Shaking a leg and hot to trot: the effects of body size and temperature on running speed in ants

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Abstract. 1. Data were compiled from the literature and our own studies on 24 ant species to characterise the effects of body size and temperature on forager running speed.

2. Running speed increases with temperature in a manner consistent with the effects of temperature on metabolic rate and the kinetic properties of muscles.

3. The exponent of the body mass-running speed allometry ranged from 0.14 to 0.34 with a central tendency of approximately 0.25. This body mass scaling is consistent with both the model of elastic similarity, and a model combining dynamic similarity with available metabolic power.

4. Even after controlling for body size or temperature, a substantial amount of interspecific variation in running speed remains. Species with certain lifestyles [e.g. nomadic group predators, species which forage at extreme (>60 °C) temperatures] may have been selected for faster running speeds.

5. Although ants have a similar scaling exponent to mammals for the running speed allometry, they run slower than predicted compared with a hypothetical mammal of similar size. This may in part reflect physiological differences between invertebrates and vertebrates.

Key words. Allometry, ants, body mass, locomotion, running speed, temperature.

Introduction

After growth and maintenance, locomotion represents the main energetic cost for most animals (Alexander, 1999). The speed at which an animal moves has implications for home range size, dispersal ability, foraging mode, predator avoidance, reproductive strategy, and the ability to cope with changes in climate or land use. However, to understand the fundamental role locomotion plays in shaping an animal's life history, it is first necessary to gain an understanding of how running speed is affected by both biomechanical and environmental constraints. Two variables in particular have received much attention for potentially influencing rates of locomotion: body size and temperature. Running speed in various groups of animals has been empirically observed to increase with body size (McMahon, 1975; Peters, 1983), and temperature has also been observed to have a positive effect on running speed for a number of vertebrate and invertebrate ectotherms at least up to some critical temperature (Bennett, 1990). While a variety of mechanistic explanations have been proposed for these relations, there has been little consensus on the underlying principles. More importantly, with the exception of mammals, few attempts have been made to characterise general patterns of running speed across a broad suite of species.

Ants represent an ideal group for examining the effects of body size and temperature on running speed. Ants are ubiquitous components of most ecosystems (Holldobler & Wilson, 1990) and experience a broad range of foraging temperatures, from 5 to over 70 °C at the soil surface (Christian & Morton, 1992). Species share basic morphological similarities and yet they range in size by three orders of magnitude, including both

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intra- and inter-specific variation. To our knowledge, this is the first study that examines the effects of body size and temperature on running speed across a large number of invertebrate species. Establishing these relationships and comparing them to observed relationships in vertebrates represents a test of the universality of running speed allometry.

In this paper, proposed models are reviewed for how running speed should vary with temperature and body size. Data are then presented for 24 species of ants collected from the literature and gathered in the field to evaluate these published models. Body size and temperature together are not expected to explain all of the variation in ant running speed. Oster and Wilson (1978) discussed the idea that different ant species, often of similar size or occurring in similar climates, appear to vary in *tempo* of foraging activity, and that this variation may reflect different selective foraging strategies. Running speed is clearly a critical variable determining both individual and colony level foraging efficiency. Thus, a number of ecological traits are also examined to see whether they may explain some variation in running speed after size and temperature have been accounted for.

Models

Temperature

By noting that running speed is the product of stride length and stride frequency, one can begin to predict how temperature and body size should affect running speed. Temperature affects rates of oxygen supply (Krogh, 1914; Gillooly *et al.*, 2001) as well as various kinetic properties of muscles that influence locomotor performance (Heinrich, 1981; Bennett, 1990; Marsh, 1990; Rome & Bennett, 1990). Kinetic properties include twitch contraction time (Bennett, 1990) and deactivation rate of cross-bridge cycling (Josephson, 1981; Marsh, 1990), both of which may limit limb cycling frequency. A model proposed by Gillooly *et al.* (2001; Brown *et al.*, 2004) predicts a general temperature effect on biological rates based on reaction kinetics described by a Boltzmann factor $e^{-E/kT}$, where T is temperature in Kelvin, E is the average activation energy of reactions involved in metabolism, and k is Boltzmann's constant (8.62×10^{-5} eV K^{-1}). This model accurately characterises the temperature dependence of metabolic rate over the temperature range of most biological activity (0–40 °C; Gillooly *et al.*, 2001). If stride frequency is partly determined by metabolic rate and its effects on muscle kinetics, then a Boltzmann-like effect of temperature on ant running speed is expected. Stride length is expected to depend solely on ant morphology and therefore should be independent of temperature.

Body size

Much debate has revolved around how running speed should scale with body mass (Table 1). Here a thorough discussion of all of the relevant biomechanical theory is not attempted, although the model of dynamic similarity has received recent support (Alexander & Jayes, 1983; Christiansen, 2002; Alexander,

Table 1. Models relating animal mass to running speed and their predicted allometric exponents.

