responses to environmental changes that are significantly more abrupt than those that would occur in nature. ☐

Methods

Each experimental unit consisted of a single plant growing in an eight-inch pot containing field-collected soil. Plants were initially collected as seed from the field, germinated in the laboratory and added to the experimental units as one-week-old seedlings. After each 15-week growth period, plant shoots were removed and new seedlings were added to each pot. After the first generation, the source of seed was from plants of the previous generation. *B. inermis* is an obligate cross-pollinated plant. Some inbreeding can occur, but this results in seed that is significantly smaller and distorted. Therefore only out-crossed seed was used for the establishment of new generations.

The experiment consisted of 15 experimental units per treatment. The three $[CO_2]$ treatments were imposed using nine environment-controlled growth chambers. Throughout the experiment, other environmental variables were recorded for each chamber, including air temperature, relative humidity and light intensity. Apart from $[CO_2]$, we did not detect any significant difference in any measured environmental variable among treatments. Plants were randomly assigned to a different growth chamber after every five weeks, and the appropriate $[CO_2]$ was re-set. Plants were watered (400 ml) on a weekly basis and fertilized with 250 ml of low-phosphorus, Long-Ashton solution every two weeks.

At harvest, soil was collected using a 10-cm diameter corer. This soil core was then used to trap AMF for determination of AMF species richness and mycorrhizal dependency. This was achieved by mixing the soil with silica sand, adding this mix to a new eight-inch pot, planting a new seedling of *B. inermis*, letting it grow for three months, cutting off the shoots, planting a new seedling and letting it grow for two more months, and finally collecting the resulting AMF spores from a 50-g core sample. A subsample of the spores (200 randomly chosen spores) was used for species identification. The remainder (average = 548 spores) were mixed into a sterile soil/sand medium in a new eight-inch pot that was then used to grow a seedling of *B. inermis* for 12 weeks. Mycorrhizal dependency was calculated as (the biomass of *B. inermis* grown with AMF minus the biomass of plants grown without AMF) divided by the biomass of *B. inermis* grown with AMF. Plant biomass was determined after drying at 60 °C for 36 h. For [P], plant shoot tissue was ashed at 500 °C for 4 h, dissolved in aqua regia and then determined using a mass spectrometer. Root lengths were determined using an image analysis system (WinRhizo, Regent Instruments Inc.). A sub-sample of roots was collected, cleaned of soil, stained with Chlorazol Black E[25] and assessed for mycorrhizal colonization[26]. The total length of fungal hyphae was determined after extraction from a subsample of soil using the filtration method[27]. The length of living hyphae belonging to each of the different genera was assessed using direct immunofluorescence[14]. Finally, as an overall assessment of soil aggregate size distribution we measured the MWD and WSA of the 1–2 mm aggregate size class using a wet-sieving protocol[28].

