

Climbing, falling, and jamming during ant locomotion in confined environments

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Locomotion emerges from effective interactions of an individual with its environment. Principles of biological terrestrial locomotion have been discovered on unconfined vertical and horizontal substrates. However, a diversity of organisms construct, inhabit, and move within confined spaces. Such animals are faced with locomotor challenges including limited limb range of motion, crowding, and visual sensory deprivation. Little is known about how these organisms accomplish their locomotor tasks, and such environments challenge human-made devices. To gain insight into how animals move within confined spaces, we study the locomotion of the fire ant *Solenopsis invicta*, which constructs subterranean tunnel networks (nests). Laboratory experiments reveal that ants construct tunnels with diameter, D , comparable to body length, $L = 3.5 \pm 0.5$ mm. Ants can move rapidly (> 9 bodylengths per s) within these environments; their tunnels allow for effective limb, body, and antennae interaction with walls, which facilitate rapid slip-recovery during ascending and descending climbs. To examine the limits of slip-recovery in artificial tunnels, we perform perturbations consisting of rapid downward accelerations of the tunnels, which induce falls. Below a critical tunnel diameter, $D_c = 1.31 \pm 0.02 L$, falls are always arrested through rapid interaction of appendages and antennae with tunnel walls to jam the falls. D_c is comparable to the size of incipient nest tunnels ($D = 1.06 \pm 0.23 L$), supporting our hypothesis that fire ants construct environments that simplify their control task when moving through the nest, likely without need for rapid nervous system intervention.

animal locomotion | extended phenotype | locomotion control | social insect | stability

Terrestrial animals and increasingly robots must move in diverse and complex environments, including running across flat landscapes (1), swimming in sand (2), climbing rough or smooth vertical surfaces (3), and squirming through cracks (4). The bulk of discoveries of locomotor behaviors and control strategies have been made by challenging animals in the laboratory in simplified environments that are typically featureless, flat, and unconfined (5). Such simplifications have allowed discovery of general principles in locomotor modes of walking, running, and climbing (6–9). Recent studies have generated appreciation for the importance of mechanical interactions with the environment, and through biological experiment (10) and robot modeling (11, 12) have demonstrated that stable and robust movement can emerge as a result of appropriately tuned dynamics of limb–ground interaction (13, 14). For example, rapid perturbations to locomotion may be corrected by so-called “preflexes” (15) in which mechanical design of the limb and appropriate kinematics enable rapid recovery from perturbation (6, 8, 10). However, typical substrates that legged locomotors contend with differ in orientation, can deform in response to foot/body contact (1, 11), and are rough on multiple size scales (16, 17); little is known about how organisms effectively use limb/body–substrate interactions in such environments. Practically, we expect that discovery of such principles can lead to advances of robotic devices that must operate in complex conditions; such devices often suffer performance loss in natural environments (11).

In particular, the role of confinement is relatively unexplored in locomotor performance and behavior. Many subterranean-dwelling organisms live and move within confined spaces in their environments (18, 19). The morphology (20, 21), energetic costs (22–25), and genetic basis (26, 27) for creating subterranean burrows and nests, which are examples of the “extended phenotype” (28), have been studied across a diversity of organisms. However, the constraints on locomotion of individuals and groups inhabiting these environments are largely unexplored (29). Rapid locomotion within the confines of a subterranean nest is essential for inhabitants to escape or respond to predators (18, 30), evacuate during flooding (31), or transport resources and information effectively (30). However, lack of vision (18, 19, 32), limited limb mobility (18), and excessive crowding among individuals (33) would seemingly challenge efforts at rapid locomotion within confined environments. Thus, we seek to understand how such environments influence the mobility and stability of animals moving within them.

Ants are excellent organisms with which to study confined locomotion. Many ant species construct large underground nests through the excavation of soil (34). Nest shape and size—in addition to ant shape and size—varies widely across species but typically consists of vertical tunnels that connect larger chambers used for food storage and brood rearing (21, 34). A majority of an ant colony worker’s life is spent below the surface within the nest—tending to brood or performing routine nest maintenance—and only near the end of life do worker ants forage above surface (34–37). The evolutionary pressure of subterranean life has led to several adaptations among ants such as partial or complete loss of vision in some species (38, 39) and long-range acoustic (40–42) and chemical communication systems (38, 43, 44). However, almost nothing is known about how ants move through their confined nest environments.

We hypothesize that ants have developed strategies and adaptations for rapid movement within nests, particularly during crucial times such as nest reconstruction or evacuation. A species that frequently must contend with such events is the red imported fire ant (*Solenopsis invicta*). Fire ants originate from the Pantanal wetlands in South America, which are subject to seasonal rains and flooding (37). Fire ant colonies construct large and relatively complex subterranean nests (37) that can be up to 2 m deep and contain greater than 50 m in length of tunnels (45). As an invasive species in the Southern United States, fire ants have demonstrated proficiency at constructing nests within a wide range of soil conditions (37). Construction of such large nests demands the ability to move repeatedly and stably within the nest confines while transporting soil.

