Towards understanding of climbing, tip-over prevention and self-righting behaviors in Hexapoda

Dissertation

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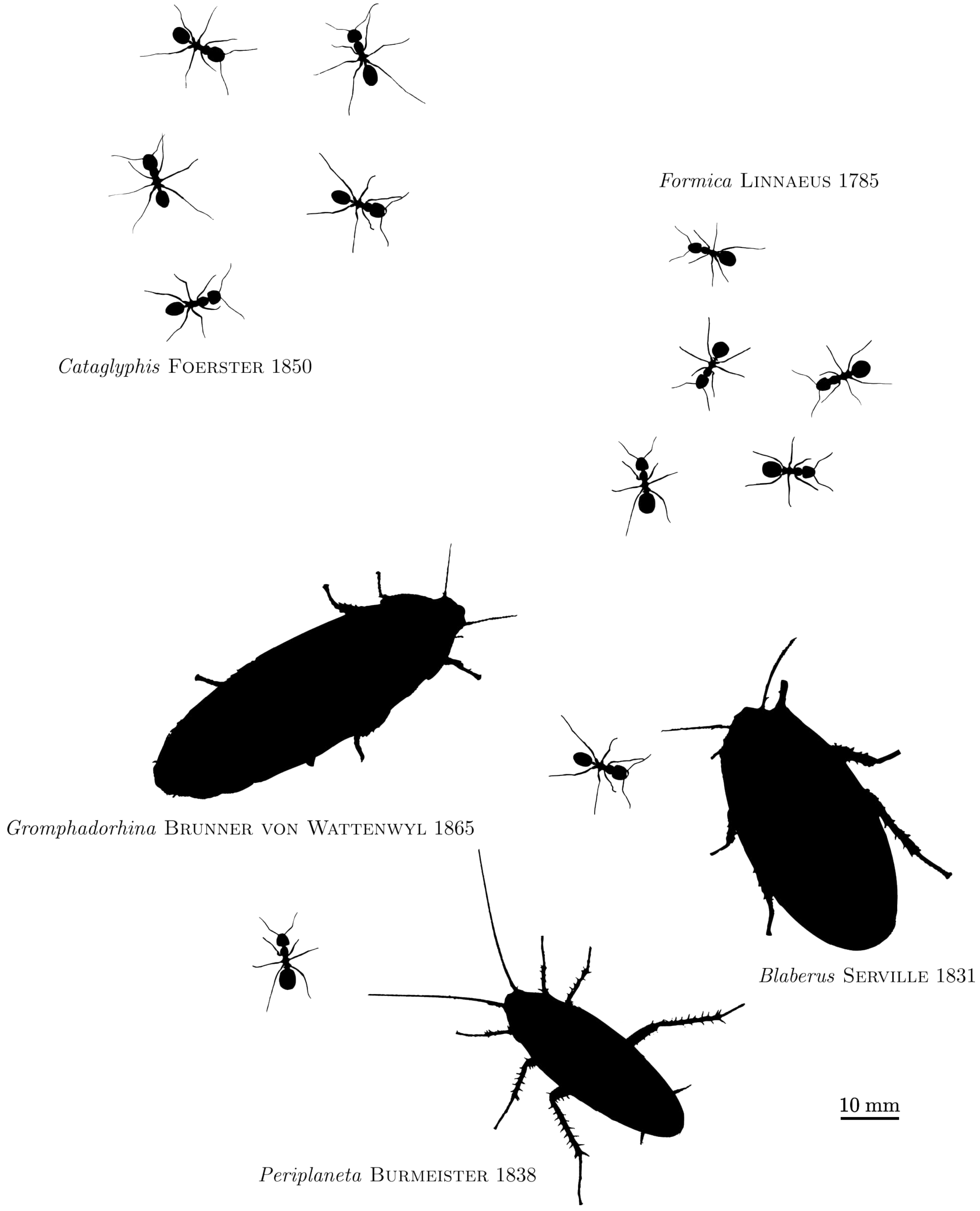
Formica LINNAEUS 1785
Cataglyphis FOERSTER 1850
Gromphadorhina BRUNNER VON WATTENWYL 1865
Blaberus SERVILLE 1831
Periplaneta BURMEISTER 1838
10 mm

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Summary

Ants and cockroaches are both known for their successful evolutionary radiation globally. For initial intrudings into such unknown terrains and the ongoing threat by diverse obstacles, the survival of the ants and cockroaches – or mobile organisms in general – relies to a large extent on a versatile locomotor system. Moreover, their locomotion behaviors may be of significant ecological impact for the turnover of biomass since, for instance, cockroaches function as mobile fermentation tanks, or ants service as ecosystem engineers. Consequently, their role as kinds of model organisms for studying the potential advantages of their locomotory morphologies and behaviors has been recognized widely across different research areas. However, biomechanical descriptions of the most basic leg functions for locomotion such as propulsion and tip-over prevention on slopes, or self-righting after toppling do not exist. Further, the few existing contact force measurements in Hexapoda, a key in explaining the functioning of legs including the feet, do not suffice to explain how these insects employ their legs to overcome inclined and declined slopes.

Thus, the present dissertation with the title "Towards understanding of climbing, tip-over prevention and self-righting behaviors in Hexapoda" quantifies via three case studies:

- (i) how desert ants engage their legs to traverse inclined and declined slopes,
- (ii) how desert and wood ants avoid toppling over on inclined slopes, and
- (iii) how Madagascar hissing cockroaches, American cockroaches, and discoid cockroaches self-right from an upside-down orientation.

The three articles have in common not only that they exemplify the importance of the versatile functionality of locomotor appendages in Hexapoda but also the ambivalence of stability in moving animals.

Key methods involve the recordings of forces and motions as well as measurements of morphological parameters with the aim of describing geometric and temporal patterns, energy landscape models, or to calculate torques, impulses, and angles. This includes novel biomechanical quantifications such as

- ground reaction impulse and force vectors of individual legs in climbing ants on inclined and declined slopes,
- torques with respect to the critical tipping axis in climbing ants (i.e., tip-over prevention behaviors), and
- potential energy landscapes to explain the self-righting behaviors in cockroaches.

The main findings include results and conclusions such as:

- Desert ants prevent tipping-over on slopes by keeping their center of gravity inside the supporting polygon (geometric strategy).

- Wood ants prevent tipping-over on slopes by pulling on the substrate; geometric changes and additional contact points such as the gaster tip or a dragging hind leg to change the supporting geometry were not necessary to stabilize its posture (adhesion strategy).
- Desert and wood ants prevent toppling dynamically (dynamic stability), because their static torques do not become equal to zero over time (no static stability).
- For desert and wood ants, the main decelerating or accelerating leg on inclined or declined slopes, respectively, is above the center of gravity.
- For desert and wood ants, the measured directional change in the lateral ground reaction forces should incorporate the advantages of direction-dependent attachment structures.
- The effect of lateral shear loading was enhanced by the lateral inwards pulling of the front legs in both ants together with the prolonged double support durations on inclined slopes.
- Additionally, the wood ants employed lateral shear loading between the front and the middle legs on steep inclined slopes.
- The measured adhesive pulling with the front legs in wood ants could increase normal load on the hind legs to prevent slipping. The leg impulse surface angle of the hind legs was flatter for the desert ants compared to the wood ants.
- Beyond that, zigzagging as a geometric sub-strategy helps ants to quickly re-orient the critical tipping axis to adjust the torques with respect to the critical tipping axis.

- All three cockroach species could self-right with a probability of 97 % within a given time of 30 s.
- In 63 % of the self-righting attempts the cockroaches could self-right on the first attempt, and on that attempt in less than one second.
- The fastest self-righting attempts took 0.46 s for the Madagascar hissing cockroach, 0.31 s for the discoid cockroach and 0.14 s for the American cockroach, whereas the median total time to achieve self-righting including failed attempts was 1.6 s, 1.1 s and 0.6 s, respectively.
- Whereas the American cockroaches used their legs (93 %) and the discoid cockroaches used their wings (46 %) or their legs (49 %) to self-right, the Madagascar hissing cockroaches used its legs only in the final stage of its righting action and relied primarily on the arching of its body which together led in 98 % of their attempts to success.

- Whereas all three cockroach species used legs to assist their self-righting actions, only two species pushed with their appendages against the ground to *initiate* the righting action (dynamic strategy). The Madagascar hissing cockroaches in contrast relied mainly on its shape changing (geometric) strategy.

- The exploitation of intertial effects (dynamic strategy) for the American cockroach and the discoid cockroach during their self-righting processes could further be verified by observing upward motions of the animals' body in 63 % and 78 % of all attempts, respectively, after the pushing of their appendages has already stopped.

- In sum, I observed diverse tip-over prevention and self-righting strategies in Hexapoda which include geometric, adhesive or dynamic mechanism.

Up to the present in December 2021 while finishing this dissertation, the published articles have been cited by studies of various research areas including neuromechanics, biological adhesion, animal navigation, paleoecology, robotics, and computer animation which exemplifies potential points of contact for future interdisciplinary research questions related to this dissertation.

To progress further in the mechanical understanding of how animals locomote on the gram and milligram scale, I suggest to simultaneously record various characteristics of the microscopic contact structures (e.g., bending and orientation of the tarsal attachment structures), ground reaction forces, and macroscopic whole-body dynamics (e.g., intra-leg dynamics, center of gravity motions). This should also include the quantification of the changing body shape to develop time-dependent intrinsic energy landscape models for locomoting organisms in addition to the proposed time-independent energy landscape models used in the present dissertation. Subsequently, this could be placed inside a second (external) energy landscape model which contains physical and ecological information about the surrounding environment with the aim of describing legged locomotion on complex terrain not only biomechanically, on the organismal level, but eventually also ecomechanically on the population or ecosystems level.

Thus, if I had more years and further funding to continue this project, I would first extend the working setup by a collection of modular and standardized obstacles and sensors which can be connected in various ways with the components of the *Open and Modular Optical Toolbox UC2* to eventually record microscopic features of the animals' contact mechanics without sacrificing a global view on the animals motion. I would then use this mobile and modular assembly to go into the fields of biodiversity hotspots to be able to observe, record, quantify, and systemize the locomotion behaviors of as many arthropods as possible in their ecological setting with the aim to map and to conserve the biodiversity of animal locomotion through complex habitats which would otherwise be lost if species go extinct and habitats are destroyed.

Zusammenfassung

Die vorliegende Dissertation mit dem Titel “Towards understanding of climbing, tip-over prevention and self-righting behaviors in Hexapoda” untersucht in drei Studien exemplarisch, wie (i) Wüstenameisen ihre Beine einsetzen um An- und Abstiege zu überwinden, wie (ii) Wüsten- und Waldameisen ein Umkippen an steilen Anstiegen vermeiden, und wie sich (iii) Madagaskar-Fauchschaben, Amerikanische Großschaben und *Blaberus discoidalis* AUDINET-SERVILL, 1839 aus Rückenlagen drehen und aufrichten.

Neuartige biomechanischen Beschreibungen umfassen unter anderem:

- Impuls- und Kraftwirkungen einzelner Ameisenbeine auf den Untergrund beim Bergauf- und Bergabklettern,
- Kippmomente bei kletternden Ameisen,
- Energiegebirge-Modelle (energy landscapes) zur Quantifizierung der Körperform von Schaben für die funktionelle Beschreibung des Umdrehens aus der Rückenlage.

Zu den konkreten Befunden zählen:

- Wüstenameisen vermeiden ein Umkippen an Anstiegen durch die Verlagerung ihres Körperschwerpunktes in die Unterstützungsfläche.
- Waldameisen vermeiden ein Umkippen an Anstiegen durch Zugbewegungen an der Unterstützungsfläche (Adhesion); eine Verlagerung ihres Körperschwerpunktes in die Unterstützungsfläche hinein oder durch Änderung der Geometrie der Unterstützungsfläche mit Hilfe zusätzlicher Kontaktpunkte (z.B. schleifende Gasterspitze oder Hinterbeine) waren aufgrund ihrer Haftkräfte nicht notwendig für deren Stabilisierung.
- Wüsten- und Waldameisen stabilisieren ihre Haltung dynamisch über die Schrittzyklen.
- Wüsten- und Waldameisen bremsen und beschleunigen in Bewegungsrichtung an Ab- und Anstiegen überwiegend mit dem Beinpaar, welches sich oberhalb des Körperschwerpunktes befindet.
- Wüsten- und Waldameisen wechseln von einem seitlichen Auswärtsdrücken (lateral pushing) beim Fortbewegen in der Ebene zu einem seitlichen Ziehen zur Körpermitte hin (lateral pulling) mit ihren Vorderbeinen bei Anstiegen und mit ihren Hinterbeinen bei Abstiegen. Die Waldameisen zeigten diesen Verhaltenswechsel nicht nur mit den Vorder- oder Hinterbeinen, sondern auch mit ihrem mittleren Beinpaar. Diese lateralen Zugbewegungen implizieren seitliche Scherkräfte, die die Kletterbewegungen vermutlich unterstützen. Die gemessenen verlängerten Bodenkontaktzeiten an An- und Abstiegen beeinflussen in diesem Zusammenhang die Wirkdauer der Scherkräfte zwischen den verschiedenen Fußaufsatzpunkten.

- Die gemessenen Zugkräfte an den Vorderbeinen der Waldameisen in Richtung der Flächennormalen bei steilen Anstiegen könnten die Druckkräfte an deren Hinterbeine auf den Untergrund vergrößern, um vermutlich ein Ausrutschen durch folglich höhere mögliche maximale Reibungskräfte zu erschweren.

