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The fast and the fractalous: speed and tortuosity trade off in running ants

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Summary

1. The thermal sensitivity of locomotor performance has often been described in terms of speed, but the trajectory of locomotion may play an equally important role in capturing prey or escaping predators. Hypotheses based on physical constraints or behavioural plasticity predict relationships between the speed and the tortuosity of running, which should affect the thermal sensitivity of locomotion.

2. We measured the speed and tortuosity of running by leaf-cutter ants over a range of temperatures from 10 °C to 40 °C. Tortuosity was estimated by the fractal dimension of each path.

3. As we expected, ants ran faster at higher temperatures, but they also followed straighter (less tortuous) paths. A negative relationship between speed and tortuosity was observed both within and among thermal environments.

4. Both biomechanical and behavioural mechanisms might have caused the observed relationship. Turning at high speeds should be more difficult because of the force needed to overcome inertia, and turning at low speeds could help ants evade a predator. Staged encounters with predators should help to define the ecological significance of the trade-off between speed and tortuosity.

Key-words: fractal dimension, locomotor performance, protean movement, speed, temperature

Introduction

The thermal sensitivity of locomotion has been a focus of physiological ecologists for several decades, tracing back to Bennett's classic study of sprinting by lizards (Bennett 1980). Generally, an individual's speed of running, jumping or swimming depends strongly on its body temperature (Huey & Stevenson 1979; Huey & Kingsolver 1989). Many ecologists believe these thermal sensitivities evolve because speed affects the ability to capture prey, evade predators and defend mates (Bennett & Huey 1990). Despite this belief, we have little direct evidence that speedy locomotion enhances the survival or fecundity of organisms (reviewed by Angilletta, Niewiarowski & Navas 2002; Husak 2006; Husak & Fox 2006; Husak *et al.* 2006). Although maximal speeds vary greatly among genotypes from different environments, this variation often does not conform to the predictions of theory (e.g., see Huey *et al.* 1989). In fact, some organisms only rarely resort to maximal speeds under natural circumstances (Hertz, Huey & Garland 1988; Irschick 2000; Jayne & Irschick 2000; Brana 2003), which might explain why speed affects survivorship at some times but not others (Jayne & Bennett 1990). Although locomotion clearly plays a critical role in most activities, perhaps ecologists over-emphasize the importance of speed.

While much attention was focused on speed, the thermal sensitivities of other aspects of locomotion received less attention. Indeed, we might judge locomotor performance as much by manoeuvrability as by speed (Howland 1974; Domenici 2002). Animals rely on complex manoeuvres to capture prey, evade predators and avoid obstacles (Domenici 2001; Maresh *et al.* 2004; Kohlsdorf & Biewener 2006). These manoeuvres require acceleration and deceleration, both of which depend strongly on temperature (Bergmann & Irschick 2006). If speed isn't the only aspect of locomotion that matters, studies of the relationships among temperature, speed and other locomotor performances could further resolve constraints on the evolution of thermal physiology.

We have several reasons to expect a relationship between speed and manoeuvrability (Table 1). First, a biomechanical constraint could directly prevent fast runners from making tight turns (but see Zollikofer 1994; Jindrich & Full 1999). Stabilizing forces enhance speed during linear movement, but turning requires destabilizing forces (Fish 2002). Given a strong biomechanical constraint, an animal's speed would

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Table 1. Hypothetical mechanisms relating the speed and the tortuosity of locomotion

		Predicted relationship	
Mechanism	Description	Within temperatures	Among temperatures
Physical constraint			
Biomechanics	High speed makes turning more difficult	Negative	Negative
Heat disorientation	High temperature disorients runners, causing wandering	None	Positive
Cold limitation	Low temperature impairs neural activity for turning	None	Positive
Behavioural plasticity			
Heat evasion	Straighter paths increases the likelihood of reaching a cooler patch	None	Negative
Predator evasion	Turning enhances escape at low speeds	Negative	Negative

