h^{-1}) for individuals and conducting an analysis of variance with an appropriate mean separation (in this case an LSD test is used). Male alates had the highest $\dot{V}_{O_2}$ (0.674±0.024), followed by workers (0.404±0.023), female alates and larvae (0.316±0.010 and 0.291±0.020, respectively), and pupae (0.227±0.015) (Table 3). Orthogonal contrasts were then used to address specific questions. Males (male alates) respire more quickly than workers and female alates (F=165.6, df=1, 278, $P<0.0001$). Workers respire more rapidly than female alates (F=11.0, df=1, 278, P=0.001), and adult females as a group (workers and alates) respire at a faster rate than immature stages (F=24.3, df=1, 278, $P<0.0001$). Since temperature significantly affected RQ in some life stages, pooling the data across temperatures was not appropriate, so we compared RQs of castes and life stages at two temperatures, 20 and 30°C. ANOVA indicated significant differences among RQs for stages (F=4.05, df=4, 43, P=0.007 and F=3.57, df=4, 39, P=0.014 for 20 and 30°C, respectively). Mean separation was carried out using an LSD test. At 20°C, mean worker RQ (0.741±0.040) was significantly greater than that of other castes and life stages ($P<0.05$) (Table 3). At 30°C, worker and female alate RQs were very similar (0.716±0.031 and 0.715±0.060, respectively), and were greater than mean RQs of males and pupae (0.565±0.012 and 0.596±0.030, respectively), while mean larval RQ was intermediate and statistically indistinguishable from all other stages ($P>0.05$). RQ differences were examined more closely using orthogonal contrasts. Adult female (workers and female alates) RQ was not significantly greater than RQ of immature stages at 20°C (P=0.16), but was greater at 30°C (F=10.6, df=1, 39, P=0.002). Worker RQ was significantly greater than female alate RQ at 20°C (F=7.84, df=1, 43, P=0.008), but not at 30°C (P=0.99). Finally, male RQ was not statistically distinguishable from that of females (workers and alates) at 20°C (P=0.067), but was significantly greater at 30°C (F=7.74, df=1, 39, P=0.008).

3.8. Comparison with other ant species

A significant regression of log-transformed, temperature-corrected $\dot{V}_{O_2}$ on log-transformed mass is not possible for our data on *S. invicta* workers. This is likely due to the low mass range in our study (see Section 3) due to movement of smaller individuals. Using mean metabolic rate for workers we can check our values against those reported for other ant species. When respiration data for *S. invicta* is converted to mean microwatts at 25°C and plotted with metabolic rate data for other ant species (data from Lighton and Fielden, 1995) (Fig. 10A), it is evident that our worker data are consistent with known values for other ants. Assuming RQ of 0.72 and Q_{10} of 2 in calculating metabolic rate of other ant species, the overall equation relating mass to standard metabolic rate (μW) for those species is:

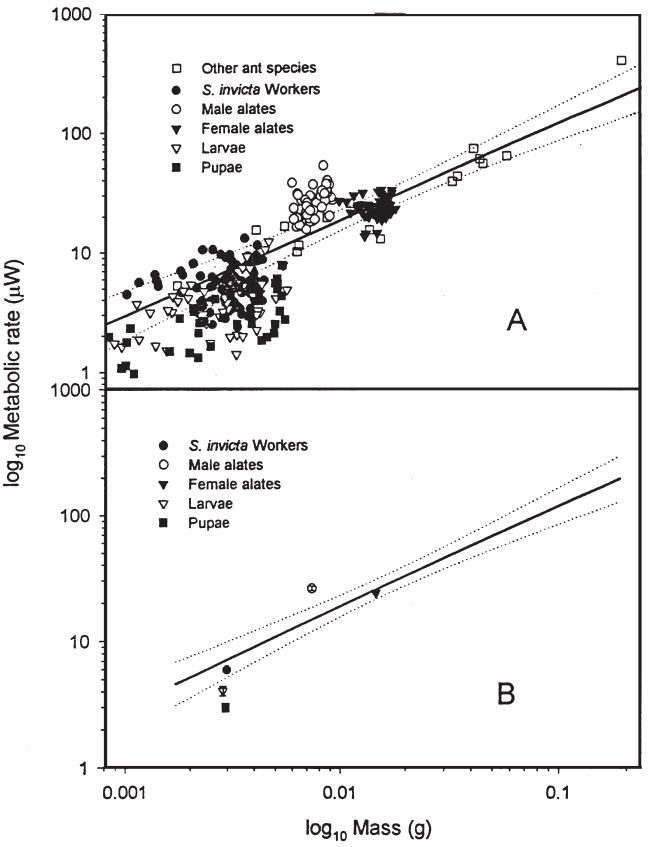

Fig. 10. Mass scaling of metabolic rate (μW) for several ant species (see citation in text). Upper graph shows all *S. invicta* data for comparison, lower graph illustrates mean values for *S. invicta* castes/life stages and overall regression line for other ant species. See text for equations. The dotted line represents the 95% confidence interval for the regression.