- Änderungen der Bewegungsrichtung an Anstiegen bietet den Ameisen darüber hinaus eine weitere Möglichkeit ihre Drehmomentbilanz zu ändern, um damit ihre Haltung weiter stabilisieren zu können.

- Alle drei Schabenarten drehten sich aus der Rückenlage mit einer Erfolgsquote von 97 % innerhalb von 30 s.

- Im ersten Drehversuch aus der Rückenlage waren 63 % innerhalb 1 s erfolgreich.

- Die schnellsten Drehversuche aus der Rückenlage dauerten 0.46 s bei Madagaskar-Fauchschaben, 0.31 s bei *Blaberus discoidalis* und 0.14 s bei der Amerikanischen Großschabe.

- Während die Amerikanischen Großschaben ihre Beine (93 %) und *Blaberus discoidalis* ihre Flügel (46 %) oder ihre Beine (49 %) zur Selbstaufrichtung einsetzten (dynamische Strategie), nutzten die Madagaskar-Fauchschaben ihre Beine nur in der Endphase ihrer aufrichtenden Aktion und nutzten vor allem Verwringungen ihres Körperstammes (geometrische Strategie), die in 98 % ihrer Versuche zum Erfolg führten.

- Das Ausnutzen von Trägheitseffekten (dynamischen Strategie) wurde für die Amerikanische Großschabe und *Blaberus discoidalis* geschlussfolgert, weil Aufwärtsbewegungen der Tiere in 63 % bzw. 78 % aller Versuche beobachtet wurden, obwohl das Drücken ihrer Beine bzw. Flügel bereits aufgehört hatte.

Bis Dezember 2021 wurden die drei veröffentlichten Fachartikel der vorliegenden kumulativen Dissertation von wissenschaftlichen Publikationen aus den Bereichen der Neuromechanik, der biologischen Adhäsions- und Grenzflächenforschung, der Tiernavigation, Paläoökologie sowie Robotik und Computeranimationen zitiert, wodurch die aktuelle wissenschaftliche Relevanz des Dissertationsthemas untermauert und in denen weitere integrative Ausblicke zu finden sind.

Die Zusammenhänge zwischen Kontaktmechanismen und der Dynamik der Fortbewegung von Tieren auf der Gramm- und Milligrammskala könnte u. a. weiter vorangetrieben werden, indem nach Möglichkeit zeitgleich Bewegungen der mikroskopischen Kontaktstrukturen (z. B. Biegung und Ausrichtung der Haftstrukturen), des gesamten Körpers (z. B. Bein- und Schwerpunktbewegungen) sowie Bodenreaktionskräfte aufgezeichnet werden. Zusätzlich könnte die bei Bewegungen auf Beinen inhärente Veränderung der Körpergeometrie in zeitabhängige (intrinsische), über die in dieser Arbeit vorgestellten zeit-unabhängigen Energie-Modelle von Körperformen hinaus, einfließen. Darauf aufbauend könnte diese in weitere (externe) Energielandschaftsmodelle eingebettet werden, welche physikalische und ökologische Informationen über die Umgebung enthalten, mit dem Ziel, die Fortbewegung auf Beinen im komplexen Gelände nicht nur biomechanisch auf Organismenebene, sondern auch öko-mechanisch auf Populations- und Ökosystemebenen zu beschreiben.

1 Introduction

A walking human requires about 2.3 joule to move a kilogram of their body mass a meter distance.[1] According to such a mass-specific measure for the metabolic cost of locomotion, humans belong to the most energy efficient legged land locomotors.[2] Horses for instance, widely appreciated for their efficient load carrying capabilities in difficult terrain, metabolize a comparable amount of mass-specific energy per meter distance.[3] Ants, on the small scale in contrast, consume about 300 to 1000 times more mass-specific metabolic energy to travel a given distance[4] compared to walking humans or horses. Surprisingly, their apparently high mass-specific metabolic cost of locomotion did not hinder their ascent to ecological dominance[5].

Despite such notable size-dependent differences in the metabolic cost of transport, the stated species have in common that they usually locomote on legs. Humans, however, may use wheeled systems and bisect[6] or even quarter[7] their metabolic cost of locomotion when cycling, while animals “are prisoners of their own morphology”[8] and limited in using tools to improve the cost of their locomotion. Thus, one may ask what are the advantages of locomoting on legs rather than rolling on wheels despite its asserted high energetic cost of transport, or “why animals don’t have wheels”[9]. Although this question is not new, it is still relevant

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[1] A minimum “energy cost of locomotion” of $2.3 \pm 0.35\,\mathrm{J \cdot kg^{-1} \cdot m^{-1}}$ for a walking speed of $1.25\,\mathrm{m \cdot s^{-1}}$ was measured on 21 subjects by: di Prampero, P. E.: The energy cost of human locomotion on land and in water, in: International Journal of Sports Medicine 1986

[2] Various data on the cost of locomotion of different organisms have been summarized, for instance, by: Full, R. J.: Mechanics and energetics of terrestrial locomotion: bipeds to polypeds, in: Wieser, W./Gnaiger, E. (eds.), Georg Thieme Verlag, 1989; Pontzer, H.: Effective limb length and the scaling of locomotor cost in terrestrial animals, in: Journal of Experimental Biology 2007; Diamond, J.: Transport mechanisms: The biology of the wheel, in: Nature 1983; Jensen, T. F./ Holm-Jensen, I.: Energetic cost of running in workers of three ant species, Formica fusca L., Formica rufa L., and Camponotus herculeanus L. (Hymenoptera, Formicidae), in: Journal of Comparative Physiology 1980.

[3] Compare for instance with the summary tables in Reilly, S. M./McElroy, E. J./Biknevicius, A. R.: Posture, gait and the ecological relevance of locomotor costs and energy-saving mechanisms in tetrapods, in: Zoology 2007; and Diamond: Transport mechanisms (see n. 2)

[4] Jensen/Holm-Jensen: Energetic cost of running in workers of three ant species, Formica fusca L., Formica rufa L., and Camponotus herculeanus L. (Hymenoptera, Formicidae) (see n. 2).

[5] Ants are considered as “ecologically dominant” and “evolutionary successful” animals by Wilson, E. O.: Success and Dominance in Ecosystems: The Case of the Social Insects, Ecology Institute, 1990; idem: Causes of Ecological Success: The Case of the Ants, in: Journal of Animal Ecology 1987.

[6] Zuntz, L.: Untersuchungen über den Gaswechsel und Energieumsatz des Radfahrers, Berlin: Hirschwald, 1899.

[7] Diamond: Transport mechanisms (see n. 2) cites various sources in his summary table.

[8] Vincent, J. F. V.: Experiments with biometerials, National Centre for School Technology, 1978.

[9] LaBarbera, M.: Why the Wheels Won’t Go, in: The American Naturalist 1983 questioned:

and worthy of elaboration within the following sections, because it helps to reason for the wide interdisciplinary interest in the understanding of the functional morphology of animal limbs in different environmental contexts, and brings together the more specific research questions of the present cumulative dissertation which ask “how ants employ their legs on slopes (i) to progress and (ii) to prevent tipping over”, and (iii) “how cockroaches self-right from and upside-down orientations after they have toppled over”.

1.1 On the versatility of segmented legs

In contrast to the aforementioned low metabolic cost of transport as possible advantageous characteristics for ecological dominance, other qualities such as the versatility of structures of the locomotor system, their robustness, and the facilitation of a continuous metabolic flow through the appendages may be more relevant for living organisms than an energy efficient locomotion in many cases.

Effectiveness may be more relevant than efficiency in locomoting animals

To be more specific, smaller animals locomote with higher costs compared to larger animals according to several allometric properties[10]. However, they may have succeeded in their niche rather by the effectiveness and multi-functionality of their locomotor appendages than by an energetically more efficient form of locomotion. For example, several ant species can inhabit trees and the soil which relies on versatile climbing and tunneling capabilities which may involve energetically more expensive motions than running a given distance on a flat surface.

Mass-specific cost of terrestrial locomotion per ground contact or per stride as a fair measure to compare the locomotor efficiency among species

However, the metabolic cost of transport for insects to climb up vertically a given distance may outperform larger animals which usually locomote on flat surfaces with ease. Thus, comparisons of the mass-specific energy expenditure have to be treated with care, since characteristics of the gait and terrain (Figure 1) should be considered as well. Moreover, by calculating the mass-specific cost of terrestrial locomotion per ground contact (ground contact cost) or stride,

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“Why animals don’t have wheels”; and Diamond: Transport mechanisms (see n. 2, p. 1) referenced in this context Gould, S. J.: Kingdoms Without Wheels, in: Natural History 1981 and asked: “Why did evolution not anticipate the most important element of human transport, the wheel?”.

[10] Pontzer: Effective limb length and the scaling of locomotor cost in terrestrial animals (see n. 2, p. 1); Full: Mechanics and energetics of terrestrial locomotion (see n. 2, p. 1); Full, R. J./ Zuccarello, D. A./Tullis, A.: Effect of variation in form on the cost of terrestrial locomotion, in: Journal of Experimental Biology 1990.

the allometric effects of size seem to diminish and remain between 1.5 and 3.1 J kg^{-1}contact time^{-1} for insects and mammals[11], or for mammals roughly between 1 and 10 J $\text{kg}^{-1}$$\text{stride}^{-1}$[12], respectively. According to those two gait-normalized efficiency measures, differently sized animals would locomote comparably efficiently in their individual stride-sized worlds. Taken together, an energetically efficient locomotion may not be as relevant for the animals as the effectiveness or versatility of the locomotory system, and different efficiency measures lead to different conclusions in comparing the species with respect to size.

Obstacle diversity

A similar reasoning may also explain "why animals don't have wheels"[13]. The exemplified comparison in the beginning of the introduction assumes that the wheels of the bicycle can roll. Rolling wheels require a solid substratum with relatively small irregularities compared to the height of the wheels. In addition, the surface needs to be sufficiently rough to prevent slipping. Thus, the apparently efficient cyclist would probably rank behind many of the given examples in Diamond[14]'s summary table about the cost of transport, or its progression would even be impossible, if the pseudo-competition among the various motion systems had taken place on a slope with, for instance, loose granular material such as sand. Moreover, characteristics such as the turning radius and the width of the bicycle reduces its maneuverability compared to various legged designs with many degrees of freedom which facilitate creative postural changes to wriggle through confined spaces. Of course, stunt riders are, for instance, capable of extraordinary jumps and turns on complex terrains, but the functioning of the bicycle still relies on relatively solid surfaces, a moderate inclination, a sufficient track width, and relatively wide turning radii.

Since most organisms do not live in road-like habitats with relatively flat, solid, and predictable surface characteristics, wheeled locomotion may not be as functional as legged forms of locomotion. Natural terrestrial environments have none-homogeneous ground properties, and they are scattered with many irregular obstacles: Vegetation confines the track width, granular and loose material hampers traction, smooth surface areas lead to slipping, inclines increase the risk for toppling over and falling, a sticky ground may lock the animal, wind can unbalance, accelerate or decelerate the animals, and walls or holes could even block the

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[11] Full/Zuccarello/Tullis: Effect of variation in form on the cost of terrestrial locomotion (see n. 10, p. 2).

[12] Heglund, N. C./Taylor, C. R.: Speed, stride frequency and energy cost per stride: how do they change with body size and gait?, in: Journal of Experimental Biology 1988.

[13] LaBarbera: Why the Wheels Won't Go (see n. 9, p. 1).

[14] Diamond: Transport mechanisms (see n. 2, p. 1).