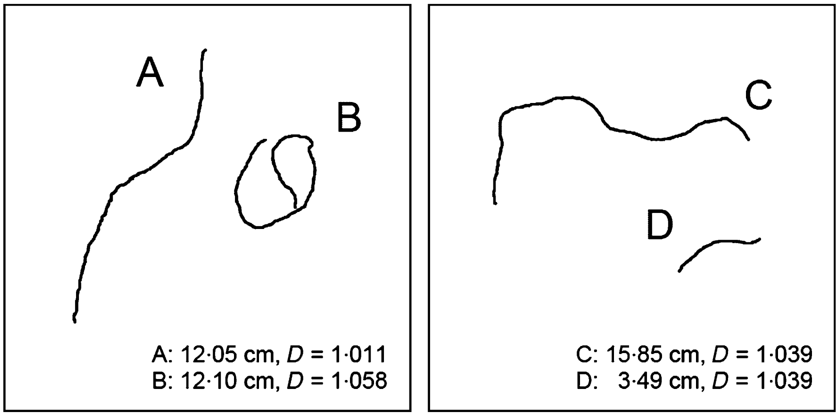

Fig. 1. Representative paths demonstrating the utility of fractal analysis. Paths A and B are similar in length, but differ substantially in fractal dimension (*D*). Paths C and D are similar in fractal dimension, but differ substantially in length.

relate negatively to the tortuosity of its path. Second, high temperatures impair neural function (Robertson 2004). If the neural processes associated with stabilizing and destabilizing effects respond differently to hyperthermia, loss of orientation could precede loss of speed. In this case, speed would correlate positively with tortuosity over some range of high temperatures. Third, low temperatures could reduce both speed and manoeuvrability by limiting the biochemical processes required for locomotion (Hochochka & Somero 2002). This mechanism would generate a positive correlation between speed and tortuosity over some range of low temperatures. Finally, a relationship between speed and directionality might arise from a plastic defensive strategy. For example, an individual that cannot attain high speeds could adopt a tortuous route, in hopes of confusing or escaping a predator through protean movement (Humphries & Driver 1967; Driver & Humphries 1988). This last mechanism would generate a negative correlation between speed and tortuosity.

To distinguish among these ideas, we quantified the effects of temperature on the speed and the trajectory of running by leaf-cutter ants (*Atta sexdens*). These ants routinely forage along exposed trails and occasionally must escape from predators or parasites (e.g., see Erthal & Tonhasca 2000). We forced ants to run over a range of temperatures and calculated the tortuosity of each path as a fractal dimension. Recently, fractal analysis has become a popular way to characterize the tortuosity of animal movements (Uttieri *et al.* 2005; Caldwell & Nams 2006; Haynes & Cronin 2006). For a given distance, a more tortuous trajectory yields a greater fractal dimension (Fig. 1). The fractal dimension of any path must lie between 1·0 and 2·0, with the former representing a path that lies perfectly straight and the latter representing a path that completely covers a surface (Benhamou 2004). Here, we show that the tortuosity of running relates very strongly to the speed of an animal, reflecting either biomechanical constraints or behavioural plasticity.

Methods

We sampled ants from a mixture of wild and captive colonies at the University of São Paulo, Brazil. Wild ants were collected from two colonies on the university's campus; we sampled individuals that were walking along trails (n = 20 from each colony). Captive ants were sampled from 19 colonies raised in the laboratory (n = 176; 4–10 ants per colony). Because leaf-cutter ants die within days of being isolated from their colony (Silva *et al.* 2003), all measures of locomotion began within a few hours of sampling and ended on the same day.

We used a repeated measures design, in which each ant ran at three temperatures: 10 °C, 20 °C and 30 °C. The same random order of temperatures (30 °C, 10 °C and 20 °C) was used for all individuals. We also ran another set of ants from five captive colonies at 40 °C. These ants (n = 40) were not included in our repeated measures because we knew some individuals would undergo heat stress (Angilletta *et al.* 2007). Although we might have chosen to expose ants to 40 °C after all other measures, we also wanted to closely regulate the duration of exposure before running. Logistically, using a separate group of ants was the easiest way for us to minimize thermal stress while controlling for thermal history.