Model	Reference	Allometric exponent
1. Geometric similarity	Hill (1950)	0
2. Elastic similarity	McMahon (1975)	1/4
3. Static stress similarity	McMahon (1975)	2/5
4. Dynamic similarity	Alexander and Jayes (1983)	1/6
5. Metabolic power	Schmidt-Nielsen (1984)	1/12
6. Dynamic similarity × metabolic power	Proposed here	1/4

2005). Dynamic similarity assumes geometric similarity in form as well as simple linear scaling of all times and forces involved in locomotion. As an example, the motion of two pendulums of different length swinging through the same angle is dynamically similar. In fact, a number of authors have suggested that the limbs and body of a walking or running animal can be viewed as an inverted pendulum (McMahon, 1975; Biewener, 2003). Dynamic similarity predicts that stride frequency scales with leg length as $f \propto L^{-1/2}$ (just as the frequency of a pendulum varies as the inverse square root of its length) and assuming isometry ($L \propto M^{1/3}$) then body mass should scale with stride frequency as $f \propto M^{-1/6}$. Assuming that stride length is proportional to leg length in a geometrically similar animal, then $l \propto M^{1/3}$, and thus running speed scales as $v \propto M^{1/6}$. For a collection of East African mammals, Pennycuick (1975) found stride frequency to scale as $f \propto M^{-0.17}$, and Garland (1983) noted that for 106 mammal species ranging from shrews to elephants, $v \propto M^{0.17}$ in apparent accordance with the dynamic similarity model. Closer examination of Garland's and other complete mammal datasets (Christiansen, 2002; Iriarte-Diaz, 2002), however, suggests a more complex relationship between running speed and body size better characterised either by non-linear scaling, or by fitting two or more separate scaling relationships to the data. Iriarte-Diaz (2002) found that the model explaining the most variation in running speed broke the data into mammals <30 kg ($v \propto M^{0.24}$) and mammals >30 kg ($v \propto M^{-0.16}$). At larger sizes, mechanical stress on musculoskeletal design presumably becomes an important constraint that smaller animals do not face (Christiansen, 2002; Iriarte-Diaz, 2002; Biewener, 2003).

The above model is strictly biomechanical (as are models 1–3 in Table 1), in that it depends solely on the scaling of body proportions and the consequent forces that might be generated for a given limb length or muscle contraction. What these models lack is an explicit treatment of how energy available for locomotion scales with body size. Oxygen supply to tissues is a function of metabolism and typically scales with $M^{3/4}$ (Kleiber, 1932; Peters, 1983). A similar scaling has been observed for absolute rates of oxygen consumption ($VO_{2\ max}$), the activity of myosin ATPase, the volume density of mitochondria, and the rate of muscle shortening (Lindstedt *et al.*, 1985). In contrast to how energy supply scales with body size, the absolute cost of locomotion typically scales with $M^{2/3}$ (Taylor *et al.*, 1982; Schmidt-Nielsen, 1984). Thus, larger animals should have more available metabolic power, which should scale as $M^{3/4}/M^{2/3}$ or

$M^{1/12}$, which Schmidt-Nielsen (1984) argued should be linearly related to running speed. Schmidt-Nielsen (1984) also allowed for a slightly higher exponent for this running speed allometry given that maximum metabolic power may increase with body size faster than the $M^{3/4}$ of resting metabolic rate.

If biomechanical and energetic constraints on stride frequency are multiplicative, then combining the frequency-leg length prediction from dynamical similarity with the body size allometry predicted by available metabolic power yields:

$$f \propto L^{-1/2} M^{1/12} \propto M^{-1/6} M^{1/12} \propto M^{-1/12} \qquad (1)$$

assuming that leg length scales as $M^{1/3}$. If stride length scales linearly with leg length, then the running speed allometry is given as

$$v \propto lf \propto M^{1/3} M^{-1/12} \propto M^{1/4}. \qquad (2)$$

Finally, by remembering that temperature is expected to affect stride frequency through its exponential effect on biochemical kinetics and muscle contraction rates, a full model of the body size and temperature dependence of running speed can be described as

$$v \propto M^{1/4} e^{-E/kT}. \qquad (3)$$

Thus, a number of models exist that predict that running speed should increase with body mass raised to some power between 0 and 0.4. Full (1997) estimated the exponent for a group of 32 insects at 0.10, while Peters (1983) reported values of 0.29–0.36 for various beetle groups based on the studies of Buddenbrock (1934) and Hempel (1954). In general, the allometric models presented here are for comparisons of *physiologically similar speed* across species. While some researchers have used maximum speed for constructing these relationships (e.g. Garland, 1983; Christiansen, 2002), others have used characteristic speeds such as the trot-gallop transition in mammals (e.g. Heglund *et al.*, 1974; McMahon, 1975). Here, the assumption is made that the sustained running speed achieved by ants when foraging represents such a physiologically similar speed for comparison.

Methods and data

Data collection

Data were collected on ant running speed from 19 published studies on 22 different species, as well as our own unpublished data on six species (Appendix 1). Studies were identified by searching Web of Science and Google Scholar using the following key words: *ant* AND (*velocity* OR *running speed* OR *locomotion*). All search results and relevant citations within those results were examined and all data on running speed as a function of body size and/or temperature that were provided in either raw or graphical form were extracted. With one exception (*Cataglyphis bicolor*, see below), the data are for sustained running speeds of unladen ants measured over a distance of 0.5–2 m, with the ants typically travelling away from the nest on a

roughly linear trajectory. Studies reporting temperature most often reported air temperature, often near the soil surface, and it is assumed that this is well correlated with ant body temperature.

Data for *Acromyrmex versicolor* and *Messor pergandei* were collected by A.H.H. and F.B. near Bahía Kino, Sonora, Mexico from 9–15 March 2002. Unladen running speed was measured for ants from five colonies of each species over relatively even, obstacle-free terrain. Air temperature was recorded simultaneously with each speed measurement at 1–2 mm above the ground. Ants were collected and stored in individual airtight vials, and wet mass was measured to the nearest 0.1 mg 7 days after collection. Hind femur length (suture with the trochanter to articulation with the tibia) was measured to the nearest 0.1 mm, and was used to estimate total hind leg length based on the femur-hind leg relationship established for a subset of individuals.