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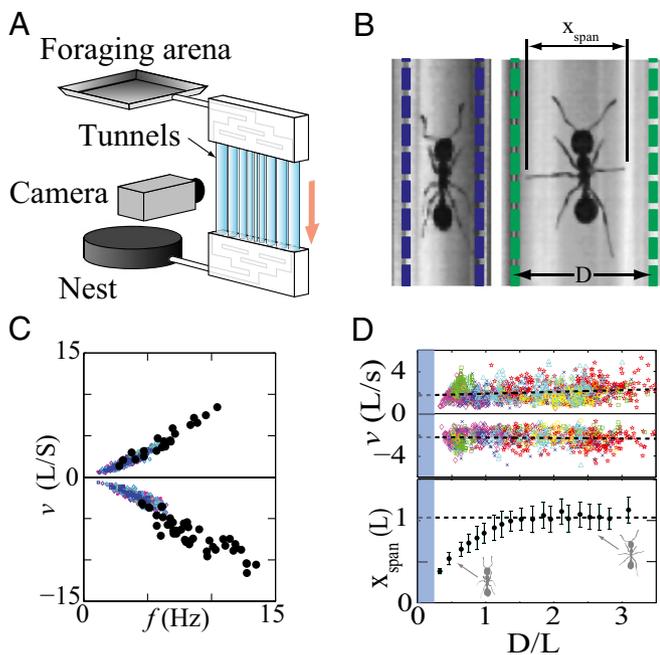


Fig. 2. Climbing posture and antennae use in glass tunnels. (A) Schematic of climbing biomechanics experiment. (B) Posture of ascending ant in a 2 mm diameter tunnel (Left; $D = 0.60$ L) and in a 6 mm diameter tunnel (Right; $D = 1.36$ L). Right image shows posture variable, x_{span} , measured in experiment. (C) Stride frequency and speed relationship for glass tunnels (colored points) and ant-created tunnels (filled black circles). (D, Upper) Speed versus D/L . Color indicates colony. Dashed lines are linear fits described in the text. Blue box indicates the minimum predicted tunnel diameter in which an ant could fit. (D, Lower) Lateral limb span (mean \pm SD) as a function of normalized tunnel diameter. Dashed line indicates constant limb span of $x_{span} = 1.04 \pm 0.14$ L independent of tunnel diameter.

a foraging arena and nest through glass tubes of diameters, $D = 1.0$ – 9.0 mm (in increments of 1 mm). We will refer to these glass tubes as “glass tunnels.”

We found that ants rapidly ascended (2.0 ± 0.8 L·s⁻¹, $n = 1,621$ ants) and descended (2.3 ± 0.7 L·s⁻¹, $n = 990$ ants) in the glass tunnels (Figs. S4 and S5). The kinematic relationship between stride frequency and speed (Fig. 2C) was fit by the function $v = ax^2 + bx$ for both the ascending ($a = 0.039 \pm 0.003$ L·s; $b = 0.41 \pm 0.01$ L) and descending ($a = -0.018 \pm 0.005$ L·s; $b = -0.49 \pm 0.02$ L) climbs (Figs. S6 and S7). The speed–frequency relationship of ascent did not significantly differ among the ant-constructed tunnels and the glass tunnels of diameters, $D = 0.3$ – 0.4 mm (comparable to that of the self-constructed tunnels; $F_{2,361} = 1.8150$, $P = 0.1643$). We did, however, find a small but significant difference in functional form of the speed–frequency relationship during descent ($F_{2,252} = 113.9$, $P < 0.001$). To test maximal performance within ant-constructed tunnels, we induced an alarm response among the colony by exhaling into the tunnel entrance. Within ant-constructed tunnels, ants rapidly descended (6.9 ± 2.1 L·s⁻¹; $n = 21$) and ascended (4.1 ± 1.8 L·s⁻¹; $n = 45$) at speeds greater than observed in the glass tunnels and surprisingly were able to move at speeds greater than 9 L·s⁻¹ within the confined, simulated nest environment.