All measures of locomotion were made in a walk-in environmental chamber. Ants were placed in this room about 1 h before the first run to ensure that they reached the desired temperature. Each ant was stored under a small plastic cup (150 mL) that was inverted on a table. The temperature of the table was confirmed with an infrared thermal gun (Rayngner ST30, Raytek Corp., Santa Cruz, CA). After all ants were run at a given temperature, we changed the temperature of the room and waited for the ants to reach the new target temperature. During this time, ants remained inside their respective cups. In this way, we completed the entire series of runs in a single day while also giving ants 2–3 h of rest between runs. Ants assigned to run at 40 °C were exposed to this temperature for only 20 min before their run.

At each temperature, we used a pen to record the escape path of each ant for a fixed duration. Each ant was placed under its plastic cup on a sheet of white paper. After a few seconds, the cup was removed and a hand (holding a pen) was immediately placed behind the ant. Generally, ants responded to the hand by running in the opposite direction. During this process, the pen was used to trace the ant's path without touching the ant. Another researcher used a stopwatch to ensure that the ant's path was recorded for 3 s (maximal deviation = 0·1 s).

We used a computer program to calculate the total length and fractal dimension of each path. First, we scanned the tracings at 150 dpi to create a digital record of each run on an array of 1275 × 1650 pixels. These digital images were converted to x–y coordinates in ArcView 3·2 and were imported into Fractal 4·08 (Nams 2004) for analysis. To convert the length of each path (i.e. distance covered in 3 s) from pixels to centimetres, we divided the length by the number of pixels in 1 cm at 150 dpi (59 pixels). By dividing the length of each run by its duration (3 s), we arrived at an estimate of speed. The tortuosity of each run was estimated by its fractal dimension (D, scale range = 1–100, 30 steps; e.g., see Fig. 1). Prior to statistical analyses, fractal dimensions were log-transformed to meet the assumptions of linearity and homoscedasticity (log of $D - 1$; Nams 2004).

We used two complementary analyses to examine the factors that influenced running performance. First, we used an anova for repeated measures to assess the effects of temperature and colony on running speed and fractal dimension. Runs at 40 °C were excluded from this analysis because they involved a different set of ants. When data violated the assumption of sphericity, we computed thermal effects using a manova (see Potvin, Lechowicz & Tardif 1990). This first type of analysis would tell us not only whether locomotor performance depended on temperature, but also whether thermal dependence varied among ants from different colonies. Second, we used a GLM to assess the relationship between running speed and fractal dimension at each temperature. In this analysis, speed was a continuous independent variable (fixed factor) and colony was a categorical independent variable (random factor). This second type of analysis would tell us whether these two characteristics of running performance were functionally related.

Results

Temperature strongly affected the speed and the tortuosity of running (Fig. 2). Running speed increased with increasing temperature for all ants (main effect: Wilk's λ = 0·12, $F_{2,179}$ = 660, P < 0·00001), but the degree to which speed depended on temperature varied greatly among ants from different colonies (interaction effect: Wilk's λ = 0·61, $F_{40,358}$ = 2·48, P < 0·00001). From 10 °C to 30 °C, the Q_{10} of running speed averaged 2·5 (± 0·1) and ranged from 2·0 to 3·1 among colonies. The ranked performances of individuals were highly consistent among temperatures (Kendall's coefficient = 0·79), suggesting variation in speed at each temperatures reflected variation in capacity or motivation among individuals.