Data for *Atta colombica* were collected by A.H.H. on Barro Colorado Island (BCI), Panamá on 7 and 9 November 2003. Unladen running speed was measured for outbound ants from a single colony running over a 1-m section of concrete walkway. Air temperature was recorded simultaneously with each speed measurement 1–2 mm above the ground. On the same day, wet mass was measured to the nearest 0.1 mg, and hind femur length was measured and converted to hind leg length as described above.

Unladen running speed was measured for outbound ants from two *Nomamyrmex esenbeckii* colonies and three colonies of both *Eciton burchellii* and *E. hamatum* by S.P. on BCI between September 2002 and September 2003. Mean air temperature during each measurement period was estimated from BCI weather station data (recorded at 15-min intervals). Hind leg length (from the suture with the trochanter to the end of the last tarsal segment) was measured to the nearest 0.1 mm. Dry mass was estimated from leg length based on species-specific regressions (S. Powell, unpubl.data; *E. burchellii*: $DM = 0.0198 \, L^{2.28}$; *E. hamatum*: $DM = 0.0397 \, L^{2.03}$; *N. esenbeckii*: $DM = 0.0087 \, L^{3.17}$, R^2 for all relations ≥ 0.99). Dry mass values were converted to wet mass using the relationship presented in Bartholomew *et al.* (1988) for *E. hamatum*: $DM = 0.314 \, WM$.

Analyses

Ordinary least squares regression (OLS) on log-transformed values was performed to characterise intra-specific running speed allometries as a function of either body size or leg length. Intra-specific allometries are possible because of the tremendous variation in body size within species, and they are helpful in testing allometric models because ecological variation across species is held constant. Because temperature is expected to affect running speed via the Boltzmann relationship and its effects on metabolic rate, OLS regression was performed on the natural log of running speed as a function of $1/kT$ where k is Boltzmann's constant (8.62×10^{-5} eV K^{-1}) and T is temperature in Kelvin. The slope of this relationship is an estimate of the average activation energy of metabolism, which is expected to be ~ 0.65 eV (Gillooly *et al.*, 2001). OLS was chosen over reduced major axis

(RMA, or Model II) regression because while both dependent and independent variables are expected to have measurement error, the dependent variable (running speed) is expected to have additional error as a result of environmental variation (e.g. trail traffic, path obstacles, motivational state).

Species were categorised with respect to a number of ecological variables reflecting diet, foraging mode, and territoriality (Holldobler & Wilson, 1990). With respect to diet, species were categorised as being herbivores, omnivores, or predators. Leaf-cutting ants ultimately derive most of their nutrition from cultivated fungi, but they were classified as herbivores because they actively forage for leaves to serve as the fungal substrate. Foraging mode was distinguished by whether species foraged in a group (e.g. group predators), recruited nestmates to a food source, or whether individual ants foraged solitarily. Finally, species were classified by how they use space. Species that hold absolute territories (i.e. actively defend a territorial boundary at all times) were distinguished from those that do not, and nomadic species were classified as cyclic or non-cyclic depending on the regular nature of their emigrations. From species-specific temperature and size relations, the expected running speed at standardised mid-range values (28 °C, 5 mg, 6 mm) were calculated for the sake of comparison among and between these ecological groupings.

Results

Temperature

Our database includes temperature measurements made from 6 to over 60 °C and running speeds ranged from <1 to 50 cm s^{-1}. On average, a particular species experienced a range of 20 °C while foraging, and individuals of all species ran faster at higher temperatures (Fig. 1a). The slope of the Boltzmann relationship, an estimate of the average activation energy of metabolic processes, ranged from 0.15 to 0.93 with a mean value of 0.47 (Table 2). For a number of species, running speed appeared to level off above some critical temperature. Furthermore, species that were observed foraging at higher temperatures tended to have shallower (less negative) slopes (Fig. 1b). The shallowest slope was for *Cataglyphis bicolor*, an ant of arid regions that is active at air

temperatures exceeding 60 °C (Harkness, 1979). It must be noted that this species was the only species for which running speed was measured for laden ants. However, while unladen ants might run faster than laden ants at a given temperature, there is no reason to expect that carrying a standardised load (1–2 mm cheese crumbs) should affect the slope of the temperature-running speed relationship. It has been included in this study because it is one of only two species foraging at the extreme end of the temperature spectrum. Other species with shallow slopes include three species of *Pogonomyrmex* (*barbatus*, *desertorum*, and *occidentalis*) which all forage up to or beyond 50 °C.

Temperature explained on average 66% of the variation in running speed within species (Table 2). Across species variation exists independent of temperature, as indicated by the range of normalisation constants (vertical displacement of regression lines) in Fig. 1a. The majority of this inter-specific variation is spanned by variation within a single species, *A. colombica*, which was measured over a narrow range of temperatures (Fig. 1a, filled symbols). As will be seen in the following sections, >90% of the variation in *A. colombica* running speed is explained by body size. While data for body size do not exist for many of the species in Fig. 1a, evidence from *A. colombica* suggests that body size may explain much of this residual variation.