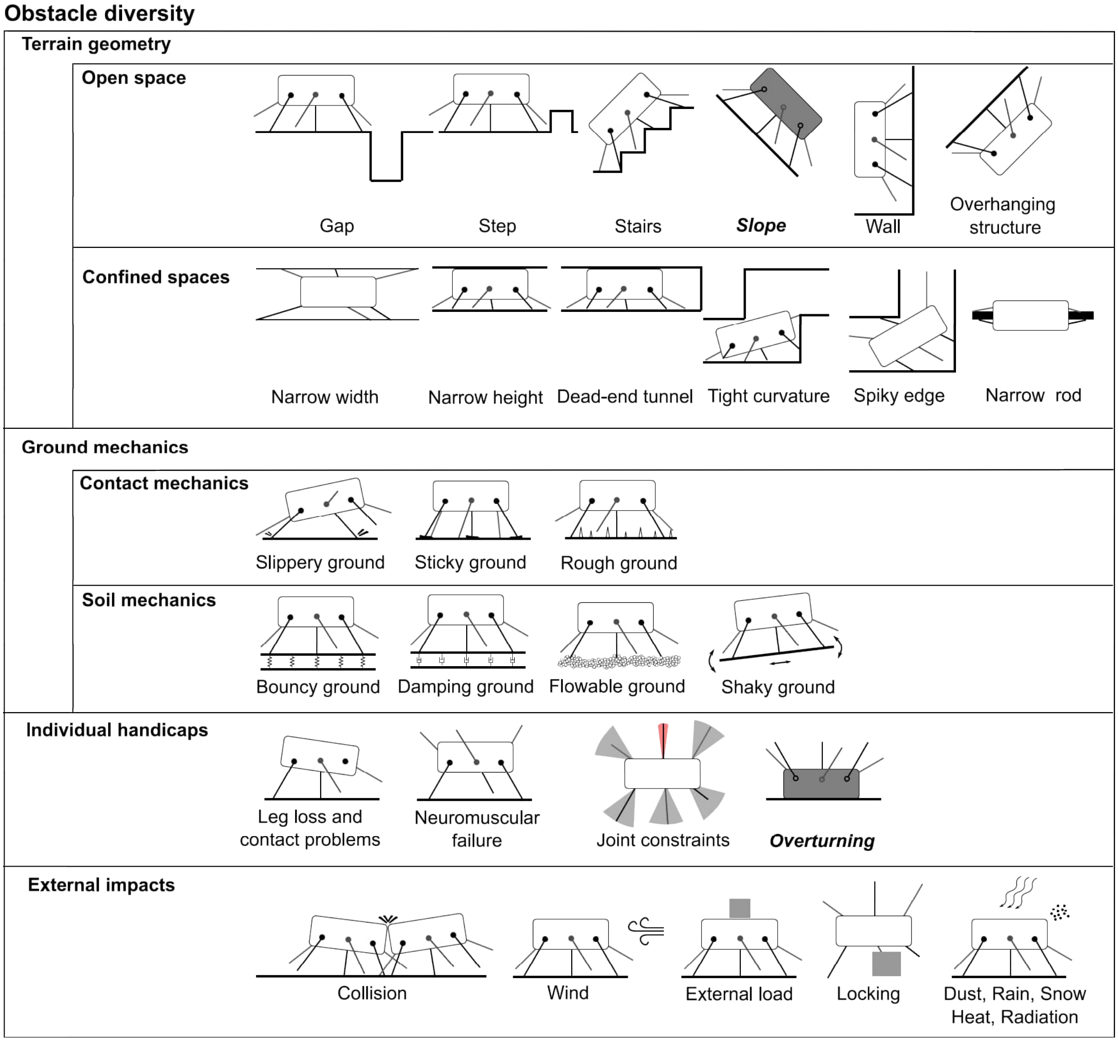

Figure 1: *Obstacle diversity.* One attempt to illustrate and group an extract of the diversity of obstacles which terrestrial animals may face while roaming their land habitats. Imagine how wheeled motion systems would react to such hurdles. Another classification can be found, for instance, in the article “Robots on the Move: Versatility and Complexity in Mobile Robot Locomotion” by Nie/Pacheco Corcho/Spenko wherein the size of the obstacle relative to a robot provides the basis for the groupings. The present dissertation aims to describe and examplify the diverse motion behaviors of Hexapoda on slopes and in overturning situations (gray-emphasized mosaics).

advancement completely (Figure 1). For instance, desert ants, often specialized for rapid runs on open flat salt pans, can also climb in their confined underground nest. Thus, as mentioned before, a low cost of transport or an energetically efficient way of moving around may not be as crucial as the utility and reliability of the locomotory system in such complex habitats. Moreover, in order to radiate successfully into unknown habitats, animals need to be highly versatile so that they may cope with unexpected and new obstacles. With wheeled locomotory architectures they probably would not have conquered arboreal habitats, confined spaces in the soil, riparian zones with flowable substrates, or rock formations, for instance.

Segmented legs facilitate a terrain-adaptive supporting geometry

Segmented legs facilitate various motion behaviors in overcoming diverse obstacles. For example, the positioning of the feet enables animals with legs to circumvent or to climb over barriers, to change their temporal stepping pattern and their spatial supporting geometry which, in turn, affects the relative location of their center of gravity with respect to the current tipping axes. This subsequently enables legged systems to make terrain-adaptive adjustments of various locomotion performance measures such as ground clearance, pace width, critical tipping angle, gradeability, turning radius, and weight distribution. As opposed to this, rolling systems with their continuous ground contact, relatively wide turning radius, limited rolling capability on bumpy, slippery, and soft ground are more constrained in avoiding or surmounting such disturbing structures. Imagine how wheeled motion systems would react to the hurdles illustrated in Figure 1. Hence, probably the most important reason why land animals may not employ rolling wheels on axles for their progression is because wheels cannot be employed in many natural environments which include obstacles such as granular or soft substrates, steps, walls, or gaps, for instance (Figure 1).

Whole body rolling motions as a secondary form of locomotion

Even though the majority of land animals do not exploit the mechanism of freely spinning wheels on axles, some still utilize whole-body rolling motions (Figure 2). Thereby, the rolling motion can be powered actively by muscle contraction or passively by external forces such as wind or gravity. For instance, the caterpillars of *Pleurotya ruralis* SCOPOLI 1763 and *Cacoecimorpha pronubana* HÜBNER, 1799 actively employ reflex coiling[15] for its high-speed backward rolling[16] escape behavior. The mantis shrimp *Nannosquilla decemspinosa* RATHBUN 1910 can roll actively

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[15] Brackenbury, J.: Caterpillar kinematics, in: Nature 1997.

[16] Idem: Fast locomotion in caterpillars, in: Journal of Insect Physiology 1999.

with "rapid series of backward somersaults"[17] on smooth sand. It can even climb up slopes as steep as 30 deg in the laboratory on a wooden substrate. The huntsman spider *Cebrennus rechenbergi* JÄGER 2014 can escape actively up- or downhill with its flic-flac behavior[18]. Other spiders such as *Carparachne aureoflava* LAWRENCE 1966 and *Carparachne alba* LAWRENCE, 1962 harness gravity whereas an unidentified salticid uses wind for their passive cartwheeling[19]. Wind-driven rolling motions have also been observed in larvae of the tiger beetle *Cicindela dorsalis media*[20] LECONTE, 1856. The salamander *Hydromantes platycephalus*[21] CAMP, 1916, the pangolin *Manis* sp.[22], and ants of *Myrmecina graminicola*[23] LATREILLE 1802 can coil themselves into a spheroid or ball-like position to roll down slopes as escape mechanism. As a final example, scarab beetles *Scarabaeus semipunctatus* FABRICIUS, 1792 form dung balls and roll them with their hind legs.[24]

Taken together, there are several organisms capable of free wheel rolling on land (i.e., rolling without a spinning wheel on an axle). However, all of them employ their rolling behaviors only as a secondary form of locomotion in suitable areas with sufficiently steep downslopes (gravity-driven wheeled locomotion) or at least gentle upslopes with solid surfaces where external forces such as wind or gravity can drive the animal (Figure 2), or in escaping situations where it is often more important to escape randomly and fast somewhere than controlled but slower to a specific direction. For their primary form of locomotion all of the listed examples still employ their locomotor appendages for walking or running gaits.

Freely spinning wheels on axles are difficuilt to nurture

Alongside the environmental constraints of wheeled locomotion, anatomical con-

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[17] Caldwell, R. L.: A unique form of locomotion in a stomatopod—backward somersaulting, in: Nature 1979; Full, R. et al.: Locomotion like a wheel?, in: Nature 1993.

[18] Jäger, P.: Cebrennus Simon, 1880 (Araneae: Sparassidae): a revisionary up-date with the description of four new species and an updated identification key for all species, in: Zootaxa 2014.

[19] Henschel, J. R.: Spiders wheel to escape, in: South African Journal of Science 1990.

[20] Harvey, A./Zukoff, S.: Wind-Powered Wheel Locomotion, Initiated by Leaping Somersaults, in Larvae of the Southeastern Beach Tiger Beetle (Cicindela dorsalis media), in: PLOS ONE 2011.

[21] García-París, M./Deban, S. M.: A Novel Antipredator Mechanism in Salamanders: Rolling Escape in Hydromantes platycephalus, in: Journal of Herpetology 1995.

[22] Tenaza, R. R.: Pangolins Rolling Away from Predation Risks, in: Journal of Mammalogy 1975.

[23] Grasso, D. A. et al.: Rolling away: a novel context-dependent escape behaviour discovered in ants, in: Scientific Reports 2020; Giannetti, D. et al.: Unlike rolling stones: not every Myrmecina species actively rolls away from danger (Hymenoptera, Formicidae), in: The European Zoological Journal 2022.

[24] Scholtz, G.: Scarab beetles at the interface of wheel invention in nature and culture?, in: Contributions to Zoology 2008.

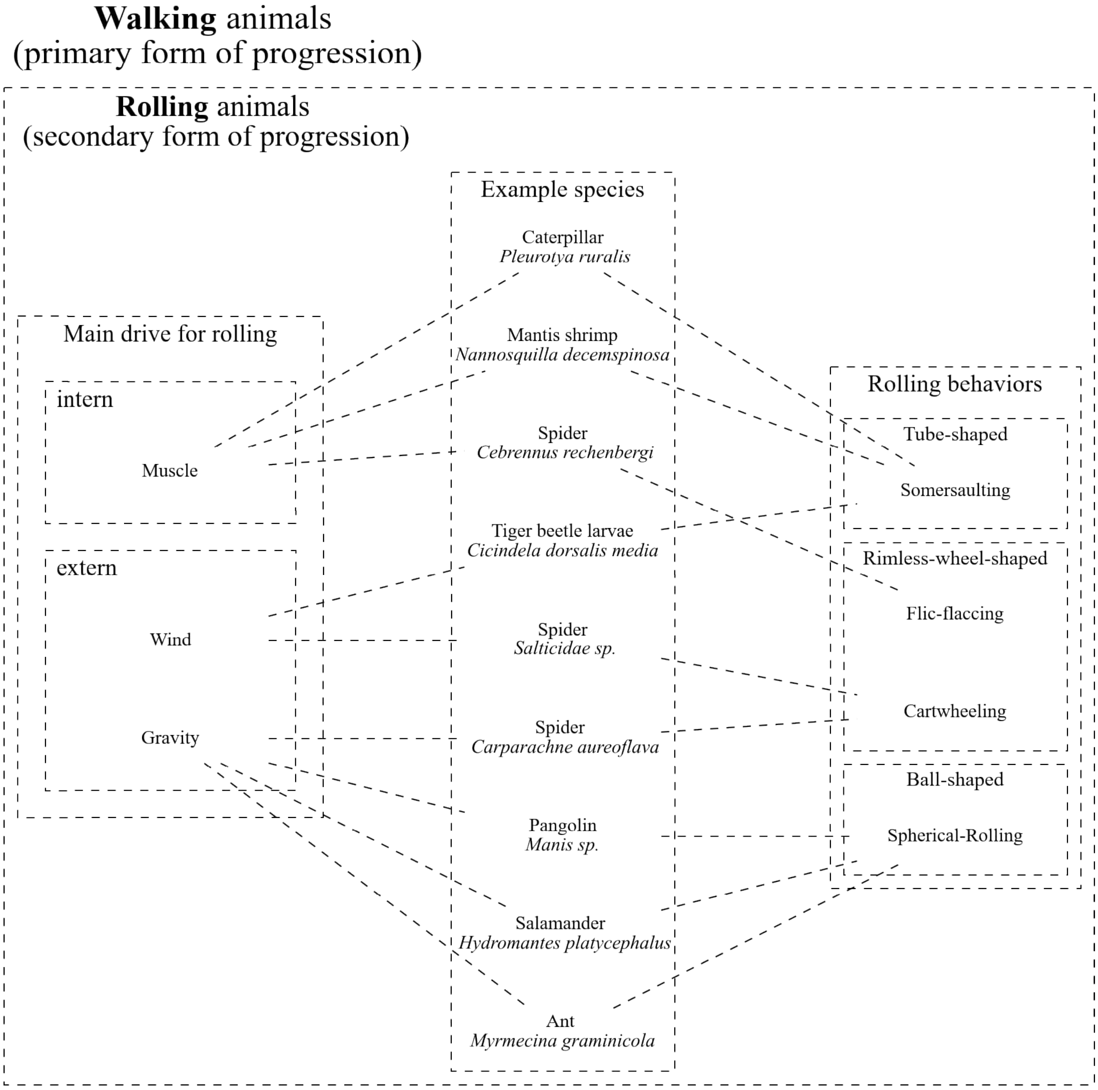

Figure 2: Examples of rolling motions employed by animals as a secondary form of progression besides their primary walking locomotion.

straints of spinning wheels in organisms have been discussed, too. First, animals have difficulties in nurturing and self-healing freely spinning wheels. This is because blood vessel and nerve impulses may not bridge the gap between the axles and the wheels. Even though freely rotating biological structures have been found in the micrometer scale for swimming bacteria[25], this mechanism of a rotating

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[25] Berg, H. C./Anderson, R. A.: Bacteria Swim by Rotating their Flagellar Filaments, in: Nature 1973; Berg, H. C.: The Rotary Motor of Bacterial Flagella, in: Annual Review of Biochemistry 2003; Furuta, T. et al.: Gap compression/extension mechanism of bacterial flagellar hook

flagella would probably not work for terrestrial animals on the centimeter or meter scale. One important reason for the functioning of the rotating flagella is that their metabolic transport relied mainly on electrochemical gradients. Larger organisms, in contrast, depend on flowing body fluids which enable a more voluminous transport of nutrients and removal of metabolic waste. Obviously, it is difficult to bypass freely rotating structures with structures to channel flowing body fluids such as blood or hemolymph. However, non-metabolized external (retractable) wheels for passive rolling could still have evolved, as Diamond[26] or Scholtz[27] pointed out while referring to claws[28] and "dead cellular material such as hair or horn"[29], and bio-lubricants could reduce the friction on its inner bearing. On the downside, even if such hypothetical non-metabolized wheels could have evolved they still face abrasion on its outer parts which need to be replaced, and the aforementioned difficuilties in rough terrain.