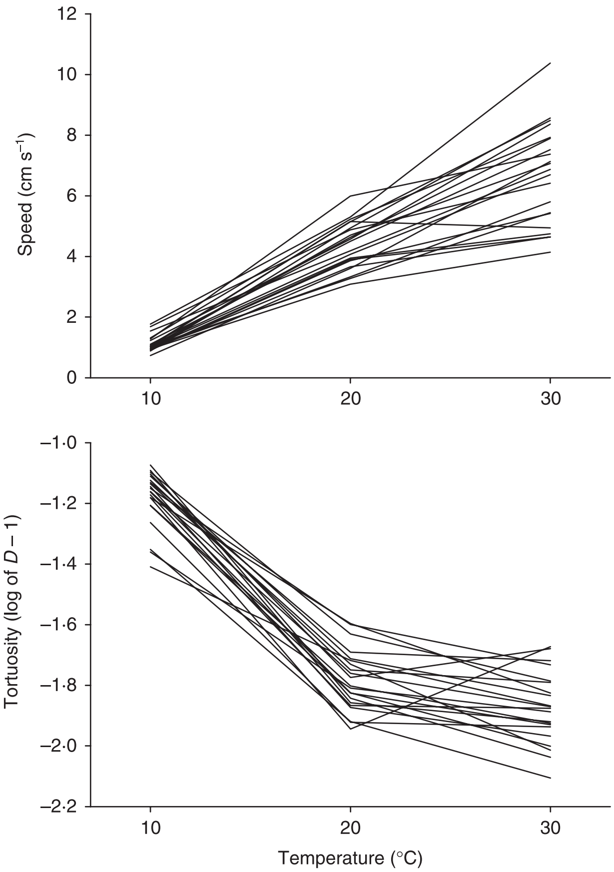

Fig. 2. Thermal sensitivities of the speed and the tortuosity of running. Each line represents the mean curve for ants of a single colony. Upper panel: Speed generally increased with increasing temperature. Lower panel: Tortuosity generally decreased with increasing temperature. Note that values of 0 and –3 for the logarithm of $D - 1$ correspond to fractal dimensions of 2 and 1·001, respectively.

In contrast, the tortuosity of running–estimated as the fractal dimension of the path–decreased sharply with increasing temperature (main effect: MS = 25·33, $F_{2,360}$ = 550, P < 0·00001). The thermal sensitivity of tortuosity also differed among colonies (interaction effect: MS = 0·07, $F_{40,360}$ = 1·47, P = 0·04). As with speed, the rank of tortuosity among individuals was highly consistent among temperatures (Kendall's coefficient = 0·71). Given the concordance of rankings based on speed and tortuosity, we were not surprised that speed and tortuosity covaried negatively among temperatures (Fig. 2). We were more interested to discover that speed and tortuosity also covaried when temperature was held constant. At each of the four temperatures, ants that ran faster also followed less tortuous paths (Fig. 3). When we

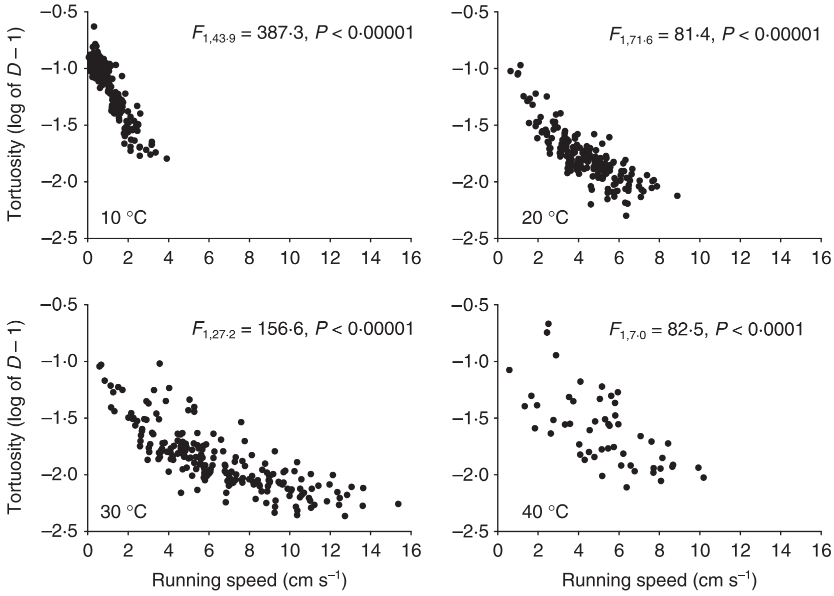

Fig. 3. The tortuosity of a path was negatively related to the speed of locomotion. A negative relationship was observed at each of four temperatures. An estimate of the effect at each temperature was derived from a mixed model ANCOVA. Note that values of 0 and –3 for the logarithm of $D - 1$ correspond to fractal dimensions of 2 and 1·001, respectively.

combined the data for all temperatures, tortuosity appeared to have decreased nonlinearly with increasing speed. Consistent with this interpretation, an ANCOVA revealed significant heterogeneity of slopes among temperatures (MS = 1·73, $F_{3,640} = 87\cdot17$, $P < 0\cdot00001$).

