

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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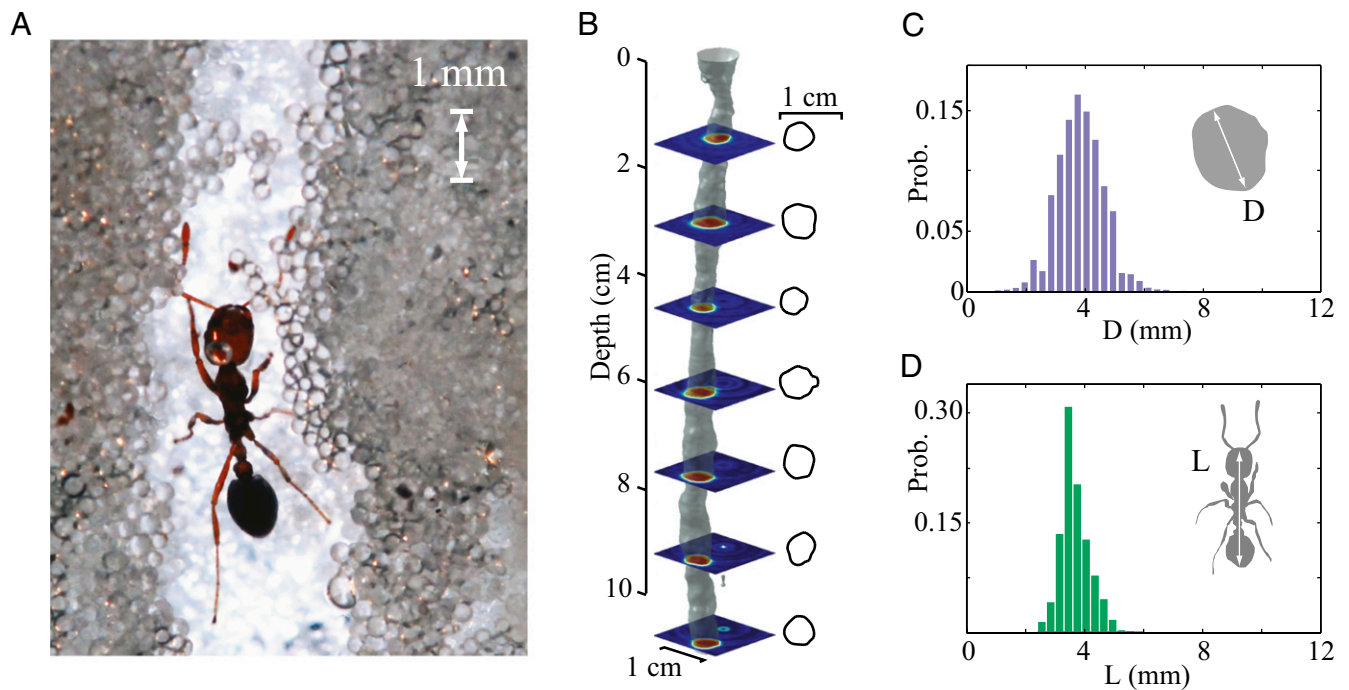


Fig. 1. Fire ants create and move through subterranean tunnels (Photo credit: Laura Danielle Wagner). (A) Image shows fire ant worker climbing within an ant-constructed tunnel against a clear glass pane. (B) X-ray CT scan reconstruction of a fire ant tunnel segment. (C) Probability distribution of tunnel cross-sectional diameter, D. In A–C, the substrate consists of wetted 250 micron approximately spherical glass particles. (D) Probability distribution of ant body length, L (measured from head to gaster), in laboratory climbing experiments.

In this article we seek to identify principles of locomotion within confined environments that challenge animals with a different set of locomotive constraints than in above-ground study. We investigate the effects of subterranean confinement (tunnel diameter) on the mobility and stability of the fire ant (*S. invicta*). We show that climbing in confined environments is a robust mode of high-speed locomotion, in which slips, falls, and frequent collisions with the environment do not necessarily prevent high-speed ascent and descent. We also demonstrate an unusual stabilizing response of fire ants when dislodged from the tunnel wall—the use of antennae as limb-like appendages to arrest and jam falls. Overall, we find that stable locomotion within subterranean environments is a function of the local tunnel morphology within which the organisms move. We hypothesize that the principle of off-loading locomotor control to the environment can be used by animals in confined environments and can inspire the next generation of mobile robots.