1. Körner, C. & Bazzaz, F. A. *Carbon Dioxide, Populations, and Communities* (Academic Press, San Diego, 1996).
2. Luo, Y. & Mooney, H. A. *Carbon Dioxide and Environmental Stress* (Academic Press, San Diego, 1999).
3. Luo, Y. & Reynolds, J. F. Validity of extrapolating field CO_2 experiments to predict carbon sequestration in natural ecosystems. *Ecology* **80,** 1568–1583 (1999).
4. IPCC. Climate Change 2001: Synthesis Report. in *A Contribution of Working Groups I, II, and III to the Third Assessment Report of the Intergovernmental Panel on Climate Change* (eds Watson, R. T. & the core writing team) 1–398 (Cambridge Univ. Press, Cambridge, 2001).
5. Bazzaz, F. A. The response of natural ecosystems to the rising global CO_2 levels. *Annu. Rev. Ecol. Syst.* **21,** 167–196 (1990).
6. Ward, J. K. & Kelly, J. K. Scaling up evolutionary responses to elevated CO_2: lessons from *Arabidopsis*. *Ecol. Lett.* **7,** 427–440 (2004).
7. Sinead, C. & Bell, G. Phenotypic consequences of 1,000 generations of selection at elevated CO_2 in a green alga. *Nature* **431,** 566–569.
8. Rillig, M. C., Treseder, K. K. & Allen, M. F. in *Mycorrhizal Ecology* (eds van der Heijden, M. G. A. & Sanders, I.) 135–160 (Springer, Berlin, 2002).
9. Treseder, K. K. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. *New Phytol.* **164,** 347–355 (2004).
10. Staddon, P. L. & Fitter, A. H. Does elevated atmospheric carbon dioxide affect arbuscular mycorrhizas? *Trends Ecol. Evol.* **13,** 455–458 (1998).
11. Allen, M. F. *Ecology of Mycorrhizae* (Cambridge Univ. Press, Cambridge, 1991).
12. Smith, S. E. & Read, D. J. *Mycorrhizal Symbioses* 2nd edn (Academic, London, 1997).
13. Klironomos, J. N., Ursic, M., Rillig, M. & Allen, M. F. Inter-specific differences in the response of arbuscular mycorrhizal fungi to *Artemisia tridentata* grown under elevated atmospheric CO_2. *New Phytol.* **138,** 599–605 (1998).
14. Treseder, K. K., Egerton-Warburton, L. M., Allen, M. F., Cheng, Y. & Oechel, W. C. Alteration of soil carbon pools and communities of mycorrhizal fungi in chaparral exposed to elevated carbon dioxide. *Ecosystems* **6,** 786–796 (2003).
15. Wolf, J., Johnson, N. C., Rowland, D. L. & Reich, P. B. Elevated CO_2 and plant species richness impact arbuscular mycorrhizal fungal spore communities. *New Phytol.* **157,** 579–588 (2003).
16. Klironomos, J. N. Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology* **84,** 2292–2301 (2003).
17. Klironomos, J. N. in *Microbial Biosystems: New Frontiers* (eds Bell, C. R., Brylinsky, M. & Johnson-Green, P.) 845–851 (Proc. 8th Int. Symp. on Microbial Ecology, Halifax, 2000).
18. Hart, M. M. & Reader, R. J. Taxonomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. *New Phytol.* **153,** 335–344 (2002).
19. Rillig, M. C., Wright, S. F., Allen, M. F. & Field, C. B. Rise in carbon dioxide changes soil structure. *Nature* **400,** 628 (1999).
20. Piotrowski, J. S., Denich, T., Klironomos, J. N., Graham, J. M. & Rillig, M. C. The effects of arbuscular mycorrhizae on soil aggregation depend on the interaction between plant and fungal species. *New Phytol.* **164,** 365–373 (2004).
21. Van der Heijden, M. G. A. *et al.* Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396,** 69–72 (1998).
22. Goverde, M., Van der Heijden, M. G. A., Wiemken, A., Sanders, I. R. & Erhardt, A. Arbuscular mycorrhizal fungi influence life history traits of a lepidopteran herbivore. *Oecologia* **125,** 362–369 (2000).
23. Gange, A. C., Brown, V. K. & Alphin, D. M. Multitrophic links between arbuscular mycorrhizal fungi and insect parasitoids. *Ecol. Lett.* **6,** 1051–1055 (2003).
24. Rillig, M. C. Arbuscular mycorrhizae and ecosystem processes. *Ecol. Lett.* **7,** 740–754 (2004).
25. Brundrett, M. C., Piché, Y. & Peterson, R. L. A new method for observing the morphology of vesicular-arbuscular mycorrhizae. *Can. J. Bot.* **62,** 2128–2134 (1984).
26. McGonigle, T. P., Miller, M. H., Evans, D. G., Fairchild, G. L. & Swan, J. A. A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. *New Phytol.* **115,** 495–501 (1990).
27. Miller, R. M., Reinhardt, D. R. & Jastrow, J. D. External hyphal production of vesicular-arbuscular mycorrhizal fungi in pasture and tallgrass prairie communities. *Oecologia* **103,** 17–23 (1995).
28. Kemper, W. D. & Rosenau, R. C. in *Methods of Soil Analysis Part 1. Physical and Mineralogical Methods* 2nd edn (ed. Klute, A.) 425 (Agronomy Monograph No. 9, American Society of Agronomy, Madison, 1986).

Directed aerial descent in canopy ants

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Numerous non-flying arboreal vertebrates use controlled descent (either parachuting or gliding *sensu stricto*[1,2]) to avoid predation or to locate resources[3–7], and directional control during a jump or fall is thought to be an important stage in the evolution of flight[3,8,9]. Here we show that workers of the neotropical ant *Cephalotes atratus* L. (Hymenoptera: Formicidae) use directed aerial descent to return to their home tree trunk with >80% success during a fall. Videotaped falls reveal that *C. atratus* workers descend abdomen-first through steep glide trajectories at relatively high velocities; a field experiment shows that falling ants use visual cues to locate tree trunks before they hit the forest floor. Smaller workers of *C. atratus*, and smaller species of *Cephalotes* more generally, regain contact with their associated tree trunk over shorter vertical distances than do larger workers. Surveys of common arboreal ants suggest that directed descent occurs in most species of the tribe Cephalotini and arboreal Pseudomyrmecinae, but not in arboreal ponerimorphs or Doli-choderinae. This is the first study to document the mechanics and ecological relevance of this form of locomotion in the Earth's most diverse lineage, the insects.