Body size

For the species considered here, intra-specific variation in body mass ranged from two to 70-fold, and across all species mass ranged from 0.3 to 36 mg. For eight of the nine relationships and seven of the eight species examined, running speed increased with body mass (Fig. 2a, Table 3). For the six highly significant body mass-running speed scaling relationships ($P < 0.0001$), the mean exponent was 0.24, ranging from 0.14 to 0.34. The relationship for *Formica fusca*, the one species to show a weak negative effect of body mass, was only evaluated for six individuals over a narrow range of sizes. Body mass explained between 4 and 79% of the variation in running speed, and the significant inter-specific variation in standardised running
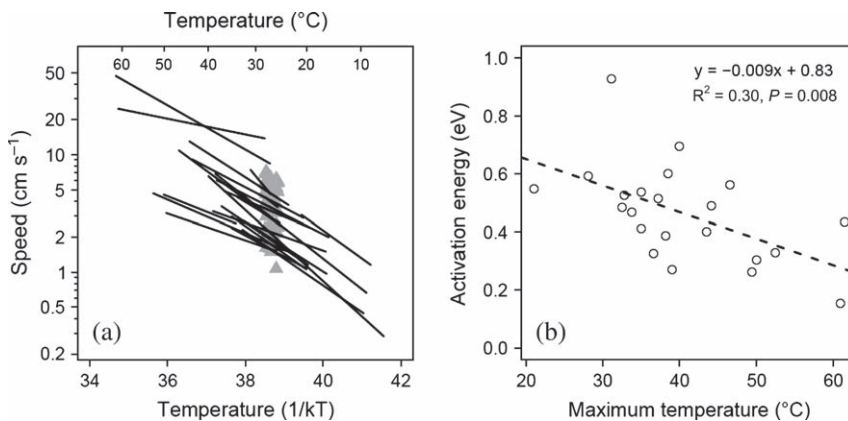

Fig. 1. (a) Regression lines depicting the relationship between temperature and running speed for 19 ant species from 22 different studies. Data points are not shown for clarity. The natural log of running speed is plotted as a function of 1/kT, where k is Boltzmann's constant and T is temperature in Kelvin. Grey triangles represent the variation in running speed for a single species, *Atta colombica*, over a narrow range of temperature. (b) The relationship between the maximum temperature at which each ant species was observed running and the negative slope of the temperature-running speed relationship, an estimate of the average activation energy of metabolism.

Table 2. Summary of the relationships between temperature and running speed. Regression results are for the natural logarithm of running speed as a function of 1/k*T*, where k is Boltzmann's constant and *T* is temperature in Kelvin. Numbers in species names refer to different studies in the order listed in Appendix 1. Slopes reported are negative one times the actual values, representing an estimate of the average activation energy in eV.

Species	Min temp (°C)	Max temp (°C)	N	Slope	95% CI [LL, UL]	Speed at 28 °C (cm/s)	r^2	P-value
Acromyrmex versicolor	16.2	32.5	49	0.49	0.32, 0.65	2.07	0.43	<0.0001
Aphaenogaster senilis	6.0	40.0	14	0.70	0.52, 0.88	2.34	0.86	<0.0001
Atta colombica2	25.6	28.1	64	0.6	−0.48, 1.70	4.29	0.02	0.27
Atta colombica3	27.0	31.1	28	0.93	0.69, 1.16	5.16	0.72	<0.0001
Cataglyphis bicolor	28.2	60.9	66	0.15	0.12, 0.19	13.71	0.58	<0.0001
Dorymyrmex goetschi	16.4	39.0	19	0.27	0.09, 0.46	2.28	0.36	0.007
Formica rufa1	8.2	21.0	30	0.55	0.48, 0.62	5.06	0.90	<0.0001
Leptogenys nitida	20.0	35.0	4	0.54	0.11, 0.97	1.85	0.94	0.030
Leptogenys schwabi	20.0	35.0	4	0.41	0.20, 0.63	1.66	0.97	0.014
Linepithema humile	25.2	33.8	21	0.47	0.43, 0.51	3.09	0.97	<0.0001
Liometopum apiculatum	9.0	38.5	38	0.60	0.56, 0.64	3.16	0.97	<0.0001
Messor pergandei1	19.5	36.6	25	0.33	0.14, 0.51	3.45	0.37	0.001
Messor pergandei2	20.6	43.5	69	0.40	0.35, 0.45	4.27	0.79	<0.0001
Messor pergandei3	15.9	38.2	36	0.39	0.30, 0.48	3.71	0.69	<0.0001
Ocymyrmex barbiger	27.2	61.6	96	0.43	0.39, 0.48	8.81	0.82	<0.0001
Pogonomyrmex barbatus	23.8	52.4	68	0.33	0.17, 0.49	1.81	0.21	0.0001
Pogonomyrmex desertorum	25.8	49.5	61	0.26	0.06, 0.46	1.62	0.11	0.011
Pogonomyrmex maricopa	25.0	46.5	50	0.56	0.47, 0.66	3.08	0.73	<0.0001
Pogonomyrmex occidentalis	34.1	50.0	15	0.30	0.11, 0.49	2.06	0.47	0.005
Pogonomyrmex rugosus	23.5	44.2	61	0.49	0.42, 0.56	4.96	0.77	<0.0001
Solenopsis invicta	9.5	32.8	28	0.53	0.44, 0.62	1.67	0.85	<0.0001
Tapinoma sessile	19.7	37.2	29	0.52	0.46, 0.57	2.02	0.94	<0.0001

speed suggests that ecological factors play an important role in determining species-specific normalisation constants. For a standardised body size (5 mg), the army ants (*Eciton* and *Nomamyrmex* species) were the fastest, while the leaf cutter *A. versicolor* and the wood ant *Formica rufa* were the slowest.

The running speed allometry for *A. colombica* was noticeably curvilinear (Fig. 2a, dotted line), with a quadratic function on log-transformed variables explaining 94% of the variation in speed (compared with 79% for a linear fit). This curvilinear allometry is largely explained by the fact that relative leg length declines with worker size in *A. colombica* (a decelerating leg length allometry; Feener *et al.*, 1988, A. H. Hurlbert, unpubl. data), while for other species the leg length allometry is generally constant (A. H. Hurlbert and F. Ballantyne, unpubl. data; S. Powell, unpub.data) or slightly accelerating (Powell & Franks, 2006). Plotting running speed as a function of leg length controlled for the potentially non-linear scaling between body size and leg length, and running speed was determined to be a simple power function of hind leg length for all species examined, although this relationship was not significant for *M. pergandei* (Fig. 2b). The scaling exponent varied from 0.42 to 0.99, and leg length explained between 7 and 92% of the variation in running speed (Table 4). Again, for a standard leg length (6 mm), army ants typically ran faster than other ant species.