Results and Discussion

Shape and Form of Excavated Fire Ant Tunnels. To examine the interaction of fire ants with the tunnels that they constructed, we first measured the size and shape of nest tunnels excavated by fire ant workers (body length $L = 0.35 \pm 0.05$, $n = 2,611$ measurements) in three-dimensions in a laboratory experiment using an X-ray computed tomography (CT) system (Fig. 1 and Fig. S1). We allowed isolated groups of fire ant workers to excavate tunnels within an 8 cm diameter, and 12 cm deep, cylindrical volume of laboratory soil (wet approximately spherical glass particles, see below) over the course of 20 h. The tunnels were roughly circular in cross-section (Fig. 1B, Fig. S2, and SI Text), and the effective cross-sectional diameter (SI Text) within the tunnels was $D = 3.7 \pm 0.8$ mm ($n = 2,262$ observations from 10 experiments).

To determine if the soil substrate had an effect on tunnel shape and size, we repeated this experiment using different substrate

combinations of particle diameter (50, 210, and 595 μm ; See Table S1 for polydispersity) and soil moisture content (1%, 3%, 5%, 10%, 15%, 18%, and 20% by mass). We challenged worker groups from eight separate colonies to excavate tunnels in each substrate combination and collected 168 separate X-ray CT tunnel excavation observations (Fig. S3). We found a significant effect of both particle diameter ($F_{2,136} = 10.48$, $P < 0.0001$) and soil moisture content ($F_{6,136} = 5.38$, $P < 0.0001$) on excavated tunnel depth, indicating that substrate had a strong effect on digging proficiency. Soil moisture content had a nonlinear effect on tunnel depth. Tunnel depth was small at low soil moisture and rose to a maximum at intermediate soil moisture contents of 10–15%, above which tunnel depth decreased again at high soil moisture (SI Text).

Importantly, however, we found no significant effect of soil moisture ($F_{6,106} = 1.06$, $P = 0.39$), particle diameter ($F_{2,106} = 1.56$, $P = 0.21$), or the interaction of moisture and particle size ($F_{12,106} = 1.47$, $P = 0.15$) on the tunnel diameter (SI Methods). Moreover, tunnels constructed in the laboratory and observed in X-ray CT were similar in diameter to tunnels found in natural fire ant nest mounds (4.4 mm) (46), nest entranceways (3–4 mm) (45), and incipient nests (3.1 ± 0.1 mm) (47), although tunnels deeper within natural nests may be larger in size (6.0 ± 3.0 mm) (46). Our results demonstrate that during tunnel founding, fire ants show a relatively fixed behavioral program by building tunnels of approximately the same diameter in a variety of conditions. This suggests that the diameter of the tunnel could be important in fire ant locomotion.

Tunnel Size Effects on the Biomechanics of Confined Climbing. To investigate the biomechanics of locomotion within tunnels, we monitored fire ants climbing within ant-constructed tunnels within Quasi-2D arenas (Fig. 1A and Movies S1–S3) and smooth cylindrical glass tubes (Fig. 2A and B). We tracked the position of ascending and descending ants freely trafficking between