The tropical forest canopy is home to a large fraction of the Earth's species, and ants are an important part of the associated fauna[10]. Canopy ants exhibit numerous adaptations that promote an arboreal lifestyle, such as modified 'sticky' tarsi that allow them to cling to surfaces[11,12]. Despite these adaptations, large numbers of ants fall from trees in tropical forests, a result of being dislodged by wind or by arboreal mammals or birds[13,14]. Moreover, *Cephalotes atratus* workers will voluntarily drop off tree trunks when approached by a foreign object[15]. This is paradoxical because worker ants lack wings, and the likelihood of any ant rejoining its colony after falling to the forest floor 30 m below is presumably quite low. Here we show that falling *Cephalotes* spp. rarely reach the forest floor. Instead, they control their aerial descent such that they glide back to their host tree trunk, preventing a landing in the understory and facilitating a rapid return to the nest.

Observations of this behaviour in *C. atratus* during previous studies in Panama[16], and recent video recordings in Peru (see Supplementary Videos), showed that falling individuals of *C. atratus* follow a consistent J-shaped path leading back to their associated tree trunk. The trajectory is characterized by three distinct stages: (1) a vertical drop (uncontrolled parachuting); (2) a rapid directional adjustment with body alignment towards the tree; and (3) a steep but directed glide to the trunk. By painting the gaster and hind legs of the ants white, we determined that *C. atratus* workers align their abdomens towards the trunk during the adjustment stage, and that the subsequent glide to the trunk occurs abdomen-first and dorsal side up over the entire transit.

We quantified the consistency of directed descent behaviour by dropping 120 marked *C. atratus* workers from the lower crown branches (about 27 m) of their resident tree near Iquitos, Peru, under windless conditions. A strong majority of the ants (85%) successfully landed on the trunk. This success rate far exceeds that expected for a parachuting insect exhibiting undirected horizontal drift during free fall (8%; *G*-test, $P < 0.0001$; see 'Null model' in Methods). Upon making contact with the trunk, ants generally adhered there or tumbled downwards a few metres before gaining a foothold, at which point they began to climb the tree. Marked ants typically returned to the same branch, often walking near the original drop point, within 10 min of the fall. This is the first quantification of controlled descent in ants, and the first record of any macroscopic animal consistently gliding backwards to reach a target. Furthermore, a pair of experiments (see Supplementary Information) documents that return success does not depend on familiarity with the colony's host tree, and that the ants align to the target tree regardless of their initial orientation when dropped.
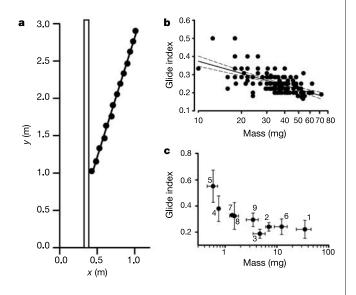
Some ants partly rely on visual stimuli to relocate their nest after foraging[17,18]. Thus, we predicted that directed descent behaviour in ants depends on their ability to visually locate a tree trunk during a fall. Individual *C. atratus* workers were experimentally blinded by covering the eye with white enamel paint. Control ants and blinded ants also received white paint on the dorsal surface of the head. Blind *C. atratus* workers regained the trunk with significantly lower frequency (average ± 1 s.d. = 10.0 ± 4.61%) than controls (84.5 ± 11.52%; $P < 0.0001$). The frequency with which blind ants landed on the trunk did not differ from that expected by undirected horizontal motion (*G*-test, $P > 0.17$; see 'Null model'). Ants used in other experiments occasionally directed their descent towards the beige climbing rope or nearby lianas, suggesting that light-coloured upright linear objects serve as important visual cues for alignment.