$$\text{Standard Metabolic Rate} = 753(\pm 1.39)\ \text{Mass}^{0.799(\pm 0.077)}$$

(F=108.8, df=1, 15, $P<0.0001$, r^2=0.8788). We assume reasonable values for Q_{10} and RQ because available data are fragmentary, and our assumed values approximate those generally found in studies of insect metabolic rate. For species-specific values (where available), see Lighton and Fielden (1995). Regression of temperature-corrected metabolic rate on mass for *S. invicta* adults (workers, males, and female alates) yields the equation:

$$\text{Standard Metabolic Rate} = 1242(\pm 1.27)\ \text{Mass}^{0.888(\pm 0.046)}$$

(F=370.32, df=1, 185, $P<0.0001$, r^2=0.6668). If we exclude males, which have a significantly higher respiratory rate than other castes (see results above), the equation becomes:

$$\text{Standard Metabolic Rate} = 708(\pm 1.22)\text{Mass}^{0.816(\pm 0.04)}$$

(F=468, df=1, 130, $P<0.0001$, r^2=0.7827). This equation

and the equation above for other ant species share a common mass scaling exponent of 0.813 (*t*-test, *P*=0.85).

4. Discussion

It is important when considering the results of any study of metabolic rates to carefully consider the conditions under which measurements were obtained. To obtain accurate and consistent measures of O_2 consumption and CO_2 production, and to quantify movement, it may be necessary to employ methods which may not lend themselves to natural behavior of the experimental animals. Confinement of a lone ant in a plastic syringe containing dry, CO_2-free air is certainly far from the natural conditions under which ants go about their daily activities. Movement, possibly induced by placing experimental animals in unnatural surroundings, is a serious concern in studies of metabolic rates. Male alate *S. invicta* ventilated discontinuously, with few exceptions, with dry, CO_2-free air flowing over them (Vogt and Appel, personal observations) and vigorous movement disrupts the discontinuous gas exchange cycle (Lighton, 1990). Tschinkel (1993) reported that male alates would not stop moving under his respirometry conditions (constant volume respirometer in the presence of KOH). Observations of alates in the laboratory confirm that alates exhibited very little or no movement when confined individually in sealed syringes during our experiments. It may be that the conditions under which we measured respiration in this study were less disruptive to the male alates. Additionally, low standard errors about the means at high temperature (see Fig. 3) are likely indicative of little or no variability due to movement of individuals. Investigators have observed increasing activity of male ants as the time of mating flight drew near (Nielsen, 1985); it may be that our collections were made shortly after eclosion of male alates in the mounds we sampled. A separate study of discontinuous gas exchange in male alates was conducted using ants from the same collections, and all males (*n*=44) assumed a quiescent state and ventilated discontinuously at several temperatures (Vogt and Appel, personal observations). Female alates ventilated discontinuously almost without exception under the same conditions as males (Vogt and Appel, personal observations) except at temperatures of 30°C and above. At 25°C ventilation was discontinuous but very rapid, and at 30°C the cycle broke down but there was no apparent increase in locomotory activity of female alates.

Ants of all castes in undisturbed, intact laboratory colonies exhibit occasional, brief periods of activity, and attempts to modify the behavior of experimental animals or obtain ideal conditions for measurement of basal metabolic rate (i.e., depriving subjects of food prior to a study) can adversely affect the animals in some instances (Speakman et al., 1993). By filming workers during incubation we were able to control for locomotory and escape behavior, again insuring that our data reflects the standard metabolic rate. Filming of workers was necessary due to the high level of activity observed in many individuals. *S. invicta* workers are rather small relative to most other ant species investigated to date and may have been induced to move about by desiccating conditions in respirometers filled with dry air. *S. invicta* workers can die under desiccating conditions within 6–7 h (Hood and Tschinkel, 1990); however, workers in our study were confined for no more than three hours. Additionally, Jaffe and Hebling-Beraldo (1990) hypothesize that individuals of highly social species of ants exhibit more activity than individuals of less socially complex species, resulting in higher metabolic rates. *S. invicta* exists in large, highly social colonies, and only approximately 19% of our workers remained inactive enough to be included in our analyses.

We did not have concerns about locomotory activity with larvae and pupae, which are non-motile. Larval respiratory rates may be influenced by the presence of workers through feeding activity; in our study, larvae were confined in respirometers without workers. No attempt was made to starve individuals for any amount of time prior to our measurements, and digestive processes may have accounted for some of the variability in respiratory rates between individuals.