Discussion

Both the mean and the variance of speed increased between 10 °C and 30 °C, and then decreased between 30 °C and 40 °C (see Figs 2 and 3). The distribution of speeds at 10 °C was severely skewed, but distributions at higher temperatures were either normal or slightly skewed (Fig. 4). The skewed distribution of speed at 10 °C likely resulted from the boundary for speed at 0 cm s^{-1}.

Differences in the mean and the variance of speed could have been caused by thermal effects on physiological capacity or behavioural motivation. In particular, the greater variance at higher temperatures could reflect an ectotherm's ability to use multiple strategies at a high temperature (i.e. slow tortuous runs or fast straight runs). Despite this possibility, several facts suggest the increased variance resulted from differences in locomotor capacity among individuals. First, the thermal sensitivity of running in ants ($Q_{10} = 2\cdot5$) fell within the range of values typically observed for locomotor capacity (reviewed by Rome, Stevens & John-Alder 1992). This thermal sensitivity also resembled those for standard metabolic rate ($Q_{10} \approx 2-3$, see Clarke 2004), a trait unaffected by motivation. Second, relative speeds of individuals were consistent among temperatures, suggesting variation in performance at a given temperature resulted from variation in physiological state. Third, the thermal sensitivity of physiological performance usually varies among genotypes, potentially leading to greater variance in performance at higher temperatures (e.g., see Gilchrist 1996). Based on these observations, the patterns of speed in ants might have resulted entirely from the thermal dependence of physiological capacity. Still, we cannot rule out the possibility that ants differed in their motivation to sprint during the experiment.

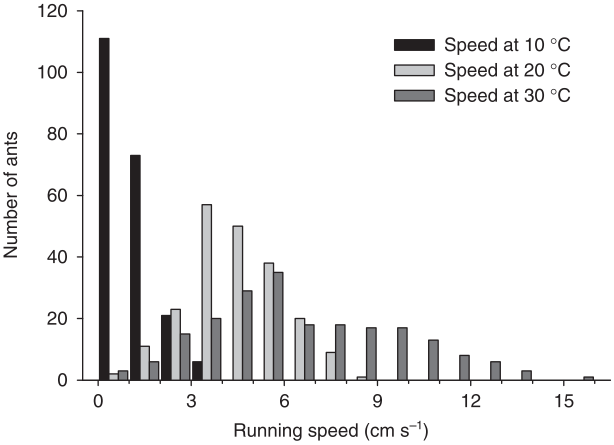

Fig. 4. The variance of running speed increased with increasing temperature. Distributions at 10 °C and 30 °C deviated significantly from normal (Shapiro Wilk's test; $P < 0\cdot0001$ and $P < 0\cdot01$, respectively), but the distribution at 20 °C did not ($P = 0\cdot90$). The distribution for another set of ants running at 40 °C also appeared normal ($P = 0\cdot87$; data not shown). Despite the skewed distribution of speeds at 30 °C, a distinct peak in the distribution existed and the mean and median speeds differed by only 2 cm s^{-1}.

We summarized five hypotheses about the relationship between speed and tortuosity during locomotion (Table 1). These hypotheses were based on either physical constraints or behavioural plasticity. For running ants, we observed a strong negative relationship between speed and tortuosity within and among thermal environments. Therefore, we reject two of the hypotheses based on physical constraints (heat disorientation and cold limitation) because they predict a positive relationship. A third hypothesis (heat evasion), based on behavioural plasticity, predicts a negative relationship among thermal environments but no relationship within thermal environments; therefore, we also reject this hypothesis as a convincing explanation for our data. The remaining hypotheses (biomechanics and predator evasion) could potentially explain the observed relationship.