Ant gliding performance was analysed from two-dimensional reconstruction of body trajectories obtained within a flight arena (Fig. 1). Of 28 filmed ants, six successfully glided to and landed on a target column within the camera's field of view. Equilibrium glide speeds averaged 4.3 m s^{-1} for these six ants, and the equilibrium glide angle (that is, the angle between the flight path and the horizontal; Fig. 1) averaged 75.0° (range 73.0°–77.9°), corresponding to a lift:drag ratio of 0.27. Although this value is modest relative

to the shallow glides and high lift:drag ratios exhibited by many gliding vertebrates, such glides by ants are nonetheless impressive given the absence of dedicated lift-generating surfaces and the typical Reynolds number during flight (mean value of 4,110 based on body length). By comparison, a cylinder with length:diameter ratio of four (approximating *C. atratus* workers) will attain a maximum lift:drag ratio of 0.22 at the same Reynolds number (calculated following the resolved-flow analysis in ref. 19). For arboreal ants falling from tall trees, absolute glide angle may be less relevant than the ability to effect stable motion oriented towards the home trunk.

Worker body size (mass) is highly variable within *C. atratus*, and spans two orders of magnitude among species within the genus *Cephalotes* (Fig. 1). We examined the effects of body size on directed descent performance by measuring the vertical distance travelled between the drop point and trunk contact. Glide performance increased (that is, vertical drop distance decreased) with decreasing worker body size in *C. atratus* (Fig. 1). We attribute this to smaller individuals attaining a minimum viable glide velocity (U_{min}; ref. 3) more rapidly than larger individuals during the parachuting phase of the descent.

This size dependence was duplicated interspecifically, further documenting the widespread distribution of directed descent within the myrmicine tribe Cephalotini (Fig. 1). The flattened, flanged morphology typical of Cephalotini is more developed in smaller species[20,21] and probably enhances their lift:drag ratio. However, dorsoventral flattening does not seem to be a prerequisite for directed descent in ants—several species in the subfamily Pseudomyrmecinae controlled their descent when dropped (Sup-

Figure 1 Flight dynamics and performance of *Cephalotes* workers. **a**, Representative aerial trajectory for a *C. atratus* worker gliding to and landing on a vertically aligned white fabric column. Time interval between points is 1/30 s. The regression is given by: $y = 3.22x − 0.41$, $R^2 = 0.996$, $P < 0.001$. Equilibrium glide velocity averaged 4.53 m s^{-1}; body mass was 0.047 g. **b**, Glide index (horizontal distance travelled per unit vertical drop) as a function of body size in 140 *C. atratus* workers collected from six different colonies (11–45 ants per colony). Some points are hidden by overlap. Mass was measured in the laboratory (59% of points) or estimated in the field (41%) from head width (see Supplementary Information). Solid line is the least square regression. Glide index = $−0.097$ ln(mass) + 0.596; $R^2 = 0.355$; $P < 0.0001$; dashed lines are 95% confidence limits. **c**, Average (±1 s.d.) glide index versus mass for minor workers of nine *Cephalotes* spp. Numbers refer to species listed in Supplementary Table 1. For glide index means, $n = 2$ drops for *C. pallens* (point 7); $n > 2$ for all others. For mass means, $n = 1$ for *C. grandinosus* (point 4); $n > 7$ for all others. Horizontal distance ranged from 2.0 to 2.5 m in **b** and from 1.0 to 2.5 m in **c**.

plementary Table 1); these are more cylindrical ants that lack lateral body flanges.

Directed aerial descent is not exhibited by all arboreal ants. Although it appears to be widespread in the Cephalotini and common in Pseudomyrmecinae, it is rare or absent among tested species in other groups of arboreal ants (Dolichoderinae, ponerimorphs and Formicinae). The following characteristics are consistent with this taxonomic distribution and may be evolutionarily correlated with directed descent behaviour: (1) arboreal nesting; (2) frequent foraging at branch tips (for example, for pollen, nectar and homopteran exudates); (3) relatively costly workers (for example, small colony size and/or heavily armoured individuals); (4) morphology permitting a broad range of abdominal movement[21,22] (for example, the presence of a post-petiole); (5) good vision and diurnal activity (promoting the use of high-contrast visual cues); and (6) evolutionary origins in flooded forests (where predation pressure from surface-feeding fish[23] may be extreme). Note that *Daceton armigerum* and *Camponotus* cf. *canescens* are taxonomically distinct from the Cephalotini and Pseudomyrmecinae, but both showed controlled descent behaviour (see Supplementary Table 1). *D. armigerum* meets the criteria proposed above[24] whereas *C.* cf. *canescens* does not (at least for lack of a post-petiole). This suggests that further comparative studies throughout the tropics, exploiting the 100+ species that can live in a small patch of forest canopy[14], will help refine our understanding of the ecology and evolution of directed aerial descent in ants. □