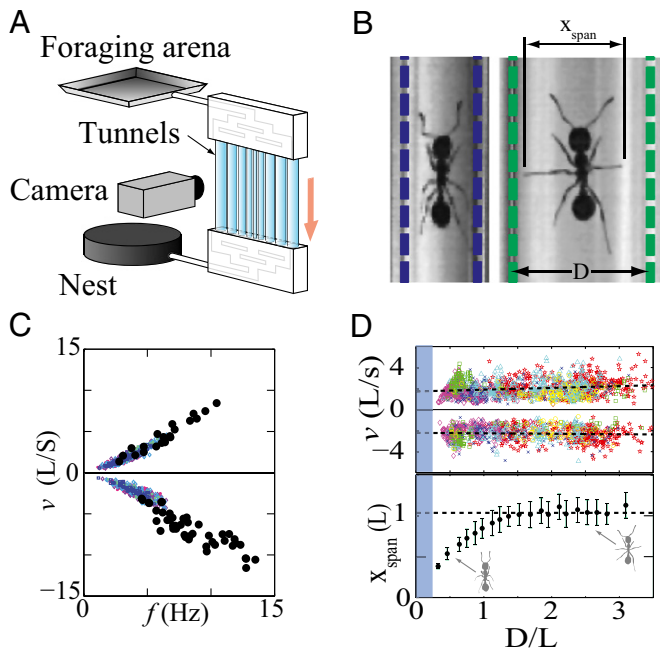


Fig. 2. Climbing posture and antennae use in glass tunnels. (A) Schematic of climbing biomechanics experiment. (B) Posture of ascending ant in a 2 mm diameter tunnel (Left; $D = 0.60$ L) and in a 6 mm diameter tunnel (Right; $D = 1.36$ L). Right image shows posture variable, x_{span} , measured in experiment. (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

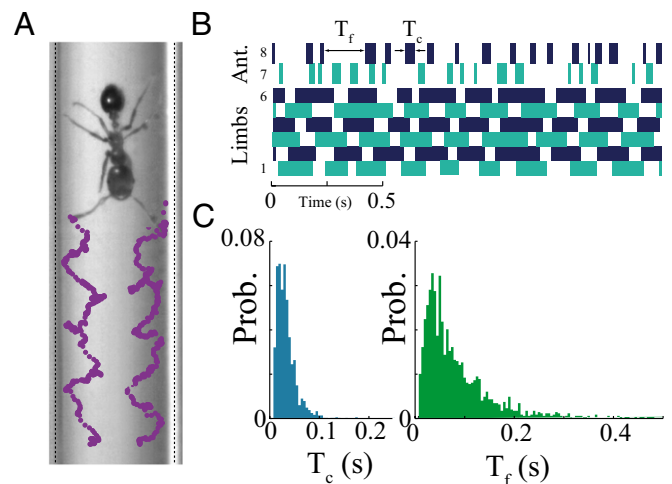


Fig. 3. Antennae use in confined locomotion. (A) Image of ant descending in a tunnel with tracked position of antennae tips shown in purple. $D = 3$ mm. (B) Stepping and antennae contact diagram for a vertical descent in a tunnel. Light and dark blue highlight limbs that form alternating tripods during locomotion: (1) right hind, (2) right fore, (4) left fore, (5) left mid, (6) left 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 .

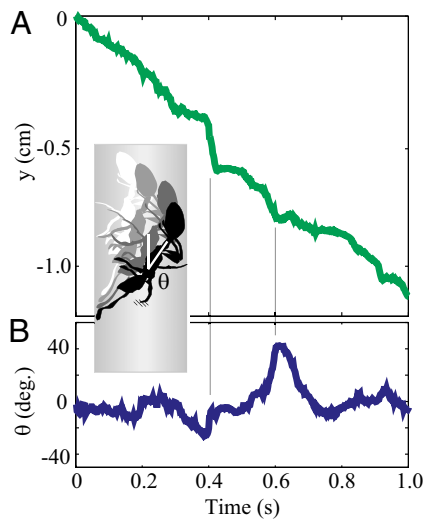


Fig. 4. Kinematics and slip recovery during tunnel climbing within an ant-constructed tunnel. (A) Vertical position of ant while descending (Movie S3). (B) Body angle (θ) with respect to tunnel axis. Two slip recovery events are highlighted by vertical gray lines. During slip events antennae and limbs are jammed against the wall and the body pitches into the tunnel wall (illustration).

away from the body to generate forward thrust. In the compact posture, to generate thrust force, we hypothesize that the rows of 50–350- μm -long spiny hairs along the limb (Fig. S8) are used in concert with limb substrate friction to engage asperities in the climbing substrate and allow the limb to push. Such multifunctional limb design has been previously shown to aid in rapid locomotion on horizontal substrates through the engagement of spiny limb hairs with rough surfaces (49).