Versatile leg functions

At this point, one could further argue that nature may provide other biological designs for successful land locomotion which neither rely on wheels nor on legs (Figure 3). For instance, earthworms crawl with peristaltic motions, leeches loop, and snakes move in several different ways. Although they all move successfully without legs, they still lack the versatility or multi-purpose functionality of legs.

To be more specific, potential grasping, embracing, and adhering capabilities of segmented limbs with fine structures on the feet may help animals to climb on and cling to vertical or overhanging structures. Of course, snakes may also climb up trees legless with their lasso locomotion[30], for example, but this requires the embracing of the whole trunk, whereas legs with adhesive capabilities may again be more versatile for coping with diverse vertical and overhanging obstacle geometries.

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as the molecular universal joint, in: Journal of Structural Biology 2007; LaBarbera: Why the Wheels Won't Go (see n. 9, p. 1); Diamond: Transport mechanisms (see n. 2, p. 1); Yamaguchi, T. et al.: Structural and Functional Comparison of Salmonella Flagellar Filaments Composed of FljB and FliC, in: Biomolecules 2020; Mandadapu, K. K. et al.: Mechanics of torque generation in the bacterial flagellar motor, in: Proceedings of the National Academy of Sciences 2015.

[26] Diamond: Transport mechanisms (see n. 2, p. 1).

[27] Scholtz: Scarab beetles at the interface of wheel invention in nature and culture? (see n. 24, p. 6).

[28] Diamond: Transport mechanisms (see n. 2, p. 1).

[29] Scholtz: Scarab beetles at the interface of wheel invention in nature and culture? (see n. 24, p. 6).

[30] Savidge, J. A. et al.: Lasso locomotion expands the climbing repertoire of snakes, in: Current Biology 2021.

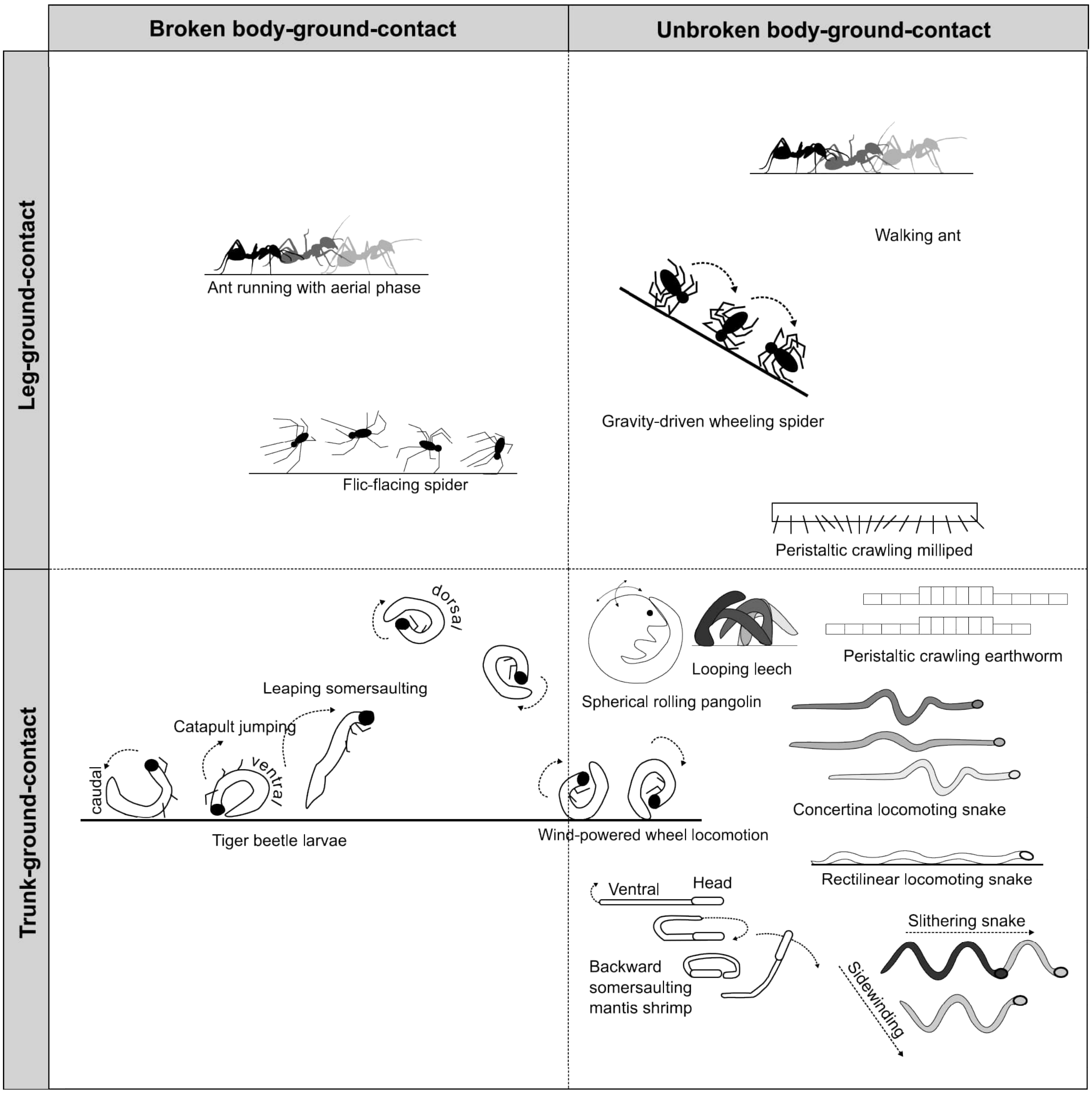

Figure 3: *Tiny extract of terrestrial locomotion diversity.* Grouping of several terrestrial locomotion behaviors with respect to (i) the consistency of ground contact of any body part while the representative animal is in motion and (ii) the use of legs or the trunk as the main propulsive structure which is in contact with the ground. Imagine how the various designs could possibly encounter the obstacles in Figure 1.

Moreover, legs “with highly-recurved claws”[31] can favor the formation of collective structures (self-assemblages, social mechanics, collective actions)[32]. For that, individuals attach together to build up, for instance, living bridges, ladders, chains, and rafts. According to Anderson/Theraulaz/Deneubourg[33] at least 18 different kinds of such collective structures are known for insects alone.

Beyond that, legs not only support locomotion on land surfaces, but also in sub-terrestrial materials, in air, and, in or on water (interfacial legged locomotion). For example, many fossorial animals take advantage of limb-based propulsion and burrowing[34], or, terrestrial “gliding animals are able to use limb and whole-body movements to effect axial or torsional maneuvers”[35], or “rowing motions”[36] help ants to “generate thrust at the water surface”[37] and swim[38]. Thus, legs not only enable species to move on solid substrates, but also in fluidlike environments, and they may also function to support the animals for their transitioning between those environments. This is of high ecological relevance, because the capability of employing medium-changing-maneuvers such as lift- or take-offs, landings, and beachings enables animals to radiate into new habitats.

Beyond those examples, which aimed to illustrate the advantages of the highly versatile functions of legs for locomoting in unstructured environments, legs also equip the animals with several multi-purpose non-primary locomotive capabilities. For instance, segmented legs with grasping capabilities support motions for collecting and intaking nutrients, holding and carrying items, building nests and traps, grooming and body care as well as mating and agonistic behaviors. Furthermore, segmented limbs can cushion the body during phases of dormancy and assist motions to righten the body from a lying posture or from an unintended

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[31] Anderson, C./Theraulaz, G./Deneubourg, J.-L.: Self-assemblages in insect societies, in: Insectes Sociaux 2002.

[32] Reid, C. R. et al.: Army ants dynamically adjust living bridges in response to a cost–benefit trade-off, in: Proceedings of the National Academy of Sciences 2015; Lioni, A. et al.: Chain Formation in Œcophylla longinoda, in: Journal of Insect Behavior 2001; Sponberg, S.: The emergent physics of animal locomotion, in: Physics Today 2017; Mlot, N. J./Tovey, C. A./Hu, D. L.: Fire ants self-assemble into waterproof rafts to survive floods, in: Proceedings of the National Academy of Sciences of the United States of America 2011.

[33] Anderson/Theraulaz/Deneubourg: Self-assemblages in insect societies (see n. 31).

[34] Morinaga, G./Bergmann, P. J.: Evolution of fossorial locomotion in the transition from tetrapod to snake-like in lizards, in: Proceedings of the Royal Society B: Biological Sciences 2020.

[35] Dudley, R. et al.: Gliding and the Functional Origins of Flight: Biomechanical Novelty or Necessity?, in: Annual Review of Ecology, Evolution, and Systematics 2007.

[36] Yanoviak, S. P./Frederick, D. N.: Water surface locomotion in tropical canopy ants, in: Journal of Experimental Biology 2014.

[37] Ibid.

[38] Schultheiss, P./Guénard, B.: Kinematic study of six mangrove ant species (Hymenoptera: Formicidae) reveals different swimming styles and abilities, in: Myrmecological News 2021.

overturned position after a plunge. In addition, several sensory organs evolved on or in legs[39]. Therewith, legs can function as a kind of multi-purpose "smart appendage" to assist animals not only in their locomotion but also in their sensing, communication, orientation, and navigation. Moreover, the evolutionary scenario from a tube-like body to a tube-like body with outgrowths of some function (e.g., unsegmented appendages, as stump legs in *Onychophora* or bristles in *Polychaete*) may have led to an explosion of potential function with the development of stiff, articulated limbs (personal note by B. Boudinot on 25th of December 2021).

In summary

Finally, all those examples in the current section can certainly be extended with more locomotive and non-locomotive functions of segmented limbs. I think it is sufficiently exemplified how segmented limbs function as versatile tools for many animals in interacting with their environment. However, while all those (qualitative) elaborations may not be new, the functional descriptions of leg action often miss quantifications with mechanical concepts such as ground reaction forces, torques, impulses, or the trajectories of the leg segments to answer how, for instance, Hexapoda accelerate and decelerate, carry their load, or prevent tipping-over. Before I motivate further why I chose to study such leg functions in Hexapoda, in particular on ants and cockroaches (Section 1.4), I first draw attention to possible applications in Section 1.2 which may have been inspired by early methods and concepts, systematizations and quantifications of the diverse (natural) leg actions (Section 1.3).

1.2 Recent developments in the emulation of leg functions

Animal-driven transport in difficuilt terrain

The awareness of the versatility of legged motion systems in rich environments (see Section 1.1) should at least be as old as the domestication of animals. For instance, dogs may have been used since the Upper Paleolithic as pack animals for "tracking, hunting or transport of large, 'ice-age' game"[40]. Horses, camels,

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[39] See for instance Figure 1 and Table 1 of Delcomyn, F./Nelson, M. E./Cocatre-Zilgien, J. H.: Sense Organs of Insect Legs and the Selection of Sensors for Agile Walking Robots, in: The International Journal of Robotics Research 1996 for several mechanoreceptors, or Field, L. H./ Matheson, T.: Chordotonal Organs of Insects, in: Evans, P. D. (ed.), Academic Press, 1998 on the section 3.5 about the diversity, structure, and function of chordotonal organs on insect legs on page 25ff.

[40] Germonpré, M. et al.: Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: osteometry, ancient DNA and stable isotopes, in: Journal of Archaeological Science 2009.

elephants, donkeys, or cattle, for instance, are still kept in certain regions carrying and pulling heavy items in complex terrain, and sheep, goats or cattle are still kept for grazing on steep hillsides which are difficult to access and cultivate otherwise. Equipped with saddles, carts, or sleds, legged animals have enabled us to move faster and/or further with heavier loads on bumpy roads, sandy desert tracks, or snowy paths.

Motorized vehicles with spinning wheels rely on costly landscape transformations

However, with industrialization many of these animal-driven transport mechanisms have been substituted by motorized vehicles which rely on spinning wheels on axles and require, as previously elaborated, railways or flattened roads with tunnels and bridges for their functioning. Thus, while legged animals can adjust their gait and posture to traverse various obstacles, the terrain has to be customized in large measure for the wheeled motorized vehicles. This obviously evolves much effort in the initial transformation of whole landscapes and in their later maintenance, and should therefore be considered in a measure for a more comprehensive equation for a total cost of transport (Section 1). Moreover, while such human made artificial tracks and environmental engineering can be done on Earth, it may be much more difficult in future extraterrestrial surroundings.

The space race and the need for remote-controlled legged motion systems

At least since the space race with the first landings of human-made remote-controlled vehicles on extraterrestrial surfaces, the question of emulating the design of biological motion systems for a versatile, robust, and efficient exploration of unknown terrains has become urgent. That is because a suitable environment for rolling wheels cannot be expected on other celestial bodies and roads may not be built without any preceding pioneering mission which can stand the harsh conditions out there. Thus, according to the elaborations in Section 1.1, rovers should have legs instead of wheels to be best prepared for coping with as many as possible unforeseen obstacles. Surprisingly, none of the deployed rovers relied purely on segmented legs with feet[41]. The main drawbacks are still seen in controlling the many degrees of freedom of articulated legs with its immanent high mechanical complexity and "potential points of failure"[42], and high degree of power consumption[43]. Similarly, Cao et al.[44] point out that the "state-of-the-art legged robots"

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[41] Ellery, A.: Planetary Rovers: Robotic Exploration of the Solar System, Berlin Heidelberg: Springer-Verlag, 2016; Kolvenbach, H.: Quadrupedal Robots for Planetary Exploration, Doctoral Thesis, ETH Zurich, 2021.

[42] Idem: Quadrupedal Robots for Planetary Exploration (see n. 41).