Methods

Study areas

Ants were dropped from trees on Barro Colorado Island, Panama (09.15° N, 79.85° W), at the La Selva Biological Station, Costa Rica (10.43° N, 84.02° W), and in western Amazonian forests within 150 km of Iquitos, Peru (03.75° S, 73.25° W; Supplementary Table 2). Vouchers were deposited at the National Museum of Natural History (Washington DC), Smithsonian Tropical Research Institute (Panama), and the Museo de Historia Natural Javier Prado (Peru).

Drop tests

Workers were grasped in the midthoracic region with forceps, held a few centimetres to one side of a branch, and dropped. Each ant was scored according to whether or not it made contact with the trunk before reaching the ground. All drops were initiated during periods of still air, as determined by lack of leaf motion in the surrounding vegetation and by the straight trajectories of dropped inanimate objects. Ants that passed near the tree but landed out of sight (that is, on the side of the tree opposite the observer) were excluded from quantitative analyses (4.5% of the total number of ants dropped; scoring them as misses did not affect the results). Ants were examined for the presence of all appendages before dropping.

Vertical drop distances for performance tests were measured with a string of flags. The string was weighted at one (free hanging) end and secured to the tree at the other, such that it was near or touching the trunk surface over most of its length. Flags were spaced at 1.0-m intervals. Drop points were established in the tree crown, and horizontal distances were measured relative to the attachment point of the string. Vertical drop distances were measured to the point where the ant passed or struck the string, and were estimated to the nearest 0.5 m (0.25 m for drop distances <4 m).

Null model

A falling object will land directly beneath its drop point unless it is acted on by a lateral force (for example, wind) or its aerodynamic profile changes (for example, a parachuting insect moving its appendages). For a drop point on a branch located 2.0 m horizontal from the central axis of the tree trunk, an ant falling in still air but haphazardly moving >2.0 m horizontally relative to the drop point should strike a 1.0 m diameter tree trunk in eight of every 100 falls. The average diameter of trees used for drops was 0.73 m (Supplementary Table 2), thus the null is an overestimate. Incorporating trunk curvature does not substantially increase the null probability at horizontal distances >2.0 m. Ants that did not glide tended to land laterally >2.0 m relative to the drop point (for example, vision experiment), meeting the most fundamental model assumption.

All experiments followed the same general protocol: 10–30 ants from the same colony were dropped from two drop points (branches) separated by 100–180 radians in a tree. Foraging workers from different colonies were used in each replicate. Whenever possible, different trees and source colonies were used for different experiments. Proportional data were arcsine square-root transformed before analysis. The vision experiment was conducted in five replicate trees, and data were analysed with a split-plot analysis of variance (ANOVA) testing for effects of replicates, branches within replicates, and vision manipulation.

Video recordings and glide dynamics

Ants were held transiently at a height of 8 m, and were then dropped approximately 50 cm in front of a vertically aligned white fabric column (width 36 cm) that visually simulated a flat tree trunk. A tripod-mounted digital video camera (Canon ZR10) was positioned approximately 6 m from and orthogonal to glide trajectories of ants to the fabric column, of which the camera's field of view covered approximately the final three vertical metres. Video frames were downloaded into a microcomputer video editor at 30 frames s^{-1}, and individual frames were then digitized to obtain coordinates of the centroid of the moving ant as a function of time. A horizontal calibration frame located directly behind the plane of glide trajectories was used to determine absolute spatial coordinates. Positional data were evaluated using the program Quicksand[25] to obtain translational velocities as a function of time. Equilibrium glides by ants were defined as those glide intervals during which instantaneous translational velocity varied by no more than 5% from the average value for the time interval under consideration. Once such intervals were identified, equilibrium glide angles were determined from the slopes of linear regressions of the associated positional coordinates. A deadweight drop (plastic cylinder 5 cm long by 1.5 cm diameter filled with water) was used to validate the accurate reconstruction (that is, to within 1%) of translational acceleration under gravity alone. Ambient wind was monitored during experiments; no gliding trials were conducted when wind speed exceeded 0.5 m s^{-1}. Body mass of the six ants exhibiting equilibrium glides averaged 47.8 mg; their body length averaged 11.6 mm.