Slip-Recovery Through Rapid Jamming. Fire ants possess a pair of elbowed antennae capable of a wide range of articulated motion about the head (Fig. 3A). While ascending and descending, ants rapidly placed antennae in contact with the tunnel walls (Movie S1 and Fig. 3A). In the glass tunnels, antennae-wall contact time was $T_c = 29 \pm 23$ ms (Fig. 3C; $n = 1,840$ contacts from 54 climbs) during head-first descent. The time between contacts was $T_f = 82 \pm 81$ ms (Fig. 3C). The rapid and repeated antennae-wall contact is important for tactile and chemo-sensing within the subterranean environment (34). However, observations of ants slipping within glass and natural tunnels (Movie S4) led us to hypothesize that these sensory appendages could also have important biomechanical functions for climbing in confined spaces.

During high-speed ascent and descent in both glass and ant-constructed tunnels, ants exhibited slips that were rapidly corrected through antennae and limb contact with the tunnel surface (Fig. 4 and Movies S1, S2, and S3). Ants rapidly arrested short downward slips (in which the instantaneous downward velocity exceeded $15 \text{ mm}\cdot\text{s}^{-1}$) within 82 ± 21 ms ($n = 456$ slips among 54 individuals) within glass tunnels of all sizes. During head-first slips, antennae were placed against the tunnel wall before arrest in 92% of the observed slip arrests (422 antennae contacts out of 456 slips). Excluding slips in which antennae began in contact with the wall, the time between slip onset and antennae-wall contact was 32 ± 22 ms ($n = 265$).

We briefly compare our observations of tunnel falling with the more extreme case of gliding among arboreal ants, in which ants in free fall can direct their motion during falls of hundreds to thousands of body lengths (50). During aerial descent among canopy ants, gliding from a tree branch to a lower location on the tree aids in evasion from predators that may be on branches or on the forest floor. In the crowded and dark nest, long-distance-

directed aerial descent would be unsuccessful due to poor navigational ability and space constraints (lack of vision and tactile sensation from antennae). However, we hypothesize that the rapid slip arrest we observe in high-speed tunnel locomotion (Movie S3 and Fig. 4) is an important mode of locomotion in confined environments, such that repeated slips or “microfalls” can enhance rapid descent.

Our observations indicate that antennae are rapidly and readily used for slip correction when climbing in confined spaces. In the case of larger slips, the antennae deformations also suggest that antennae provide significant mechanical support to the falling ant (Movie S4 and Figs. S9–S11). Morphological adaptations to subterranean life are well documented (51); here we have observed that fire ant antennae—which are evolved from ancestral arthropod limbs (52)—retain partial functionality as locomotion appendages. Antennae can act effectively like seventh and eighth limbs to arrest falls and maintain stability during climbing in tunnels.

Rapid fall arrest by bracing antennae against a tunnel wall relies on the ability to quickly jam limbs and body against opposing locations along the tunnel wall. Thus, we hypothesized that the ability to rapidly arrest slips through body jamming would be sensitive to tunnel diameter. To test this hypothesis we subjected ants climbing within glass tunnels to perturbations consisting of a rapid downward translation of the tunnels (Fig. 24 and Movie S5). Glass tunnels were mounted to a vertical air piston controlled through a computer. The piston translated the tunnels downward 5 mm, at which point the motion was stopped in less than 2.5 ms upon impact with the mounting plate. The final downward speed of the tunnels before impact was estimated to be 0.66 m/s; ants were thus subject to a mechanical perturbation of ~ 27 g upon stopping. The perturbations used in this experiment are substantially larger than what ants experience during jostling by neighbors in the natural environment. However, high-speed perturbation-response experiments challenge the fastest neural response times of locomoting organisms, and thus help to determine the role of body kinematics and morphology in rapid locomotion stabilization (6, 10, 53, 54).

We found that 52% (1,092 falls out of 2,584 perturbations) of the perturbation experiments did not lead to ants being displaced from the tunnel wall (Fig. S12A). This indicates that the fire ant