[43] Ellery: Planetary Rovers (see n. 41); Hirose, S. et al.: Fundamental considerations for the design of a planetary rover, in: IEEE, 1995.

[44] Cao, F. et al.: Insect–computer hybrid legged robot with user-adjustable speed, step length and walking gait, in: Journal of The Royal Society Interface 2016.

still cannot compete with their biological model organism especially concerning aspects such as energy efficiency, controllability, and robustness.

Cars are about to get feet

After touching on some potential advantages and drawbacks of wheeled and legged locomotion systems within the previous sections, I now want to recall one of the opening questions: “Why don’t animals have wheels?”[45]. The answer may be as simple as Diamond[46] phrased for a similar context about the attempts in emulating swimming fish: “Thus, the puzzle is not why fish failed to evolve propellers, but why engineers failed to evolve oscillating flexible foil.”[47] However, this was published in 1983 and now, almost 40 years later, promising legged vehicles and micro-robots have been engineered within the last 10 to 15 years which may soon take over some tasks on earth or on extraterrestrial explorations.[48]

Recent explosion in engineered legged motion systems

Advances in robotics and neighboring fields resulted in several dynamic walking legged robots, which are able to negotiate different obstacles in natural settings. In this context, Kolvenbach[49] referred to Bellicoso et al.[50] and noted in his dissertation from 2021 about “Quadrupedal Robots for Planetary Exploration” that the “increasing maturity of the technology has allowed the robots to leave the lab and start being used in real-world applications”, and that “it is only a matter of time since this technology becomes suitable for exploring other celestial bodies”. For instance, the quadrupedal robot *ANYmal* can “cope with stairs and obstacles of heights up to 33 % of the robot’s length”[51], and it can recover after a fall[52]. It can also change its poses, swing trajectories, and footholds to avoid collisions

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[45] LaBarbera, M.: Why the Wheels Won’t Go, in: The American Naturalist 1983.

[46] Diamond: Transport mechanisms (see n. 2, p. 1).

[47] Ibid.

[48] For instance, Kolvenbach: Quadrupedal Robots for Planetary Exploration (see n. 41, p. 12), p. 10, Bellicoso, C. D. et al.: Advances in real-world applications for legged robots, in: Journal of Field Robotics 2018, or Fankhauser, P.: Perceptive Locomotion for Legged Robots in Rough Terrain, Doctoral Thesis, ETH Zurich, 2018, p. 4ff summarize the current state of the art in legged robots.

[49] Kolvenbach: Quadrupedal Robots for Planetary Exploration (see n. 41, p. 12).

[50] Bellicoso et al.: Advances in real-world applications for legged robots (see n. 48).

[51] Jenelten, F. et al.: Perceptive Locomotion in Rough Terrain - Online Foothold Optimization, in: IEEE Robotics and Automation Letters 2020; Robotic Systems Lab (ed.): Perceptive Locomotion in Rough Terrain - Online Foothold Optimization, 2020, URL: `https://www.youtube.com/watch?v=ViecsBmjusI`.

[52] Hwangbo, J. et al.: Learning agile and dynamic motor skills for legged robots, in: Science Robotics 2019.

or to crawl within confined spaces[53], and its legs can be equipped with wheels to combine some "advantages of legged and wheeled locomotion" (roller-walking robot)[54]. Furthermore, the quadrupedal robot *SpaceBok* can walk with point feet and passive-adaptive planar feet on granular slopes[55]. Kolvenbach[56] recognized the quadrupedal robots *BigDog* (2008)[57] and *Spot Mini* (2016)[58] from Boston Dynamics as the breakthrough robots for dynamic all-terrain negotiations, which also includes successful walking on slippery surfaces and waterfronts without falling. I would add the anthropomorphic biped *Atlas* (2013) to this list of breakthrough robots, since it can maintain "its balance through a variety of rapidly changing, high-energy activities" such as jumps, beam balancing, vaults, and somersaults in synchronicity with a second robotic companion.[59]

Furthermore, mono-pedal jumpers can now achieve "78 % of the vertical jumping agility of a galago"[60], stance phase balance, "dynamic transitions between standing, hopping, and standing again"[61] as well as "precise jumps to narrow targets"[62] with a jump distance standard deviation of 1.6 cm.[63] In addition, locomotion-

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[53] Buchanan, R. et al.: Perceptive whole-body planning for multilegged robots in confined spaces, in: Journal of Field Robotics 2021; Robotic Systems Lab (ed.): Perceptive Whole Body Planning for Multi-legged Robots in Confined Spaces, 2020, URL: https://www.youtube.com/watch?v=C2e0JTdwid0.

[54] Idem (ed.): Hybrid Locomotion for Wheeled-Legged Robots (Presentation), 2020, URL: https://www.youtube.com/watch?v=tf_twcbF4P4; Bjelonic, M. et al.: Rolling in the Deep – Hybrid Locomotion for Wheeled-Legged Robots using Online Trajectory Optimization, 2020, URL: http://arxiv.org/abs/1909.07193.

[55] Robotic Systems Lab (ed.): Traversing Steep and Granular Martian Analog Slopes With a Dynamic Quadrupedal Robot, 2021, URL: https://www.youtube.com/watch?v=VNPdlgvWWAY&t=427s; Kolvenbach, H. et al.: Traversing Steep and Granular Martian Analog Slopes With a Dynamic Quadrupedal Robot, 2021, URL: http://arxiv.org/abs/2106.01974; Kolvenbach: Quadrupedal Robots for Planetary Exploration (see n. 41, p. 12).

[56] Idem: Quadrupedal Robots for Planetary Exploration (see n. 41, p. 12).

[57] Raibert, M. et al.: BigDog, the Rough-Terrain Quadruped Robot, in: IFAC Proceedings Volumes 2008; Boston Dynamics (ed.): BigDog Evolution, 2011, URL: https://www.youtube.com/watch?v=xqMVg5ixhd0.

[58] Idem (ed.): Introducing Spot (previously SpotMini), 2016, URL: https://www.youtube.com/watch?v=tf7IEVTDjng.

[59] e.g. idem (ed.): Atlas Update, 2013, URL: https://www.youtube.com/watch?v=SD6Okylclb8; idem (ed.): Atlas | Partners in Parkour, 2021, URL: https://www.youtube.com/watch?v=tF4DML7FIWk

[60] Haldane, D. W. et al.: Robotic vertical jumping agility via series-elastic power modulation, in: Science Robotics 2016.

[61] Yim, J. K. et al.: Precision Robotic Leaping and Landing Using Stance-Phase Balance, in: IEEE Robotics and Automation Letters 2020.

[62] Ibid.

[63] Yim et al.: Precision Robotic Leaping and Landing Using Stance-Phase Balance (see n. 61); BiomimeticMillisys (ed.): Salto-1P Leaping and Landing, 2020, URL: https://www.youtube.com/watch?v=_EhVY65e7W0.

assisting structures such as active robotic tails can "enhance stabilization and maneuverability"[64]. Beyond these examples of non-adhesive legged robots, *StickyBot* can adhere and crawl with gecko-inspired sticky feet along vertical smooth surfaces.[65]

Alongside those notable advances in engineering legged robots within the meter and centimeter range, so-called "micro mobile robots ($<$10 cm)"[66] are equipped with remarkable features, too. This includes, for instance, sprawled posture locomotion with up to four body-lengths per second[67], surface electrochemical actuators which operate at low voltages (200 µV) and low power (10 nW)[68], the capability to not only crawl but also to jump and control simultaneously the "trajectory by adjusting both crawling speed and jumping take-off speed"[69], or "robotic metamorphosis by origami exoskeletons"[70].

Cyborgs

Last but not least, for "insect-computer hybrid legged robots"[71], or cybernetic organisms (cyborgs), which are built on the plan of living insects as "Nature's ready-made robot platform"[72], speed, step length and walking gait can now be user-adjusted by stimulating muscles with microcontrollers. Such cyborgs require

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[64] Saab, W./Rone, W. S./Ben-Tzvi, P.: Robotic tails: a state-of-the-art review, in: Robotica 2018.

[65] Stanford (ed.): Stanford's 'Stickybot,' a Gecko-like robot, climbs vertical services, 2010, URL: `https://www.youtube.com/watch?v=o5lMJtQOKSY`; Cutkosky, M.: StickyBot III, 2021, URL: `http://bdml.stanford.edu/twiki/bin/view/Rise/StickyBotIII`; Kim, S. et al.: Whole body adhesion: hierarchical, directional and distributed control of adhesive forces for a climbing robot, in: IEEE, 2007.

[66] Asamura, K./Nagasawa, S.: A micro hexapod robot for swarm applications assembled from a single FPC sheet, in: Japanese Journal of Applied Physics 2021.

[67] Baisch, A. T./Sreetharan, P. S./Wood, R. J.: Biologically-inspired locomotion of a 2g hexapod robot, in: IEEE, 2010; Goldberg, B. et al.: Power and Control Autonomy for High-Speed Locomotion With an Insect-Scale Legged Robot, in: IEEE Robotics and Automation Letters 2018.

[68] Miskin, M. Z. et al.: Electronically integrated, mass-manufactured, microscopic robots, in: Nature 2020; Nature Video (ed.): March of the microscopic robots - YouTube, 2020, URL: `https://www.youtube.com/watch?v=2TjdGuBK9mI&t=140s`.

[69] Jung, G.-P. et al.: An integrated jumping-crawling robot using height-adjustable jumping module, in: 2016; UC Berkeley (ed.): SALTO - Teaching an old robot new tricks, 2019, URL: `https://www.youtube.com/watch?v=qFmeHPVtKOo`.

[70] Miyashita, S. et al.: Robotic metamorphosis by origami exoskeletons, in: Science Robotics 2017; Massachusetts Institute of Technology (MIT) (ed.): Robot Origami: Robot self-folds, walks, and completes tasks, 2015, URL: `https://www.youtube.com/watch?v=ZVYz7g-qLjs`.

[71] Cao et al.: Insect–computer hybrid legged robot with user-adjustable speed, step length and walking gait (see n. 44, p. 12).

[72] Ibid.

neither a human-made "complex structural design nor complicated locomotion control algorithms"[73]. At the same time, they function with about 100 times less power compared to robots of a comparable size[74]. Since this pragmatic approach uses the already existing sophisticated natural structures, it relies mainly on the understanding of the stimulation of muscles and the design of a matching interface between the living creatures and the computer units to control the motion of the organism (bio-actuator) or possibly to translate sensory information into human-readable information (bio-sensor). However, such hybrids cannot easily be transformed to a larger form for transporting purposes for instance, as they have a limited biological lifespan, and they can only be operated within narrow temperature ranges and in non-bio-hazardous environments.

Robotics-inspired biology

This list of some recent developments in engineered legged robots or cybernetic organisms is not intended to be exhaustive nor exclusive.[75] It illustrates that the current integrative approaches in life sciences, robotics, material science, machine learning, and neighboring fields are highly applicable for new designs of human-made legged motion systems. Moreover, robotic experiments are also being flipped to generate new hypotheses and to reason in biology (robotics-inspired biology[76]), which will be taken up in the subsequent Section 1.3. Foresightful, Marey[77] motivated already in 1874 such integrative and comparative approaches and wrote in the introduction of his book "Animal Mechanism":

> "The comparison of animals with machines is not only legitimate, it is also extremely useful from different points of view. It furnishes a valuable means of making the mechanical phenomena which occur in living beings understood, by placing them beside the similar but less generally known phenomena, which are evident in the action of ordinary machines. In the course of this book, we shall frequently borrow

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[73] Cao et al.: Insect–computer hybrid legged robot with user-adjustable speed, step length and walking gait (see n. 44, p. 12).

[74] Ibid.

[75] More on early legged robots is written in, for instance, Raibert, M. H./Hodgins, J. K.: Legged Robots, in: Boston: Academic Press, 1993, p. 321 or Reeve, R. E.: Dynamic Walking: A Step Forward?, in: Tzafestas, S. G. (ed.), Dordrecht: Springer Netherlands, 1999, p. 337 ff. Bellicoso et al.: Advances in real-world applications for legged robots (see n. 48, p. 13) and Kolvenbach: Quadrupedal Robots for Planetary Exploration (see n. 41, p. 12) summarize the recent advances for legged robots.

[76] Gravish, N./Lauder, G. V.: Robotics-inspired biology, in: Journal of Experimental Biology 2018.

[77] Marey, E.-J.: Animal mechanism: a treatise on terrestrial and aërial locomotion. New York, D. Appleton and co., 1874.

> from pure mechanics the synthetical demonstrations of the phenomena of animal life. The mechanican, in his turn, may derive useful notions from the study of nature, which will often show him how the most complicated problems may be solved with admirable simplicity."[[78]]

Outlook

In summary, it seems that new legged robots, in particular from the last 10 to 15 years, are advancing in exploiting inertial effects for their locomotion (dynamic locomotion) to balance, walk, run or jump more in an animal-like fashion compared to their preceding prototypes. Simultaneously, the orientation and segmentation of the robots' legs are approaching their biological templates more and more. This can not only be seen in mimicking the outer obvious morphologies but also in attempts to utilize nonlinear properties "mechanically intelligent"[79] by implementing elastic and dissipative structures, for instance.

However, while great progress becomes obvious in walking robots which exchange tractive and compression forces with the ground, climbing robots relying on adhesion, or normal pulling forces, are rare. Here, the outcomes of a modeling study reasoned *why* we should look further into the coordination of the legs and their contact mechanics in climbing Hexapoda, because it showed that "climbing [with leg adhesion] favors the tripod gait"[80], the gait which Hexapoda usually employ. Thus, biomechanical analyses of locomoting Hexapoda should be of particular interest to understand the benefits of their gait, posture and contact mechanics with respect to climbing tasks.