The effect of mass on respiratory rates of ants has been investigated by many authors (e.g., Peakin and Josens, 1978; Jensen, 1978; Jensen and Neilsen, 1975; Nielsen, 1985; Lighton, 1989). Rigorous testing of hypotheses requiring comparative data between species necessitates similarity among methods. Activity is a primary concern for researchers investigating mass scaling relationships and energetics, and ours is the first study on *S. invicta* respiration to control for worker activity during measurement of respiratory rates. Fig. 10B illustrates mean metabolic rates of the castes and life stages of *S. invicta* compared to data from Lighton and Fielden (1995) from several other ant species.

Some interesting differences exist in the metabolic rates of different castes. Males have high metabolic rates and are very lean, both adaptations for rapid flight and mating. The males sole purpose is reproduction, and they differ markedly from female alates and workers in physical appearance and physiology. It is worth noting that adaptation for flight in males requires large flight muscles and that males carry very little body mass in the form of fat reserves. The resulting high percentage of metabolically active tissue might explain the high mass scaling exponent (1.05) in males. It is clear that male alates differ from other castes with respect to metabolic rate and should probably be considered separately in modeling the effect of mass on respiration. The very low mass scaling exponent observed for female alates may be

due to a relatively high percentage of non-metabolically active fat. During female alate maturation prior to mating flights, the rate of fat gain exceeds the rate of lean mass gain, and mature individuals can contain approximately 50% (49±2.7%) fat (Tschinkel, 1993). It is worth noting that some female alates weighing less than 12 mg were used in our analyses (see Table 2) and these smaller individuals are likely not flight-ready.

Immature stages have low metabolic rates relative to adults. We did not differentiate between larval instars in our study, and differences in respiratory rates between instars may have accounted for some of the variation in respiratory rates (Takahashi-Del-Bianco et al., 1998). The majority of larvae in our study, however, were likely 3rd and 4th instars (see Section 2). The predicted rate of O_2 consumption in our study for larvae at 25°C (0.257 μl mg^{-1} h^{-1}) lies between the values for 3rd and 4th instar larvae determined by Takahashi-Del-Bianco et al. (1998) for *Camponotus rufipes* (Fabr.) in Brazil.

Many researchers express O_2 consumption per mass on a dry weight basis. While dry weights were not obtained in this study, we can estimate dry weight of *S. invicta* workers based on other studies (Appel et al., 1991; Calabi and Porter, 1989; Porter and Tschinkel, 1985; Vogt and Appel, unpublished data). However, to compare with studies that express mass-specific respiratory rates in μl mg dry $weight^{-1}$ h^{-1}, if percent body water is given, we can estimate mass-specific respiratory rates on a live-weight basis for those studies for comparison with our data. For example, Calabi and Porter (1989) found that their *S. invicta* workers contained an average of 53% total body water. Their medium workers (mean dry weight 0.68 mg, or 1.33 mg live weight) respire at a rate of 2.16 μl mg dry $weight^{-1}$ h^{-1}, or 1.02 μl mg live $weight^{-1}$ h^{-1} at 30°C. Their large workers (mean live weight 4.8 mg) respired at a rate of 0.73 μl mg live $weight^{-1}$ h^{-1} at 30°C. Our inactive workers, at 31°C (mean live weight 2.99 mg, or somewhere in between the size classes used by Calabi and Porter, 1989), respire at a rate of 0.53 μl mg live $weight^{-1}$ h^{-1}. The lower rate in our study is likely due to our use of individual, inactive animals and represents a better estimate of standard metabolic rate for this species (they note in their results that their data represent a 25% increase in respiratory rate from Porter and Tschinkel, 1985). Another study on *S. invicta* respiration is available for comparison (Elzen, 1986). His value at 30°C (approximately 0.6 ul mg live $weight^{-1}$ h^{-1}, estimated from figure) is only slightly (ca. 12%) greater than ours at 31°C. Finally, Porter and Tschinkel (1985) reported respiratory rates at 30°C. Their reported mass scaling exponent for workers (0.805) is very similar to that calculated herein (less male alates) and the estimated exponent for the data from Lighton and Fielden (1995). Using the equation relating respiration per individual to dry weight reported by Porter and Tschinkel (1985) we can substitute the estimated mean dry weight of our experimental animals at 31°C (1.48±0.40 mg) for comparison. Their equation is:

$$y = 1.51x^{0.805}$$

and, by substitution, the predicted respiratory rate for our workers would be approximately 2.07 μl h^{-1}. The actual observed rate in our study was 1.42±0.52 μl h^{-1}, or 69% of the predicted value. Variation in respiratory rates between studies could be due to nutritional status of colonies, seasonal differences, or quite possibly worker movement in studies which do not account for activity. We suspect that a great deal of variability in respiratory rates could be eliminated by close monitoring of activity so that active individuals or groups can be disregarded in analyses, or activity effects can be quantified and corrected for.