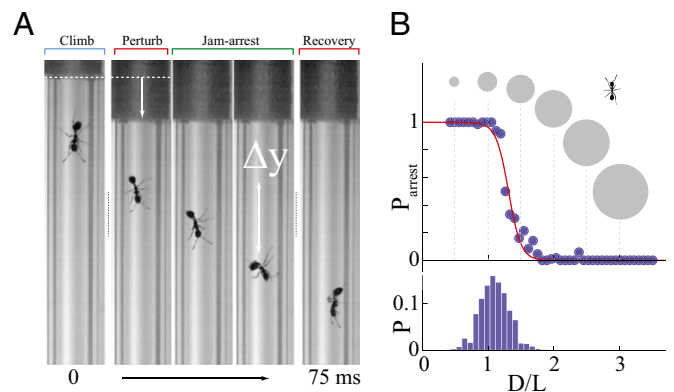


Fig. 5. Climbing perturbation experiment. (A) Image sequence of perturbation and recovery (corresponding to perturbation 1 in Movie S5). Left image is immediately before perturbation. Middle images show recovery that took place within 75 ms ($\Delta T = 30$ ms for middle three frames). After perturbation recovery ant continued downward climb (right image). (B, Upper) Probability to arrest falls, P_{arrest} , versus D/L . Line is logistic fit described in text. Gray circles are tunnel diameter drawn to scale of ant illustration. (B, Lower) Probability distribution of tunnel diameter in units of ant body length (L) for excavated tunnels (data reproduced from Fig. 1D).

tarsi and adhesive footpads are robust to substantial perturbations, consistent with other measurements of the ant's adhesive strength (55–57). However, displacement from the tunnel surface did occur in 48% of experiments, and the outcome of perturbations was strongly influenced by the interaction of ant tunnel size.

We found that tunnel diameter, with respect to ant body length, had a significant effect on the probability to fall during a perturbation experiment, with smaller tunnels aiding in the ants' perturbation resistance (Fig. S12B). The probability to fall during a perturbation increased from 36% to 73% as D/L increased from 0.4 to 3.4; the increase occurred over a narrow range around $D/L \approx 2.3$. The resistance to perturbation in tunnels of $D < 2.3 L$ was likely due to the ability of fire ants to robustly engage surfaces. When climbing vertical planar surfaces, animals have to contend with gravity, which, because the animal's center of mass is offset from the climbing surface, generates an overturning moment on the animal that must be overcome. In contrast, when climbing in small tunnels, ants may be able to minimize torque-induced gravity on the body by placing limbs laterally against walls and thus keeping the center of mass in the same vertical plane as limb contact points.

Ants perturbed from the tunnel wall either arrested their fall within a vertical distance Δy , or fell to the tunnel bottom (Fig. 5B and Movie S5). Arrest distance, Δy , increased with increasing tunnel diameter normalized by body length, D/L (Fig. S13). The upper envelope of Δy (dashed line in Fig. S13) increased linearly with a slope $67 \pm 7 \text{ mm}$ ($R^2 = 0.95$). This relationship can be understood through a kinematic argument: to arrest falls, ants extend limbs and antennae toward tunnel walls that are a further distance away within larger tunnels, and this results in longer fall distances in larger tunnels (SI Text).

The probability to arrest a fall, P_{arrest} , within a tunnel of size D/L decreased from 1 to 0 as D/L increased. We fit P_{arrest} to a logistic function, $P_{\text{arrest}} = 1/[1 + e^{\alpha(D-D_s)}]$ (Fig. 5B) and found the cutoff tunnel diameter, $D_s = 1.31 \pm 0.02 L$ ($\alpha = -10.54 \pm 1.76$), at which arrest probability decreased to below 50% (see Fig. S5 and Table S2). Within ant-constructed tunnels (of mean diameter 1.06 L; Fig. 5B, Lower) we predict that 93% of falls will be arrested. This demonstrates that ants display a high degree of climbing stability within tunnels of comparable size to those they create (1.06 L); however, an increase in tunnel diameter by 50% reduced arrest probability to less than 5%.

We hypothesized that tunnel diameter would limit the ability to recover from falls through a “jam arrest” mechanism within tunnels. Thus, we expected that D_s was governed by morphological limitations of ant limb use. We measured the lateral limb span, x_{span} , for free-falling ants and found that ants extended limbs maximally to a width of $\max(x_{\text{span}}) = 1.33 \pm 0.22 L$ independent of tunnel size when $D > 1.3 L$. This measurement is consistent with the typical midlimb span of fire ants $1.31 \pm 0.09 L$ reported in the literature (SI Text and Fig. S15) (48) and suggests ants are extending limbs maximally to re-engage the tunnel wall while falling. In tunnels whose diameter exceeded the physical reach of the ants, $D > 1.3 L$, ants were unable to engage walls and the arrest probability decreased substantially (Movie S5).