The negative relationship between speed and tortuosity could reflect biomechanical constraints on running. Turning during locomotion requires an animal to redirect the main vector of motion and rotate its body to that new direction (Jindrich & Full 1999). To do so, the animal must overcome its inertia and undergo angular motion (Zollikofer 1994). Furthermore, an animal must produce greater force to stabilize its body while turning than it does while running in a straight line. Consequently, animals encounter difficulties when attempting tight turns at high speeds. An experiment by Higham, Davenport & Jayne (2001) nicely illustrates this point. These researchers constrained lizards to escape along paths that were either straight or angled. The angled paths caused lizards to reduce their speed relative to locomotion on the straight path. In our experiment, ants were permitted to adopt any speed or angle during escape. Therefore, the relatively straight trajectories of running at high speeds make sense in light of biomechanical principles. But biomechanics cannot explain why ants followed more tortuous paths at low speeds, or why ants chose to run faster at higher temperatures despite the resulting constraint on manoeuvrability.

Behavioural plasticity to evade predators could explain not only the straight trajectories at high speeds but also the tortuous trajectories at low speeds. At high temperatures, an ant can probably evade a predator by sprinting for cover. But at low temperatures, an ant may need to rely on erratic or protean movement (Humphries & Driver 1967; Driver & Humphries 1988). Plasticity of defensive behaviour occurs frequently in other ectotherms. Generally, animals take evasive action when their body temperatures enable rapid locomotion and rely on stationary defences in other circumstances (Hertz, Huey & Nevo 1982; Crowley & Pietruszka 1983; Goode & Duvall 1989; Passek & Gillingham 1997; Shine *et al.* 2000). Furthermore, the wide ranges of speeds used at 20 °C and 30 °C should make ants less predictable than they are at other temperatures. A shift along the continuum between protean movement and linear sprinting could help ants to evade predators over a range of environmental conditions.

Importantly, both physical constraints and behavioural plasticity could have contributed to the negative relationship between speed and tortuosity. Protean movement at low temperatures could represent a behavioural strategy, while linear sprinting at high temperatures could stem predominantly from the inability to manoeuvre effectively. This interpretation assumes that ants place a premium on speed, but run as tortuously as their speed will permit. Our assumption seems reasonable considering the strong thermal sensitivity of speed (Fig. 2) and the continuous decrease in tortuosity with increasing speed (Fig. 3). Ultimately, we need additional experiments to distinguish which of these mechanisms explains the locomotion of leaf-cutter ants. Studies of evasive locomotion along constrained paths could confirm that biomechanical constraints force lower speeds during turning (Higham *et al.* 2001). Staged encounters with predators (e.g. Meager *et al.* 2006) could tell us whether tortuous locomotion at low speeds helps ants to escape successfully. The wide range of speeds and trajectories exhibited by ants (see Fig. 3) would enable us to relate these variables to the probability of escape. Furthermore, we could determine the significance of protean movement for evading predators by comparing probabilities of escape along constrained and unconstrained paths. We expect such probabilities will depend on the characteristics of the predator as much as the characteristics of the prey; for example, an endothermic predator would enjoy great mobility at a temperature that impairs the mobility of ants. Finally, we need to study locomotion in natural environments to fully understand the ecological and evolutionary significance of the trade-off between speed and tortuosity (Irschick & Garland 2001).

Although biologists have described the thermal sensitivity of locomotor performance primarily in terms of speed (Bergmann & Irschick 2006), our results confirm that other aspects of locomotion trade off with speed and deserve equal attention. In particular, turning during locomotion affects the ability to intercept or evade another organism. For example, the angle of escape greatly influences the time required for a predator to intercept its prey (Domenici 2002). A tortuous route of escape could maximize the probability of evasion when an approaching predator continuously adjusts its angle of approach. Because speed is not the only component of effective locomotor performance, direct estimates of the thermal sensitivity of activities–such as foraging (Greenwald 1974), mating (Wilson 2005) or escape (Civantos *et al.* 2004)–provide more ecologically relevant information than thermal sensitivities of speed. Such measures define the overall effectiveness of locomotor performance, without placing a premium on any single aspect of locomotion.

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