After the present section, which exemplified the advances in legged robots and the apparent technological gap in the emulation of climbing legged biological designs, I now aim to highlight some of the established approaches and concepts of studying *Animal Mechanism*[81] or *Animal Locomotion*[82] in a chronological order, because they ground the terminology, methods and discussion of this dissertation, and they help to reason further why biomechanical analyses of climbing and self-righting Hexapoda may be relevant for various research fields including robotics, functional morphology and ecology.

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[78] Marey, E.-J.: Animal mechanism: a treatise on terrestrial and aërial locomotion. New York, D. Appleton and co., 1874.

[79] Blickhan, R. et al.: Intelligence by mechanics, in: Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 2007.

[80] Ramdya, P. et al.: Climbing favours the tripod gait over alternative faster insect gaits, in: Nature Communications 2017.

[81] Marey, E.-J.: Animal mechanism: a treatise on terrestrial and aërial locomotion. New York, D. Appleton and co., 1874.

[82] Pettigrew, J. B.: Animal locomotion, or Walking, swimming, and flying, with a dissertation on aëronautics. New York, D. Appleton & company, 1874.

1.3 Potentially influential methods and concepts for the study of legged animal locomotion in a chronological order

Probably many prototypes of the cited legged motion systems in the previous section 1.2 may be related to former observations of animal motions and behaviors, and studies which did not fear to immerse into the complexity of an animal's motion system to analyze and conceptualize its functioning have contributed to the recent (erratic) advances in physical robots. Scholtz[83] argues, similarly, that humans might even have copied the wheel from the dung rolling scarab beetles. However, the initial interest to study the *Animal Mechanism*[84] and to classify them happened probably often autotelically-motivated without necessarily a purpose to design utilities, machines, or robots. Although it is vague to speculate about the incentives of the pioneering engineers and scientists and the exact roots of discoveries, certainly in the 19th century the first instruments with graphing and recording (writing) capabilities eventually led to a more widespread general interest in explaining animal motion behaviors, because their kinematics, forces, and muscle contractions could from then onwards be quantified over time.

Early apparatus to record and display animal motions

For instance, with the modifications of the first chronometers of Young[85] or kymographs of Ludwig[86] to a myographion (muscle writer), probably Helmholtz[87] and contemporaries in the 1850ies not only observed and described muscle contractions and relaxations (*Zuckung*) qualitatively, but also recorded and displayed them over time. Subsequently, the apparatus was enhanced to operate without detaching the muscle from the animal by Marey[88] to allow "the organ being left in the normal conditions of its function"[89]. Thus, this pioneering apparatus eventually led to

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[83] Scholtz: Scarab beetles at the interface of wheel invention in nature and culture? (see n. 24, p. 6).

[84] Marey: Animal mechanism: a treatise on terrestrial and aërial locomotion. (see n. 81, p. 17).

[85] Young, T.: A course of lectures on natural philosophy and the mechanical arts. London: Printed for J. Johnson, 1807, p. 772f, Figure 198.

[86] Ludwig, C.: Beiträge zur Kenntnis des Einflusses der Respirationsbewegungen auf den Blutlauf im Aortensysteme, in: Müller, J. (ed.), Berlin: Verlag von Veit Et Comp., 1847, vgl. Tafel X.

[87] Schmidgen, H.: Leviathan and the Myograph: Hermann Helmholtz's "Second Note" on the Propagation Speed of Nervous Stimulations, in: Science in Context 2015; Valentinuzzi, M. E./ Beneke, K./Gonzalez, G. E.: Ludwig: The Bioengineer [Retrospectroscope], in: IEEE Pulse 2012.

[88] Marey, E.-J.: Du Mouvement Dans Les Fonctions de la Vie: Leçons Faites Au Collège de France, 1868.

[89] Idem: Animal mechanism: a treatise on terrestrial and aërial locomotion. New York, D. Appleton and co., 1874, p. 32.

the first measurements of muscle properties over time and therefore to important insights in the actuation of the locomotor system of organisms.

Early apparatus to record and display ground reaction forces in moving humans and animals

In addition, Marey[90] published 1874 an "experimental shoe" with his pupil Mons. G. Carlet which they described as a "dynameter of pressure" to measure "the pressure of the foot on the ground, with its duration and its phases"[91]. With this, they were probably among the first who could graph the (uncalibrated) normal forces acting from the legs on the ground, or its opposites from the ground on the legs (now termed as ground reaction forces). Therewith, and with a modified version of this apparatus for a horse's hoof, they could record "step-curves"[92] and classify for bipeds and quadrupeds the "rhythm in different modes of progression"[93] what is today known as temporal stepping pattern or gait diagram. In this context, Marey[94] also talks about "reactions", which he relates to the actions of the legs on the mass of the body as follows:

> "We shall designate by this name [reactions] the movements which the action of the leg produces on the mass of the body. These movements are very complex; they are effected at the same time in every direction, and give to the trajectory which a point of the body describes in space, some very complicated sinuosities. The graphic method alone can enable us, at least as yet, to appreciate the real nature of these movements."[95]

Polygraphic measuring devices

To graph these very complex movements of a point of the body together with the pressure of the foot on the ground, they combined the register from the experimental shoe with further registers from *lever-drums* which act by inertia. The lever-drums were fixed at the pubis or the head to "receive and transmit faithfully"[96] the oscillations during various paces.[97] With this complex polygraphic

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[90] Marey: Animal mechanism: a treatise on terrestrial and aërial locomotion. (see n. 89, p. 18).

[91] Ibid., p. 113.

[92] Ibid., p. 127 f.

[93] Ibid., p. 132.

[94] Ibid.

[95] Ibid., p. 115.

[96] Ibid., p. 117.

[97] Ibid., p. 116ff.

measuring device[98], they probably initiated the quantification of the gait dynamics specifically of moving humans[99] and horses[100], or generally of legged terrestrial animals. Hence, they could find out, for instance, that “two oscillations in the vertical direction correspond with a single horizontal oscillation”[101] and relate the global dynamics of the center of gravity to the (uncalibrated) leg forces normally to the ground[102].

Geometrical chronophotography

Furthermore, they developed a complex measuring unit[103], in its combination very similar to what we are still using nowadays, to study biolocomotions by running their further developed dynamographic platform together with their geometric-chronophotographic methods[104].

Therewith, they further pioneered statements about muscular work done in moving limbs and compared the “relative amount of work done in executing various paces”[105]. Moreover, Marey[106] linked chronophotographic measures of jumping humans to the laws of ballistics[107] and to compliant properties of muscles by comparing their results to the motion of an “elastic ball falling on a hard surface from a certain height”[108]:

> “Chronophotography shows that the second jump is always higher than the first. [. . .] Now, since the height of the second jump is greater than the first, it must be admitted that the elastic force of the muscles which are contracted to break the fall, is added to the muscular action consciously brought into play for the second jump.”[109]

Neuromechanics

Thus, the development of chronophotographic methods, or “multi-exposure photographs”[110], and their application to record points of interest quantitatively on

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[98] Marey: Animal mechanism: a treatise on terrestrial and aërial locomotion. (see n. 89, p. 18), p. 126, Fig. 27.

[99] Ibid., p. 133, Fig. 34.

[100] Ibid., p. 153, Fig. 45.

[101] Ibid., p. 117.

[102] Ibid., p. 133, Fig. 34.

[103] Marey, E.-J.: Movement, trans. by Pritchard, E., Authorised ed., New York : D. Appleton and Company, 1895, p. 151, Fig.101.

[104] Ibid., p. 61, Fig. 42.

[105] Ibid., p. 158 ff.

[106] Ibid.

[107] Ibid., p. 152.

[108] Ibid., p. 161.

[109] Ibid., p. 162.

[110] McMahon, T.: Mechanics of Locomotion, in: The International Journal of Robotics Research 1984.

moving organisms eventually led, *inter alia*, not only to an augmented toolset for the liberal arts circles (e.g., light paintings), but also to a functional understanding of the diversity of locomotor morphologies in biology, and to numerical descriptions of fast animal movements which are not visible to the naked eye. Such initial physical interpretations of the recorded traces and the global dynamics of biomotions probably laid the basis for the classifications of gaits[111] and to various "template and anchor"[112] models which aim to describe substantial features of the neuromechanical functioning of legged motion systems. By "trimming away" some of the "incidental complexity of joints, muscles and neurons"[113], several locomotive functions of the biological features such as compliant legs[114], segmentation, joint design, mass distribution or posture, leg orientation or muscle attachment, may be carved out. For example, compliant legs may behave like springs to store and recoil elastic strain energy. Thereby, they can function, to save energy[115], explain the "co-existence of walking and running gaits"[116], amplify or attenuate power[117], and aid to stability (Figure 4) and robustness[118].

Neuromechanical intelligence

However, many such concepts and mathematical models have evolved over the years to illuminate various characteristics of legged locomotion systems. Sharbafi/ Seyfarth[119] summarize in the chapter "Model Zoo: Extended Conceptual Models" of their edited book *Bioinspired Legged Locomotion* several limitations and extensions of the most common locomotion models. The main merit of those conceptual

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[111] e.g. Hildebrand, M.: Analysis of Tetrapod Gaits: General Considerations and Symmetrical Gaits, in: Herman, R. M. et al. (eds.), Boston, MA: Springer US, 1976

[112] Full, R. J./Koditschek, D. E.: Templates and anchors: neuromechanical hypotheses of legged locomotion on land. In: Journal of Experimental Biology 1999.

[113] Ibid.

[114] e.g. Cavagna, G. A./Saibene, F. P./Margaria, R.: Mechanical work in running, in: Journal of Applied Physiology 1964; Alexander, R. M.: Elastic Energy Stores in Running Vertebrates, in: American Zoologist 1984; Alexander, R. M./Vernon, A.: The mechanics of hopping by kangaroos (Macropodidae), in: Journal of Zoology 1975; Roberts, T. J./Azizi, E.: Flexible mechanisms: the diverse roles of biological springs in vertebrate movement, in: Journal of Experimental Biology 2011; Alexander, R. M.: A model of bipedal locomotion on compliant legs, in: Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 1992

[115] Alexander: Elastic Energy Stores in Running Vertebrates (see n. 114).

[116] Geyer, H./Seyfarth, A./Blickhan, R.: Compliant leg behaviour explains basic dynamics of walking and running. In: Proceedings of the Royal Society B: Biological Sciences 2006; Seyfarth, A. et al.: Biomechanical and neuromechanical concepts for legged locomotion: Computer models and robot validation, in: Routledge, 2013.

[117] Roberts/Azizi: Flexible mechanisms (see n. 114).

[118] Ghigliazza, R. M. et al.: A Simply Stabilized Running Model, in: SIAM Review 2005; Rummel, J. et al.: Stable and robust walking with compliant legs, in: IEEE, 2010.

[119] Sharbafi, M. A./Seyfarth, A.: Chapter 3.6 - Model Zoo: Extended Conceptual Models, in: Butterworth-Heinemann, 2017.

models may rest inside their capability to uncover "mechanically intelligent"[120] and subsequently neuromechanical intelligent features which emerge from "interactions of nervous system, body and environment"[121], beside the value to explain functions of morphologies and motion behaviors from a biomechanical perspective. In this context, Raibert/Hodgins[122] wrote, in a nutshell:

> "We believe that the mechanical system has a mind of its own, governed by the physical structure and the laws of physics. Rather than issuing commands, the nervous system can only make "suggestions" which are reconciled with the physics of the system [body plus environment] and the task. [. . .] We think that the nervous system and the mechanical system should be designed to work together, sharing responsibility for the behavior that emerges"[123].

Self-stabilizing mechanisms

Thus, mechanically intelligent system behaviors may reside in "self-stabilizing mechanisms"[124]. For instance, Ringrose[125] demonstrated on a physical monopod robot with actuators that it can "recover automatically from minor disturbances even if it cannot detect them"[126] and associates this "reliable default behavior" without sensing with mechanical self-stability (Figure 4). He defines that a "self-stabilizing running robot has no computer, but does have actuators which go through a fixed, repeating cycle".[127] I would add here passive or active to differentiate mechanically self-stabilized systems based on the absence of any neuronal or computer activation (passive-mechanical self-stabilization in Figure 4 (a), e.g., passive walker) or the presence of a predefined neuronal or computer activation (active-mechanical self-stabilization in Figure 4 (b), e.g., death-head cockroach feedforward model without neural feedback[128]). The remaining systems, which

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[120] Blickhan, R. et al.: Intelligence by mechanics, in: Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 2007; Blickhan, R./Wagner, H./ Seyfarth, A.: Brain or muscles?, in: Recent Research Developments in Biomechanics 2003.

[121] Chiel, H. J./Beer, R. D.: The brain has a body: adaptive behavior emerges from interactions of nervous system, body and environment, in: Trends in Neurosciences 1997.

[122] Raibert/Hodgins: Legged Robots (see n. 75, p. 16).

[123] Ibid., p. 350.

[124] Ringrose, R.: Self-stabilizing running, in: IEEE, 1997.

[125] Ibid.

[126] Ibid.

[127] Ibid., p. 22.

[128] Kubow, T. M./Full, R. J.: The role of the mechanical system in control: a hypothesis of self–stabilization in hexapedal runners, in: Philosophical Transactions of the Royal Society B: Biological Sciences 1999-05-29, 1999.

depend on control through sensory-feedback (e.g., vision, strain, odor[129]) for their stabilization, I would group under the variable-neuronally stabilized field (c) in Figure 4.