Ant ecology and running speed

Half of the species in this study are classified as non-territorial, recruiting omnivores. The low number of species in other ecological categories prevents rigorous statistical evaluation of differences between groups. Running speed standardised for either temperature or body mass is shown for the different taxonomic and ecological groups in Fig. 3. For the species examined with respect to temperature, *Cataglyphis bicolor* and *Ocymyrmex barbiger* ran much faster than the other species. These two species are from different subfamilies (Formicinae and Myrmicinae, respectively), but are both non-territorial scavengers that forage solitarily at extreme soil temperatures (Harkness, 1979; Marsh, 1985). For the species examined with respect to body size, the army ants (Ecitoninae), which are nomadic group predators, were consistently faster than other species.

Discussion

Speed, size and temperature

Running speed increases with both body size and temperature for a variety of ant species with different diets and foraging strategies. Body size explains up to 94% of the variation in running speed for some species while temperature explains up to 97% for others. The mechanistic framework discussed above suggests how body size and temperature might affect how rapidly a given ant can run given some standardised level of effort. Thus, our analyses implicitly assume that the running speeds measured across these studies reflect such a standardised and comparable *foraging speed*. This assumption seems reasonable given that foraging ants must move at a speed that can be sustained for long periods of time, and other animal groups have
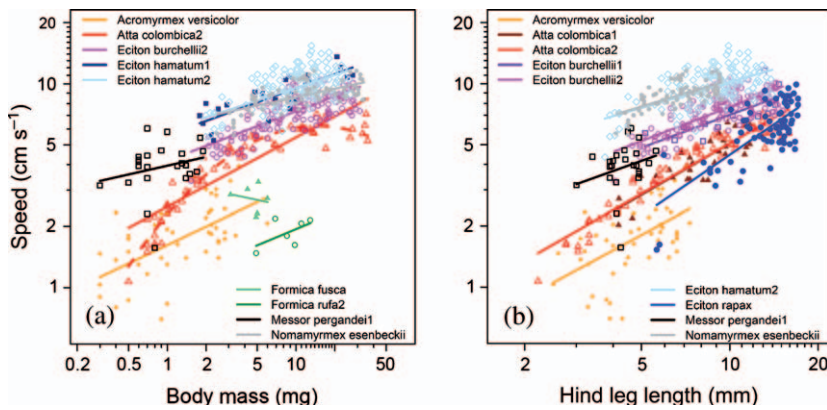
Fig. 2. The relationship between logarithmically transformed values of running speed and (a) body mass, and (b) hind leg length for different ant species. *Atta colombica* exhibits a curvilinear body mass allometry (dotted line; $\ln V = -0.14 \, (\ln M)^2 + 0.75 \, \ln M + 0.82$, $r^2 = 0.94$).

been shown to move at the speed that is energetically most efficient (Biewener, 2003). While no published study that we know of has failed to find a temperature effect on ant running speed, a number of studies found no significant effect of body size (e.g. Lighton *et al.*, 1987; Duncan & Crewe, 1993; Gomides *et al.*, 1997; Morehead & Feener, 1998). In some cases, these studies have very limited sample sizes (e.g. Jensen & Holm-Jensen, 1980, *Formica* species in Fig. 3a), or measure running speed over a broad range of environmental temperatures which may potentially obscure a body size effect (e.g. Rissing, 1982; Morehead & Feener, 1998; Lighton & Duncan, 2002). Other factors that may affect whether ants run at their optimal speed include trail traffic and encounter rates between workers (Burd & Aranwela, 2003), motivational state based on resource quality (Roces, 1993), load carriage (e.g. Lighton *et al.*, 1993), and the presence of obstacles along the foraging path (Torres-Contreras & Vasquez, 2004). In addition, Anderson and McShea (2001) found a positive correlation between colony size and running speed. However, based on our findings once most of these variables are carefully controlled for, both temperature and body size are expected to be identified as the primary predictors of running speed within most ant species.

Running speed increases with temperature in a manner consistent with the effects of temperature on metabolic rate and the kinetic properties of muscles. The slope of a plot of the natural logarithm of speed as a function of inverse temperature divided

by Boltzmann's constant ($1/kT$) is an estimate of the average activation energy of metabolism. These values estimated from species-specific running speed plots (Table 2) are in general accordance with the average activation energy typically observed for the biochemical reactions involved in metabolism (0.6–0.7 eV, Gillooly *et al.*, 2001). Interestingly, ant species that forage at extremely high temperatures (45–60 °C) tend to exhibit lower activation energies, and the rate at which speed increases with temperature decreases. This might be expected if the metabolic machinery of species adapted to extreme temperatures consists of enzymes with greater structural stability, and consequently lower catalytic potential (Somero, 1975).

The exponent of the body mass-running speed allometry ranged from 0.14 to 0.34, and for many species the 95% confidence intervals included both 0.17 and 0.25. However, across the nine studies, the allometric exponent had a central tendency of approximately 0.25. An exponent of one-quarter for the scaling relationship between body mass and running speed is consistent with both the model of elastic similarity (McMahon, 1975) and the model combining dynamic similarity (Alexander & Jayes, 1983) with available metabolic power (Schmidt-Nielsen, 1984). Body size clearly can have two potentially distinct effects on running speed. As a determinant of metabolic rate and energetic costs, body mass influences the metabolic power available for driving muscle contractions and leg turnover. More directly, longer legs imply longer strides and lower

Table 3. Summary of the relationships between body mass and running speed. Both variables were natural log transformed. Numbers in species names refer to different studies in the order listed in Appendix 1.