We return to the digging experiments—in which groups of ants constructed tunnels—to understand how ant tunnel size relates to stability in confined spaces. The average diameter of tunnels created by ants across all excavation experiments was $D = 1.06 \pm 0.23 L$. Thus it seems reasonable to assume that fire ants construct tunnels that facilitate rapid locomotion through the enablement of slip recovery by antennae and limb jamming, without hindering limb kinematics. Many other factors are likely to influence equilibrium nest tunnel size. Traffic may be important in nest tunnel size determination as it is hypothesized that larger tunnels in the nest foraging network are due to higher traffic flow in these locations (46, 58). Further, food transportation

requirements, ventilation, protection from flooding, and protection from invasion by predators or other brood raiding colonies can also influence nest structure (34). We hypothesize that the shape and size of tunnels at any time reflects the important environmental and biological factors influencing the colony at that time (37, 47). However, during incipient nest construction, such as after a flood, we expect that high-speed locomotion and excavation are important to survival.

Conclusions

We have shown that fire ants are capable of moving rapidly within their nest through the use of multifunctional limbs and antennae, which effectively engage tunnel surfaces. We found that tunnel diameter had little effect on locomotion speed over a threefold range of tunnel diameters, although body posture and limb use differed in different-sized tunnels. We also discovered that fire ant antennae were effectively used as additional limbs during locomotion. Functionality of antennae as load-bearing, locomotor appendages was a surprising result, one which highlights the importance of studying locomotion within the context of the organism's natural environment. During locomotion, antennae were rapidly and repeatedly placed in contact with the tunnel surface for sensory feedback, however the antennae's multifunctional nature also implies that antennae may be the ant's first option to rapidly recover from missteps or slips. X-ray CT indicated that fire ants constructed tunnels of appropriate size to enable utilization of the slip recovery mechanisms we observed in laboratory climbing experiments.

The ability for organisms to offload locomotion control to their environmental structures represents a new paradigm of locomotion control and a novel example of the integration of the organism's extended phenotype (the nest) for a locomotory purpose. We hypothesize that the construction of control surfaces suited to the locomotors' body size and limb kinematics reduces locomotion control requirements within subterranean environments and may be a general feature of robust control within organism-engineered substrates such as tunnels, trails, or burrows. A universal scaling of burrow cross-sectional area with body length (20)—sampled across a wide array of organisms varying by over six orders of magnitude by mass—provides evidence of the commonalities of locomotor constraints among subterranean animals. Thus, the robust locomotor control strategies for subterranean environments we have described for fire ants may apply to a diversity of subterranean animals. We also expect that our biological discoveries will provide inspiration for, and simplify control in, collective robotic devices that will have to move within confined environments such as search and rescue zones. We propose that future robot teams could enhance survival in harsh terrestrial and extraterrestrial environments through collective construction of appropriately engineered shelters and nests.

Methods

Digging Experiments. We used a custom X-ray CT system to observe tunnel excavation. Groups of 100–150 fire ant workers dug tunnels in 3.8 or 8.2 cm diameter chambers filled to a height of 12–15 cm with slightly polydisperse glass particles of diameter 50, 210, or 595 μm (Jaygo Inc.; see Table S1 for particle size distribution). We varied water moisture content in the simulated soil between 1% and 20% measured by mass. From CT reconstructions we extracted the tunnel shape using the Chan–Vese active contours method (59). We measured the effective tunnel diameter, D , as the maximum of the distance transform of the tunnel cross-section (SI Text).

Climbing Experiments. Climbs in ant-constructed tunnels were observed in quasi-2D arenas, $27 \times 34 \times 0.3 \text{ cm}$ in size, filled with wetted granular material as described in ref. 60. Ants climbed between a nest and foraging arena through glass tunnels of diameter D 1–9 mm (in increments of 1.0 mm) and length 107.0 mm (Technical Glass). Movies of climbing ants were recorded at a frame rate of 200 and 400 Hz (AOS Technologies). To observe the falling response of ants within tunnels, we performed a perturbation experiment in

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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