Blickhan/Wagner/Seyfarth[130] exemplify such self-stabilizing behaviors for instance for "the negative slope of the force-velocity relation of muscles [which] is suitable to stabilize disturbances of the velocity"[131] or the stabilizing potential of asymmetric segment lengths, co-contracting muscles, or nonlinear characteristics of biarticular structures. As benefits of self-stabilizing mechanism in hexapedal runners[132], Full/Koditschek[133] mention, for instance, the simplification of control and the "rapid response to perturbations" for a dynamic cockroach model:

> "Surprisingly, the model runs in a stable manner at the animal's preferred speed, rejecting artificially imposed perturbations! The model self-stabilizes. Perturbations alter the translation and/or rotation of the body which, consequently, provides 'mechanical feedback' by altering leg moment arms. In a sense, control algorithms are embedded in the morphology itself. Passive, dynamic feedback from a 'tuned' mechanical system may allow rapid response to perturbations and can simplify control."[134]

Ambivalence of stability

Such a rapid, or "zero-delay, intrinsic response[s] of a neuromusculoskeletal system to a perturbation" has also been termed "preflex"[135]. A preflex may facilitate stability (Figure 4), which can support (functional stability) or hamper (unfunctional stability) stance and progression. Blickhan/Wagner/Seyfarth[136] recall that it should still be possible for the locomotion system to escape from an "attractive point of operation" and to readjust it. However, a preflex may also destabilize the system, which can either (again) support (functional instability) or hamper (unfunctional instability) stance and progression. Thus, "maneuverability and stability are the opposite sides of the same medal"[137] and are both important

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[129] Dickinson, M. H. et al.: How Animals Move: An Integrative View, in: Science 2000-07-04, 2000.

[130] Blickhan/Wagner/Seyfarth: Brain or muscles? (see n. 120, p. 22).

[131] Ibid.

[132] Kubow/Full: The role of the mechanical system in control (see n. 128, p. 22).

[133] Full/Koditschek: Templates and anchors: neuromechanical hypotheses of legged locomotion on land. (see n. 112, p. 21).

[134] Ibid.

[135] Brown, I./Loeb, G.: A Reductionist Approach to Creating and Using Neuromusculoskeletal Models, in: Winters, J. M./Crago, P. E. (eds.), Springer, 2000.

[136] Blickhan/Wagner/Seyfarth: Brain or muscles? (see n. 120, p. 22).

[137] Ibid.

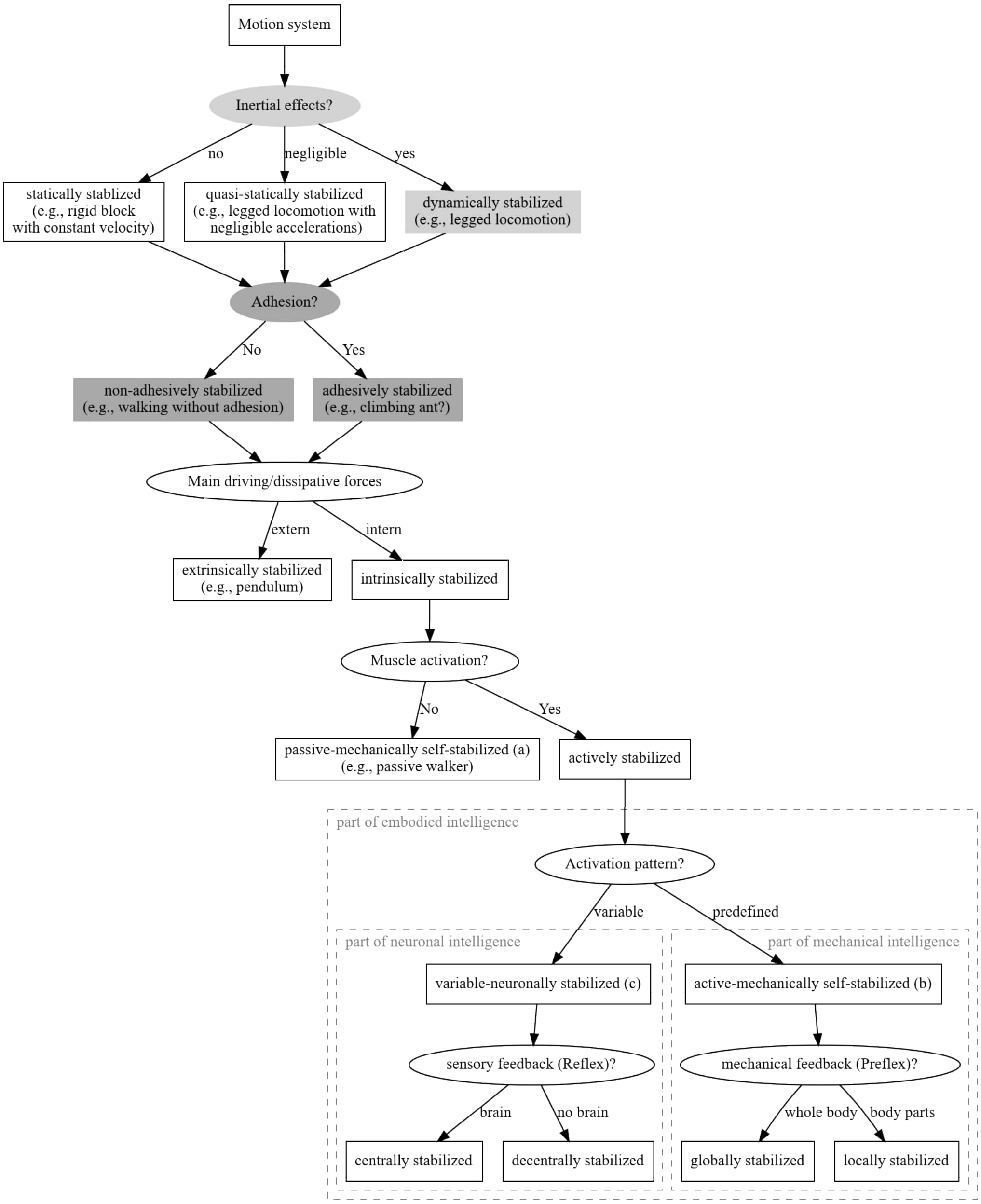

Figure 4: One possibility to structure commonly used *stability* terms in legged locomotion studies in a simplified diagram. Please note that the dark gray shaded areas fall within the scope of Article 2 (Section 2.2) about balancing strategies of ants on slopes, and that the light gray areas are linked to Article 3 (Section 2.3) about dynamic self-righting strategies in cockroaches. Please also take into account that static stability may in other writings be associated with configurations where the vertical projection of the center of gravity falls within the supporting polygon (positive stability margin). Since there may be situations where the stability margin is negative despite a balanced act (e.g., resting animal on a vertical wall), I tend to differentiate between adhesively stabilized mechanism whereby, for instance, legs can pull on the substrate to generate counter torques against toppling over, and non-adhesively stabilized actions as the counterpart (e.g., walking with no adhesion).

features for a mechanically intelligent embodied system. According to that, the biological design of the animals and the employment of their structures within the environment has to be adjusted properly, or mechanically intelligent, to exploit functionally such zero-delay responses to a perturbation. Moreover, mechanical intelligence involves, at least to my understanding, not only the capability to stabilize and destabilize a system functionally to enable stance and progression, but also features such as energy and structural efficiency, multi-functionality, recovery, safety, robustness, flexibility, or agility.

Robophysics

To study mechanically intelligent morphologies and mechanism, the "application of knowledge of the natural world to engineering problems"[138] has already been flipped to use "robots and physical models to set the course for experiments on biological systems and to generate new hypotheses for biological research"[139] (Robotics-inspired biology). Similarly, Aydin et al.[140] emphasize that systematic and automated robotic experiments can "rapidly explore a wide range of parameter space [including outside the expected parameter range] and determine the capabilities of the robot's locomotive configuration"[141] in complex real environments. With this approach, or by treating "robots as experiments"[142] in complex terrain (robophysics) rather than "afterthoughts once the control scheme has been developed mathematically and the environment has been controlled"[143], one can study the (unforeseen) complexity of locomotion which may not yet be possible to simulate and predict with computer models. Lastly, Delcomyn[144] and Webb[145], for instance, discuss in remarkable detail whether robotics can help reasoning in biology.

Thus, with the aid of physical models, functions of animal morphologies such as weight distributions, compliancy, hysteresis, elasticities, segment length ratios, contact structures, redundancies, rotational axis, asymmetries or nonlinearities,

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[138] Gravish/Lauder: Robotics-inspired biology (see n. 76, p. 16).

[139] Ibid.

[140] Aydin, Y. O. et al.: 6 - Physics approaches to natural locomotion: Every robot is an experiment, in: Walsh, S. M./Strano, M. S. (eds.), Woodhead Publishing, 2019.

[141] Idem: 6 - Physics approaches to natural locomotion: Every robot is an experiment, in: Walsh, S. M./Strano, M. S. (eds.), Woodhead Publishing, 2019.

[142] Idem: 6 - Physics approaches to natural locomotion: Every robot is an experiment, in: Walsh, S. M./Strano, M. S. (eds.), Woodhead Publishing, 2019.

[143] Idem: 6 - Physics approaches to natural locomotion: Every robot is an experiment, in: Walsh, S. M./Strano, M. S. (eds.), Woodhead Publishing, 2019.

[144] Delcomyn, F.: Insect Walking and Robotics, in: Annual Review of Entomology 2004.

[145] Webb, B.: Can robots make good models of biological behaviour?, in: Behavioral and Brain Sciences 2001.

and their motion behaviors such as gaits and postures can be verified or hypothesized. For instance, Nyakatura et al.[146] developed the physical robot *OroBOT* to prove concepts of reconstructions of the locomotion of extinct vertebrates. Moreover, Kolvenbach[147] demonstrated on their 22 kg physical robot *SpaceBok* that parallel springs within the legs reduce "energy consumption by a factor of two compared to inelastic jumps.". They showed further, that "dynamic gaits are energetically more efficient than static gaits but are riskier on steep slopes". By varying the foot morphology to study granular slope traversal performance they also showed that "point feet are less affected by slippage due to their excessive sinkage, but in turn, are prone to instabilities and tripping" whereas passive adaptive planar feet with grouser pads reduce sinkage but increase energy consumption notably when "the slope inclination approaches the soil's angle of internal friction due to shearing".

As a final example, it is known that certain animal species lower their center of gravity while traversing slopes, while others do not show this kind of adaptive locomotion behavior. Kolvenbach[148] verified in this context for their physical robot that a crouched position with a lowered center of gravity significantly increases the power consumption compared to a posture with stretched legs. As a consequence from the robotic experiment one could now hypothesize, for instance, that crouched postures oblige animals to metabolize more energy, too, and/or one could ask for the (versatile) benefits of the lowering of the animals for their locomotion if it is energetically costly. The latter question will be elaborated in Section 1.4.3 and in the published article in Section 2.2 with respect to eventual advantages for the stability in climbing ants.

1.4 Towards some research questions for this thesis

1.4.1 Miniaturization

Lower known size limits for locomoting organisms on legs

Within the last paragraph of the previous section, I have referenced studies which showed that the (functional) exploitation of inertial, gravitational, and elastic effects may help to save energy and to locomote robustly.

However, inertia and gravity may become relatively less decisive for animals the size of insects in the millimeter or micrometer range (*miniaturization*[149]), because adhesive contact forces (e.g., attachment and detachment mechanism in sticky

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[146] Nyakatura, J. A. et al.: Reverse-engineering the locomotion of a stem amniote, in: Nature 2019.

[147] Kolvenbach: Quadrupedal Robots for Planetary Exploration (see n. 41, p. 12), p. 15.

[148] Ibid.

[149] Polilov, A. A.: Small Is Beautiful: Features of the Smallest Insects and Limits to Minia-

feet), and probably dissipative internal forces (e.g., joint friction, damping), superimpose them with an increasing affect the smaller the organisms are (Figure 5). In this context, Went[150] argued that flies can walk upside down, because “gravity and adhesion are of the same order of magnitude”. For instance, Dixon/Croghan/Gowing[151] identified for *Aphis fabae* SCOPOLI, 1763 with body masses between 0.3 mg and 0.4 mg forces (expressed as weight) of about 6.4 mg. Thus, they concluded that the “adhesive force is about 20 times greater than the gravitational force tending to detach each foot”[152]. Moreover, Federle/Rohrseitz/Hölldobler[153] identified attachment forces for approximately 0.3 mg *Crematogaster (Decacrema)* ants that are on average about 146 higher than their body weight.

Zeng et al.[157] continue and point out that if “the entire creature size shrinks down to micrometers (muscle cross-section getting close to body-environment contact area), the adhesion becomes comparable with the muscle force, thus posing a great difficulty for any movement”[158]. Therewith, they estimate the “lower limit for the size of terrestrial free moving organisms”[159] to be around 140 µm based on (probably) the smallest known insect, the parasitic wasp *Dicopomorpha*[160]. At this size the “balance between achievable muscle stress and adhesive force”[161] may be achieved. Huber/Noyes[162] distinguish further between internal and external constraints which size-limit locomotion with articulated appendages and reference the mite *Cochlodispus minimus* MAHUNKA, 1976 as the lower boundary for a walking arthropod to about 80 µm.