Species	Min mass (mg)	Max mass (mg)	N	Slope	95% CI [LL, UL]	Speed at 5 mg (cm/s)	r^2	*P*-value
Acromyrmex versicolor	0.30	6.00	49	0.30	0.17, 0.43	2.62	0.32	<0.0001
Atta colombica2	0.50	36.00	64	0.34	0.30, 0.39	4.31	0.79	<0.0001
Eciton burchellii2	1.54	31.21	148	0.24	0.21, 0.28	6.19	0.59	<0.0001
Eciton hamatum1	1.79	27.44	24	0.23	0.16, 0.30	8.11	0.68	<0.0001
Eciton hamatum2	1.84	26.39	149	0.21	0.16, 0.25	8.28	0.36	<0.0001
Formica fusca	3.10	6.00	6	−0.13	−1.06, 0.79	2.69	0.04	0.71
Formica rufa2	4.90	12.90	6	0.26	−0.26, 0.79	1.61	0.33	0.24
Messor pergandei1	0.30	1.90	25	0.14	−0.10, 0.39	4.98	0.06	0.24
Nomamyrmex esenbeckii	2.43	33.75	76	0.14	0.10, 0.18	7.82	0.41	<0.0001

Table 4. Summary of the relationships between hind leg length and running speed. Both variables were natural log transformed. Numbers in species names refer to different studies in the order listed in Appendix 1.

Species	Min length (mm)	Max length (mm)	N	Slope	95% CI [LL, UL]	Speed at 6 mm (cm/s)	r^2	P-value
Acromyrmex versicolor	2.50	7.30	49	0.78	0.42, 1.14	2.08	0.29	<0.0001
Atta colombica1	4.17	12.96	31	0.84	0.66, 1.02	3.31	0.73	<0.0001
Atta colombica2	2.22	15.90	64	0.83	0.77, 0.89	3.34	0.92	<0.0001
Eciton burchellii1	5.15	14.69	12	0.54	0.23, 0.85	5.34	0.59	0.003
Eciton burchellii2	4.05	15.15	148	0.56	0.48, 0.64	5.78	0.59	<0.0001
Eciton hamatum2	3.75	13.95	149	0.42	0.32, 0.52	8.20	0.36	<0.0001
Eciton rapax	5.64	17.11	74	0.99	0.77, 1.21	2.69	0.51	<0.0001
Messor pergandei1	3.00	5.60	25	0.52	−0.33, 1.37	4.58	0.07	0.22
Nomamyrmex esenbeckii	4.10	9.40	76	0.44	0.32, 0.56	8.36	0.41	<0.0001

stride frequencies. Equation (3) can be rewritten without assuming any particular scaling of leg length and body mass, illustrating these two separate effects:

$$v \propto lf \propto L(L^{-1/2}M^{1/12}e^{-E/kT}) \propto L^{1/2}M^{1/12}e^{-E/kT}. \quad (4)$$

Although stride length and stride frequency could not be examined separately in this study (see Zollikofer, 1994), running speed was examined as a function of both leg length and body mass. Although for most species leg length and body mass were equally good predictors of running speed, *A. colombica* proved to be an insightful exception. This species exhibited non-linear scaling of running speed with body mass, but linear scaling of running speed with leg length. This difference is because of the non-linear scaling relationship between leg length and body mass, and confirms the importance of leg length over body mass

in determining running speed as suggested by the relative magnitude of their respective exponents in Equation (4). However, for species with simple leg length allometries ($L \propto M^a$) there is no reason to expect either leg length or body mass to be a better predictor.

While body size and temperature often explain the vast majority of running speed within individual species, variation between species even after controlling for size or temperature is as great as five to eightfold, respectively. Two species for which the effects of temperature were examined, *C. bicolor* and *O. barbiger*, are much faster than other species at a standardised temperature. Anderson and McShea (2001) suggested that these two desert-dwelling species have been selected to run faster in order to minimise foraging time spent at high temperatures, often exceeding 60 °C. The army ants of the subfamily Ecitoninae were the fastest species for a particular body size. The Ecitoninae
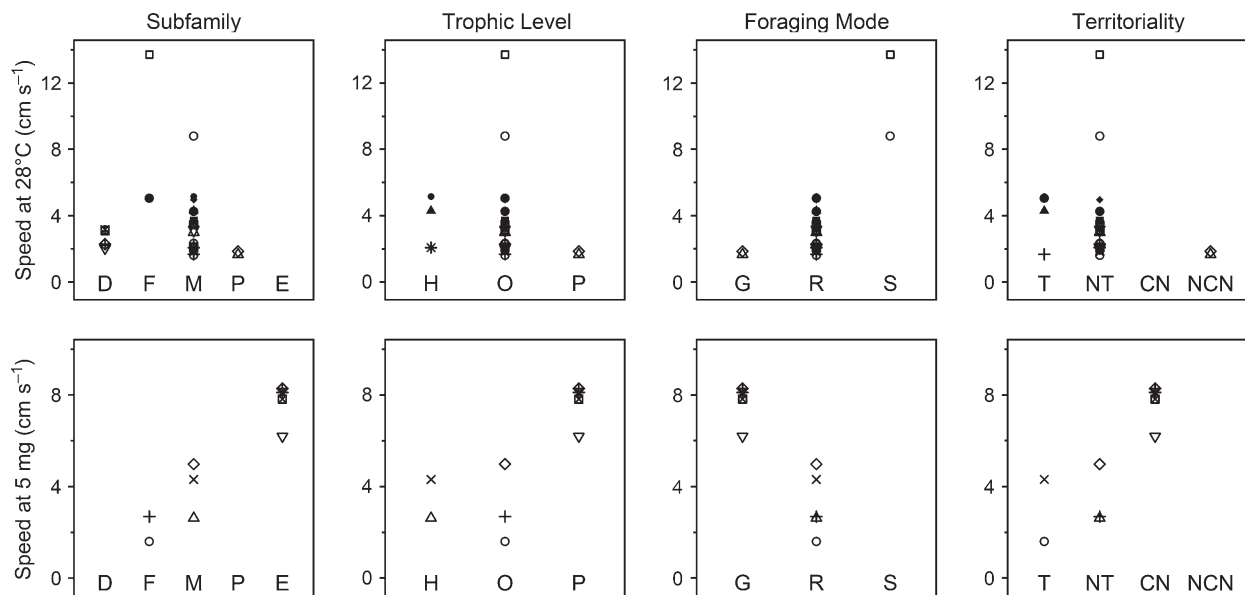