Q_{10} of *S. invicta* workers varies with temperature (Fig. 2), and can be used to make inferences about preferred temperature ranges for individuals (where they are least sensitive to temperature change). Lack of data at 40°C precludes estimation of Q_{10} at high temperatures, but is understandable in light of the critical thermal limit of fire ant workers, 39 to 41.8°C (Cokendolpher and Phillips, 1990) and their preferred temperatures (Porter and Tschinkel, 1993). Escape behavior by the ants at 40°C made measurement of standard metabolic rate impracticable. The lowest area of the Q_{10} curve (approximately 29°C) agrees closely with the maximal foraging temperature of *S. invicta* (22 to 36°C) (Porter and Tschinkel, 1987). It may be advantageous for ants to forage at temperatures where their metabolic rate is not subject to rapid increase with changing temperature (Lighton, 1989). The preferred temperature of *S. invicta* workers changes with ambient relative humidity, acclimation temperature, and hunger (Cokendolpher and Francke, 1985; Porter and Tschinkel, 1993). Interestingly, the temperature corresponding to the low point on our Q_{10} curve agrees most closely with *S. invicta's* preferred temperature at 100% relative humidity in the study by Cokendolpher and Francke (1985) (29.7±2.4°C) despite the fact that our experimental animals were incubated in dry air. The minimum Q_{10} also lies close to the preferred temperature of well-fed *S. invicta* workers as determined by Porter and Tschinkel (1993). Our experimental animals were maintained with high humidity test tube nests, and experienced high humidity conditions with the exception of the relatively brief periods of incubation.

Q_{10}s observed for other castes and life stages are illustrative of their physiological requirements and life histories. Brood (larvae and pupae) exhibit high mean Q_{10}s over our 30°C temperature range. Brood are tended by workers which move within the mound to areas of suitable temperature, resulting in effective behavioral thermoregulation (Porter and Tschinkel, 1993). High Q_{10}s of immature stages may be indicative of the ther-

moregulatory nature of the mound built by *S. invicta*, and the ability of developing brood to take rapid advantage of increases in temperature to increase respiration, and developmental rate (see Peakin et al., 1995). With Q_{10}s>3, brood was more sensitive to temperature changes than males, workers, or female alates. Interestingly, maximal respiration rates of brood in our study lies just above the preferred temperature range for brood in *S. invicta* colonies (median=31°C) (Porter and Tschinkel, 1993).

Our respirometry methods offer advantages over earlier methods used to determine respiration of *S. invicta*, not the least of which is the ability to concurrently obtain measures of CO_2 production and O_2 consumption, making analysis of RQ and estimation of metabolic substrate possible. RQs of male alates increased with decreasing mass (Fig. 5). Fat content of male alates is very low (~5%) following eclosion (MacKay, 1985), and they gain little (ca. 6%) mass during maturation (Tschinkel, 1993). Males used in our study were pooled from several colonies. We cannot say with confidence that heavier males are necessarily older individuals. Differences in mass may be due to source colony, and differences in RQ might reflect differences in fat content or stage of maturation. Female RQs were not mass-dependent but were significantly affected by temperature. Changes in RQ might reflect changes in metabolic substrate from fat to carbohydrate in preparation for activity as temperatures approach those favorable for mating flights. This hypothesis could easily be tested by collecting female alates for respiratory analysis at different times before, during, and after mating flights.

RQs of immature stages are indicative of diet. Larvae are fed bits of insects, oils, and a host of other food items high in fats, and the low observed RQ in our study indicates fat metabolism. Pupae undergoing metamorphosis rely on stored fat for energy, would be expected to have a very low RQ and in fact exhibit the lowest mean RQ of all castes and life stages. Worker RQ lies within the range expected for fat metabolism, and our workers were collected relatively late in the year when their fat content would be expected to be high (Ricks and Vinson, 1972; Tschinkel, 1993).

In conclusion, the standard metabolic rate of *S. invicta* workers and queens is similar to that reported for other ant species. Deviations from the line presented in Figs. 10A and 10B are informative and reflect the different functions and physiological characteristics of castes and life stages. As pointed out by Elzen (1986), deviations from the expected proportional relationship of oxygen consumption to mass can be addressed through examination of the biological differences between castes. Temperature and mass effects on RQ, where they occur, are more difficult to explain; however, with the advent of high-resolution, rapid respirometry equipment and techniques, hypotheses regarding changes in RQ can now be easily tested. Finally, accounting for activity of individuals allows for more rigorous testing of hypotheses concerning mass scaling phenomena and temperature effects, as well as bringing to light some important differences in activity levels of large and small individuals (to be addressed in another study). The equations presented herein should prove useful in future work on fire ant energetics, group effects, and other areas of study where metabolic rates are of interest.

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