1. Oliver, J. A. "Gliding" in amphibians and reptiles, with a remark on arboreal adaptation in the lizard, *Anolis carolinensis carolinensis* Voigt. *Am. Nat.* **85,** 171–176 (1951).
2. Moffett, M. W. What's "up"? A critical look at the basic terms of canopy biology. *Biotropica* **32,** 569–596 (2000).
3. Kingsolver, J. G. & Koehl, M. A. R. Selective factors in the evolution of insect wings. *Annu. Rev. Entomol.* **39,** 425–451 (1994).
4. Mori, A. & Hikida, T. Field observations on the social behavior of the flying lizard, *Draco volans sumatranus*, in Borneo. *Copeia* **1994,** 124–130 (1994).
5. Jackson, S. M. Glide angle in the genus *Petaurus* and a review of gliding in mammals. *Mamm. Rev.* **30,** 9–30 (1999).
6. McCay, M. G. Aerodynamic stability and maneuverability of the gliding frog *Polypedates dennysi*. *J. Exp. Biol.* **204,** 2817–2826 (2001).
7. Socha, J. J. Gliding flight in the paradise tree snake. *Nature* **418,** 603–604 (2002).
8. Maynard Smith, J. The importance of the nervous system in the evolution of animal flight. *Evolution* **6,** 127–129 (1952).
9. Dudley, R. *The Biomechanics of Insect Flight: Form, Function, Evolution* 275–287 (Princeton Univ. Press, Princeton, 2000).
10. Stork, N. E., Adis, J. & Didham, R. K. *Canopy Arthropods* (Chapman & Hall, London, 1997).
11. Orivel, J., Malherbe, M. C. & Dejean, A. Relationships between pretarsus morphology and arboreal life in ponerine ants of the genus *Pachycondyla* (Formicidae: Ponerinae). *Ann. Entomol. Soc. Am.* **94,** 449–456 (2001).
12. Federle, W., Riehle, M., Curtis, A. S. G. & Full, R. J. An integrative study of insect adhesion: mechanics and wet adhesion of pretarsal pads in ants. *Integr. Comp. Biol.* **42,** 1100–1106 (2002).
13. Haemig, P. D. Effects of birds on the intensity of ant rain: a terrestrial form of invertebrate drift. *Anim. Behav.* **54,** 89–97 (1997).
14. Longino, J. T. & Colwell, R. K. Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. *Ecol. Appl.* **7,** 1263–1277 (1997).
15. Weber, N. A. The nest of an anomalous colony of the arboreal ant *Cephalotes atratus*. *Psyche (Cambridge)* **64,** 60–69 (1957).
16. Yanoviak, S. P. & Kaspari, M. E. Community structure and the habitat templet: ant assemblages in the tropical canopy and litter. *Oikos* **89,** 259–266 (2000).
17. Wohlgemuth, S., Ronacher, B. & Wehner, R. Ant odometry in the third dimension. *Nature* **411,** 795–798 (2001).
18. Hölldobler, B. Canopy orientation: a new kind of orientation in ants. *Science* **210,** 86–88 (1980).
19. Ellington, C. P. Aerodynamics and the origin of insect flight. *Adv. Insect Physiol.* **23,** 171–210 (1991).
20. Kempf, W. W. A taxonomic study on the ant tribe Cephalotini (Hymenoptera: Formicidae). *Rev. Entomol.* **22,** 1–244 (1951).
21. de Andrade, M. L. & Baroni Urbani, C. Diversity and adaptation in the ant genus *Cephalotes*, past and present. *Stuttgarter Beitr. Naturkunde B (Geologie und Paläontologie)* **271,** 1–889 (1999).
22. Coyle, F. A. Defensive behavior and associated morphological features in three species of the ant genus *Paracryptocerus*. *Insectes Soc.* **13,** 93–104 (1966).
23. Saint-Paul, U. *et al.* Fish communities in central Amazonian white- and blackwater floodplains. *Environ. Biol. Fishes* **57,** 235–250 (2000).
24. Wilson, E. O. Behavior of *Daceton armigerum* (Latreille), with a classification of self-grooming movements in ants. *Bull. Mus. Comp. Zool. Harv.* **127,** 401–422 (1962).
25. Walker, J. A. Estimating velocities and accelerations of animal locomotion: a simulation experiment comparing numerical differentiation algorithms. *J. Exp. Biol.* **201,** 981–995 (1998).