Fig. 3. Running speed standardised by (upper panels) temperature, or (lower panels) body mass based on several taxonomic and ecological categories. Subfamily: D, Dolichoderinae; F, Formicinae; M, Myrmicinae; P, Ponerinae; E, Ecitoninae. Trophic level: H, herbivore; O, omnivore; P, predator. Foraging mode: G, group forager; R, recruiter; S; solitary forager. Territoriality: T, territorial; NT, non-territorial; CN, cyclic nomadism; NCN, non-cyclic nomadism. Symbols within a row of panels represent the same species. Open square = *Ocymyrmex barbiger*.

differ from all of the other species considered in this study because (i) they are obligate group predators, and (ii) they are nomadic and move their exceptionally large colonies on a regular schedule (Rettenmeyer, 1963; Brady, 2003). These two features of army ant ecology might be expected to select for fast running speed. First, army ants predominately prey on other ants (Rettenmeyer *et al.*, 1983) and successful group raids depend on being able to quickly overwhelm their prey with strength in numbers (Powell & Clark, 2004). Speed is therefore crucial to foraging success and selection should produce faster speeds in these strict predators than in the omnivores and herbivores that they prey upon. Second, during colony emigrations, the queen and large cohort of brood experience high mortality risk from predation and environmental factors. Thus, selection should also favour increased running speed in order to minimise the duration of emigrations and hence overall colony mortality risk.

Ants and mammals compared

Nearly all of the theory concerning running speed as a function of body size has been developed for vertebrates, most often mammals (Heglund *et al.*, 1974; McMahon, 1975; Pennycuick, 1975; Taylor *et al.*, 1982; Garland, 1983; Christiansen, 2002; Alexander, 2005). Jensen and Holm-Jensen (1980) measured the mass-specific cost of transport in ants as a function of body size, plotting those values alongside a variety of mammal data, and suggesting a general law of mechanics. A similar comparison of running speed for ants, other arthropods, lizards and mammals as a function of body size is presented (Fig. 4). Ants run slower than expected for their size based on the regression for mammals smaller than 30 kg. Ants fall below this mammal regression line even when adjusting individual running speeds to 40 °C, an approximation of mammalian body temperature. However, the allometric exponent for smaller mammals is very similar to the average exponent for ants, suggesting potentially similar mechanisms controlling the scaling of running speed for these groups.

A number of possible reasons exist for the negative displacement of ant running speeds from the mammal regression line once temperature has been taken into account. First, the vertebrate data typically represent maximum running speeds, while ants were measured at sustained foraging speeds. A hypothetical 5-mg mammal would be predicted to run at 42 cm s⁻¹, eight times faster than the median ant running speed in this study. This difference, while great, is within the up to 10-fold difference between maximal and preferred running speeds that has been observed for other taxa (e.g. Blickhan & Full, 1987; Chappell *et al.*, 2004). However, there are a number of reasons to expect ants to run slower even at a comparable level of effort as a result of biomechanical and physiological differences between arthropods and vertebrates. Aside from the fundamentally different oxygen delivery systems, insect leg muscles tend to have low mechanical advantage compared with mammals (Alexander, 1985), and are thus able to exert less force per unit body weight. Also, the musculoskeletal attachments in arthropods tend to be much stiffer than vertebrate tendons (Full, 1997)
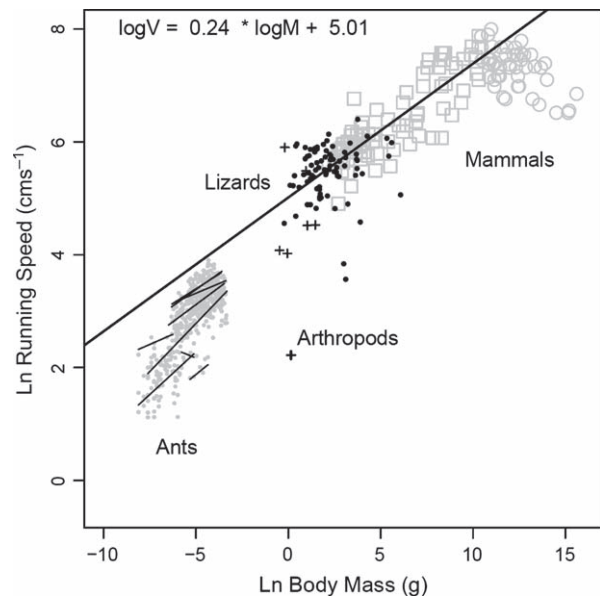