Tunnel diameter had a weak but significant effect on ascending speed (Fig. 2D, Upper), as a function of D/L [$v = m(D/L) + b$; F test for nonzero slope, $F_{1,1619} = 63.132$, $P < 0.001$; $m = 0.17 \pm 0.04$ L²·D⁻¹·s⁻¹, $b = 1.73 \pm 0.07$ L·s⁻¹]. During descent in tunnels, D/L did not have a significant effect on speed (F test for nonzero slope, $F_{1,988} = 2.740$, $P = 0.10$). We thus hypothesized that the minimum tunnel diameter through which an ant can move is

slightly larger than the animal’s head width. Fire ant head width is 0.24 ± 0.01 L (48), and this sets the lower limit of the range of observable D/L values (shaded blue box Fig. 2D). Both ascending and descending speeds near this lower limit ($D/L < 0.5$) sharply decreased (Fig. 2D, Upper), suggesting that only in the case of extreme confinement would we observe a strong effect of tunnel diameter on ascending or descending velocity. Overall, this suggests that ants move at a near constant upward and downward speed, over a wide range of tunnel sizes, while freely trafficking within the nest.

Tunnel diameter had a significant influence on climbing posture (Fig. 2D, Lower). Ants exhibited one of two stereotyped climbing postures: (i) within glass tunnels of $D > L$, ants adopted a sprawled posture in which midlimbs were extended laterally away from the body (Fig. 2B, Right), and (ii) within glass tunnels of $D < L$, midlimbs were bent and pointed posteriorly (Fig. 2B, Left). We determined the critical tunnel diameter at which this postural transition occurred by fitting

the function $x_{span} = \begin{cases} k(\frac{D}{L}) & \text{for } D < D_c \\ c & \text{for } D > D_c \end{cases}$. We determined that

in glass tunnels of diameter above $D_c = 1.03 \pm 0.01$ L the lateral limb span, x_{span} , was independent of tunnel size ($R^2 < 0.001$) with mean value of x_{span} , determined from fit parameter $c = 1.04 \pm 0.14$ L (Fig. 2D). In glass tunnels of diameter less than D_c , limb posture was altered by tunnel confinement and x_{span} subsequently decreased (Fig. 2D). For comparison with ant-created tunnels, excavated tunnel diameter was $D = 1.06 \pm 0.23$ L. Thus, ants modify their limb position depending on tunnel size, but maintain approximately the same rate of ascent and descent. Furthermore ants climbing within tunnels they construct are capable of using their spread-limb posture, which may have implications for locomotor stability.

The alteration of the midlimb posture in smaller tunnels suggests that a transition occurs in the direction of locomotor force production by the midlimb. In the sprawled posture, midlimb tarsi contact forces pull toward the body and the tarsal hooks and adhesive pads are likely engaged. In contrast, when the limb is in the compact posture, the limb pushes down and

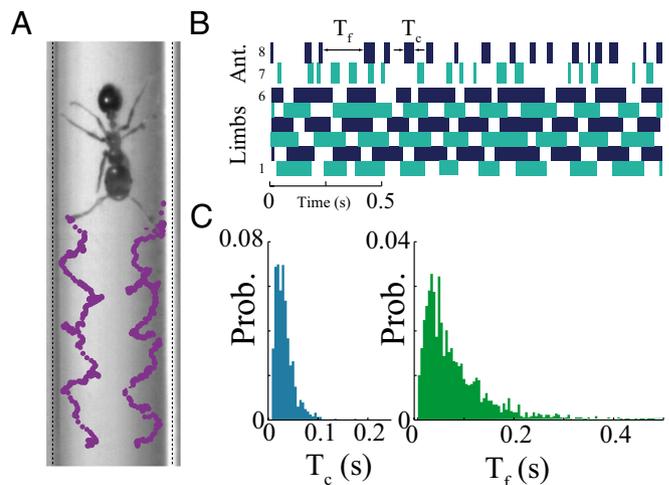


Fig. 3. Antennae use in confined locomotion. (A) Image of ant descending in a tunnel with tracked position of antennae tips shown in purple. $D = 3$ mm. (B) Stepping and antennae contact diagram for a vertical descent in a tunnel. Light and dark blue highlight limbs that form alternating tripods during locomotion: (1) right hind, (2) right fore, (3) left fore, (4) left mid, (5) left hind, (6) right hind. Right and left antennae are denoted by (7) and (8) respectively. Time of antennal contact, T_c , and time free, T_f , are highlighted. (C) Probability distribution for both T_c and T_f .

which a fixture holding the glass tunnels was mounted to a vertical, computer-controlled air piston. The air piston accelerated the tunnels from rest 5 mm downward over a time period of 0.15 s. Air piston activation was automated and triggered by ant movement, which in turn triggered the capture of high-speed video. All perturbed and unperturbed climbing experiments were performed while ants freely trafficked between the nest site and the foraging arena.

Statistics. In all experiments ant body length was measured from the base of the mandibles on the head to the tip of the gaster. Ant body length was

measured by selecting points in Matlab. Statistical tests were performed in Matlab and JMP (SAS Software). Analysis of variance was used for comparisons among treatments. In digging trials we treated colony and date as random factors in an analysis of variance. For comparing the statistical significance of nonlinear regression models to data, we used the method described in Motulsky (61). All results are reported as mean \pm SD.

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