Fig. 4. The relationship between body mass and running speed for four different animal groups. As presented in Iriarte-Diaz (2002), mammal data are split into species less than (squares) or greater than (circles) 30 kg, and regression line is fit through the smaller group. Lizard data (black dots) are from Van Damme and Vanhooydonck (2001). Arthropods (pluses) represented include beetles, crabs, and cockroaches and data are taken from citations in Full (1997). Ant data (grey dots) are those presented in Fig. 2a. Running speeds for the three ectothermic groups were adjusted to the speed expected at 40 °C based on the Boltzmann relationship (i.e. by adding $E/(kT_{obs}) - E/(kT_{40C})$) to the natural log of raw running speed, where E is the average activation energy of metabolism (assumed to be ∼0.65 eV), k is Boltzmann's constant, and T_{obs} and T_{40C} are the temperatures at which running speed was measured and 40 °C, respectively, reported in Kelvin).

which store elastic energy and allow greater running speeds (Christiansen, 2002; Biewener, 2003). However, despite these differences the similarity in scaling between ants and vertebrate groups deserves further study.

Summary

This study represents the largest known collection of data on ant running speed, with data obtained from 19 published papers as well as our own unpublished studies, and representing 24 different species. As a rule, larger, hotter ants run faster. However, the mechanistic basis for the approximately quarter-power scaling of running speed with body mass is unclear. More research is needed to fully understand how metabolic power and the biomechanics of a given morphology determine stride frequency. The effect of temperature is perhaps less controversial, but uncertainty remains regarding potential biochemical adaptations of ant species that forage at temperatures much greater than most biological activity. Running speed in ants has clear implications for both individual and colony level foraging efficiency, and our comparison across species suggests that the demands of

certain lifestyles may have selected for increased biochemical or biomechanical efficiencies. The examination of more species across a broader spectrum of life histories will facilitate the development of more refined hypotheses about the physiological and evolutionary determinants of running speed in ants.

Acknowledgements

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Appendix 1. Data sources for the present study. Data availability: uppercase letters indicate that the study examined running speed as a function of body mass (M), leg length (L), or temperature (T). Lowercase letters denote that mean body mass (m) or temperature (t) is known for the study, but was not used as an independent variable. Ecological traits: trophic group (H, herbivore; O, omnivore; P, predator); foraging mode (G, group forager; R, recruiter; S, solitary forager); territoriality (T, absolute territoriality; NT, less than absolute territoriality; CN, cyclic nomadism; NCN, non-cyclic nomadism).

Subfamily	Species	Reference	Data available	Ecological traits
Dolichoderine	*Dorymyrmex goetschi* Goetsch	Torres-Contreras and Vasquez (2004)	T	O, R, NT
	Linepithema humile (Mayr)	Shapley (1924)	T	O, R, NT
	Liometopum apiculatum Mayr	Shapley (1920)	T	O, R, NT
	Tapinoma sessile (Say)	Shapley (1924)	T	O, R, NT
Ecitoninae	*Eciton burchellii* (Westwood)	Franks (1985)	L	P, G, CN
		S. Powell (unpubl. data)	M, L, t	P, G, CN
	Eciton hamatum (Fabricius)	Bartholomew *et al.* (1988)	M, t	P, G, CN
		S. Powell (unpubl. data)	M, L, t	P, G, CN
	Eciton rapax Smith	Burton and Franks (1985)	L	P, G, CN
	Nomamyrmex esenbeckii (Westwood)	S. Powell (unpubl. data)	M, L, t	P, G, CN
Formicinae	*Cataglyphis bicolor* (Fabricius)	Harkness (1979)	T	O, S, NT
	Formica fusca Linnaeus	Jensen and Holm-Jensen (1980)	M, t	O, R, NT
	Formica rufa Linnaeus	Holt (1955)	T	O, R, T
		Jensen and Holm-Jensen (1980)	M, t	O, R, T
Myrmicinae	*Acromyrmex versicolor* (Pergande)	A. H. Hurlbert and F. Ballantyne (unpubl. data)	M, L, T	H, R, NT
	Aphaenogaster senilis Mayr	Ledoux (1967)	T	O, R, NT
	Atta colombica Guerin-Meneville	Burd (1996)	L	H, R, T
		A. H. Hurlbert (unpubl. data)	M, L, T	H, R, T
		Lighton *et al.* (1987)	m, T	H, R, T
	Messor pergandei (Mayr)	A. H. Hurlbert and F. Ballantyne (unpubl.data)	M, L, T	O, R, NT
		Lighton and Duncan (2002)	m, T	O, R, NT
		Rissing (1982)	m, T	O, R, NT
	Ocymyrmex barbiger Emery	Marsh (1985)	T	O, S, NT
	Pogonomyrmex barbatus (Smith)	Morehead and Feener (1998)	m, T	O, R, NT
	Pogonomyrmex desertorum Wheeler	Morehead and Feener (1998)	m, T	O, R, NT
	Pogonomyrmex maricopa Wheeler	Weier and Feener (1995)	m, T	O, R, NT
	Pogonomyrmex occidentalis (Cresson)	Morehead and Feener (1998)	m, T	O, R, NT
	Pogonomyrmex rugosus Emery	Weier and Feener (1995)	m, T	O, R, NT
	Solenopsis invicta Buren	Rigatuso *et al.* (2000)	T	O, R, T
Ponerinae	*Leptogenys nitida* Forel	Duncan and Crewe (1993)	m, T	P, G, NCN
	Leptogenys schwabi Forel	Duncan and Crewe (1993)	m, T	P, G, NCN