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turization, in: Annual Review of Entomology 2015; Hanken, J./Wake, D. B.: Miniaturization of Body Size: Organismal Consequences and Evolutionary Significance, in: Annual Review of Ecology and Systematics 1993.

[150] Went, F. W.: The size of man, in: American Scientist 1968.

[151] Dixon, A. F. G./Croghan, P. C./Gowing, R. P.: The Mechanism by Which Aphids Adhere to Smooth Surfaces, in: Journal of Experimental Biology 1990.

[152] Idem: The Mechanism by Which Aphids Adhere to Smooth Surfaces, in: Journal of Experimental Biology 1990.

[153] Federle, W/Rohrseitz, K/Hölldobler, B: Attachment forces of ants measured with a centrifuge: better "wax-runners" have a poorer attachment to a smooth surface, in: Journal of Experimental Biology 2000.

[155] Pianka, E. R./Sweet, S. S.: Integrative biology of sticky feet in geckos, in: BioEssays 2005

[156] idem: Integrative biology of sticky feet in geckos, in: BioEssays 2005

[157] Zeng, H. et al.: Light-Fueled Microscopic Walkers, in: Advanced Materials 2015.

[158] Idem: Light-Fueled Microscopic Walkers, in: Advanced Materials 2015.

[159] Idem: Light-Fueled Microscopic Walkers, in: Advanced Materials 2015.

[160] Mockford, E. L.: A New Species of Dicopomorpha (Hymenoptera: Mymaridae) with Diminutive, Apterous Males, in: Annals of the Entomological Society of America 1997.

[161] Zeng, H. et al.: Light-Fueled Microscopic Walkers, in: Advanced Materials 2015.

[162] Huber, J./Noyes, J.: A new genus and species of fairyfly, Tinkerbella nana (Hymenoptera, Mymaridae), with comments on its sister genus Kikiki, and discussion on small size limits in arthropods, in: Journal of Hymenoptera Research 2013.

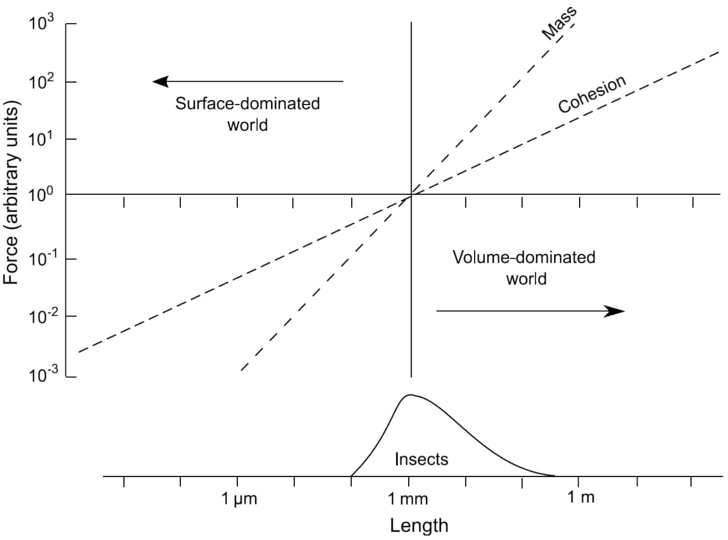

Figure 5: Conceptual diagram visualizing the boundary between a macroscopic "volume-dominated"[154]or "mass-based" world[155]and a "microscopic surface-based world"[156]where terrestrial animals are influenced, depending on their size, either more by gravity or more by cohesive forces, respectively. The figure is borrowed and modified from: Went, F. W. (1968). The size of man. American Scientist 56, 400–413. (Figure 2); Pianka, E. R. and Sweet, S. S. (2005). Integrative biology of sticky feet in geckos. BioEssays 27, 647–652. (Fig. 2);and Bonner, J. T. (2006). Why Size Matters: From Bacteria to Blue Whales. 1st ed. Princeton University Press. (p. 41).

Volume-dominated macro world

In contrast to legged organisms on the lower size limit, for a body in the "macroscopic mass- and kinetic energy-based world"[163] (volume-dominated macro world) the weight would exceed adhesive forces manyfold with the consequence that, for instance, human may not adhere to inverted surfaces. Otherwise, "to support a human's body weight, an unrealistic 40% of the body surface would have to be covered with adhesive pads"[164]. Furthermore, large toppling animals face much higher risk to get injured compared to small animals, because of their higher kinetic energy in the point of time in collision inelastically with the ground.[165]

Surface-dominated micro world

Thus, concepts from locomoting animals in the volume-dominated macro world

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[163] Pianka, E. R./Sweet, S. S.: Integrative biology of sticky feet in geckos, in: BioEssays 2005.

[164] Labonte, D. et al.: Extreme positive allometry of animal adhesive pads and the size limits of adhesion-based climbing, in: Proceedings of the National Academy of Sciences 2016.

[165] Went, F. W.: The size of man, in: American Scientist 1968.

cannot easily be transferred to the surface-dominated micro world, vice versa.[166] In particular, neither can the geometric measurements from insects and their motion data be linearly scaled to the size of humans to emulate an insect-like robot in the macro world, nor can dynamic models and physical robots from the kilogram scale be used to reason for motion behaviors of Hexapoda with adhesive forces in the milligram scale. Therefore, to deduce or validate principles of how legged animals move on the microscopic or the macroscopic scale, one has to perform measurements of them at those scales. It is a pity that the locomotion of extinct Paleozoic arthropods such as *Arthropleura* cannot be recorded any more to compare their way of progressing with the lower boundary of arthropod walking.

Success and dominance of miniaturized insects

Moreover, locomoting on a size level where neither inertial and gravitational forces nor adhesion forces can be neglected, may even beneficially influence the evolutionary success or the ecological dominance of several animal groups. A vague hypothesis in this context could be that Arthropoda, as a prominent group of such relatively small legged animals, may have exploited the benefits of both the mass related forces and the intermolecular related forces from the previously introduced "two worlds" (volume- vs. surface dominated world) for their locomotion skills, and to subsequently radiate into various habitats to become that evolutionarily successful and ecologically dominant[167] as they are. Similarly, Farisenkov et al.[168] referenced the "competition between friction and inertia" and exemplifies "success stories" of miniaturized insects, which were forced by ecological pressure to "develop extremely small bodies down to 200 µm long without losing the ability to fly"[169].

Optimal gaits may depend on size

In this context, one could further ask why arthropods which have evolved from the micrometer range[170] to at least up to the size of humans (gigantism, e.g., the original organism of a Paleozoic millipede fossil was estimated to have a width of

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[166] Went, F. W.: The size of man, in: American Scientist 1968; Pianka, E. R./Sweet, S. S.: Integrative biology of sticky feet in geckos, in: BioEssays 2005.

[167] Wilson, E. O.: Success and Dominance in Ecosystems: The Case of the Social Insects, Ecology Institute, 1990.

[168] Farisenkov, S. E. et al.: Novel flight style and light wings boost flight performance of tiny beetles, in: Nature 2022.

[169] Idem: Novel flight style and light wings boost flight performance of tiny beetles, in: Nature 2022.

[170] Huber, J./Noyes, J.: A new genus and species of fairyfly, Tinkerbella nana (Hymenoptera, Mymaridae), with comments on its sister genus Kikiki, and discussion on small size limits in arthropods, in: Journal of Hymenoptera Research 2013.

55 cm, a length of 2.63 m, and a mass of 50 kg)[171] do not walk like humans on two legs (habitual bipedalism). Bipedal gaits have been described in rapid running cockroaches for speeds above 50 body lengths per second[172], but they usually employ all of their six legs for their alternating tripod gait. Thus one could ask further why there may be no animals on the millimeter scale which usually walk on two legs, or why the small specimen do not have only two legs (morphological bipedalism)?

A modeling study indeed showed that "climbing [with adhesion] favors the tripod gait"[173], which is associated to the standard manner of how Hexapoda coordinate their legs, whereas "two-legged bipod gaits are fastest on flat terrain without adhesion"[174]. Thus, Hexapoda with adhesion capabilities may have already evolved the "optimal" gait to progress in their cluttered habitat with various inclined obstacles such as towering plants and stones. Similarly, Hughes[175] concluded with respect to static stability and "alertness" that "insects are the end-product of a process of limb reduction among terrestrial Arthropoda", because "static stability cannot be achieved with fewer than three legs on the ground"[176], and that this "feature of their locomotory mechanism is no doubt responsible, in part, for the 'alertness' which we associate with all insects, as it enables them to stop suddenly or to change direction without needing to slow down."[177]. Consequently, their coordination as well as their striking adhering and climbing capabilities has attracted interest from several research areas such as material sciences, organismal biology or robotics which led to various studies (see Section 1.1, 1.2 and 1.3) with emphasis on the description of, for instance, the dynamics of the moving organisms[178],

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[171] Davies, N. S. et al.: The largest arthropod in Earth history: insights from newly discovered Arthropleura remains (Serpukhovian Stainmore Formation, Northumberland, England), in: Journal of the Geological Society 2021.

[172] Full, R. J./Tu, M. S.: Mechanics of a rapid running insect: two-, four- and six-legged locomotion, in: Journal of Experimental Biology 1991.

[173] Ramdya, P. et al.: Climbing favours the tripod gait over alternative faster insect gaits, in: Nature Communications 2017.

[174] Idem: Climbing favours the tripod gait over alternative faster insect gaits, in: Nature Communications 2017.

[175] Hughes, G. M.: The co-ordination of insect movements. I. The walking movements of insects. In: Journal of Experimental Biology 1952.

[176] Idem: The co-ordination of insect movements. I. The walking movements of insects. In: Journal of Experimental Biology 1952.

[177] Idem: The co-ordination of insect movements. I. The walking movements of insects. In: Journal of Experimental Biology 1952.

[178] e.g. Ting, L. H./Blickhan, R./Full, R. J.: Dynamic and static stability in hexapedal runners. In: Journal of Experimental Biology 1994; Full, R. J./Blickhan, R./Ting, L. H.: Leg design in hexapedal runners, in: Journal of Experimental Biology 1991; Goldman, D. I. et al.: Dynamics of rapid vertical climbing in cockroaches reveals a template, in: Journal of Experimental Biology

the neuromuscular system[179], the functional morphology of the local attachment system[180], the external walking control of cyborg beetles[181], or the engineering of tiny locomoting legged structures[182].

Slow walking versus rapid running Hexapoda

In the context of studying the whole-body dynamics in locomoting insects, Full/Koditschek[183] differentiate in a conceptual article between slowly walking Hexapoda, such as stick insects, which depend primarily on novel and precise stepping, continuous (sensory) feedback as well as neuronal control, and rapid runners such

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2006; Reinhardt, L./Blickhan, R.: Level locomotion in wood ants: evidence for grounded running, in: Journal of Experimental Biology 2014

[179] e.g. Azevedo, A. W. et al.: A size principle for recruitment of Drosophila leg motor neurons, in: Calabrese, R. L./Doe, C. Q. (eds.): eLife 2020; Dallmann, C. J./Dürr, V./Schmitz, J.: Motor control of an insect leg during level and incline walking, in: Journal of Experimental Biology 2019; Zill, S. N. et al.: Evaluation of force feedback in walking using joint torques as "naturalistic" stimuli, in: Journal of Neurophysiology 2021

[180] e.g. Endlein, T./Federle, W.: On Heels and Toes: How Ants Climb with Adhesive Pads and Tarsal Friction Hair Arrays. In: PLoS One 2015; Federle, W./Labonte, D.: Dynamic biological adhesion: mechanisms for controlling attachment during locomotion, in: Philosophical Transactions of the Royal Society B: Biological Sciences 2019; Clemente, C. J./Federle, W.: Pushing versus pulling: division of labour between tarsal attachment pads in cockroaches, in: Proceedings of the Royal Society B: Biological Sciences 2008; Labonte, D./Federle, W.: Functionally different pads on the same foot allow control of attachment: stick insects have load-sensitive "heel" pads for friction and shear-sensitive "toe" pads for adhesion. In: PLoS One 2013; Beutel, R./Gorb, S.: Ultrastructure of attachment specializations of hexapods (Arthropoda): evolutionary patterns inferred from a revised ordinal phylogeny, in: Journal of Zoological Systematics and Evolutionary Research 2001; Beutel, R. G./Gorb, S. N.: Evolutionary scenarios for unusual attachment devices of Phasmatodea and Mantophasmatodea (Insecta), in: Systematic Entomology 2008; Gorb, S.: Attachment Devices of Insect Cuticle, 1st ed., Kluwer Academic Publishers, 2002; Gorb, S. N. et al.: Structural design and biomechanics of friction-based releasable attachment devices in insects. In: Integrative and Comparative Biology 2002

[181] e.g. Nguyen, H. D. et al.: Sideways Walking Control of a Cyborg Beetle, in: IEEE Transactions on Medical Robotics and Bionics 2020; Cao, F./Sato, H.: Insect–Computer Hybrid Robot Achieves a Walking Gait Rarely Seen in Nature by Replacing the Anisotropic Natural Leg Spines With Isotropic Artificial Leg Spines, in: IEEE Transactions on Robotics 2019; Cao, F. et al.: Insect–computer hybrid legged robot with user-adjustable speed, step length and walking gait, in: Journal of The Royal Society Interface 2016; Vo Doan, T. T. et al.: An Ultralightweight and Living Legged Robot, in: Soft Robotics 2018

[182] e.g. Goldberg, B. et al.: Power and Control Autonomy for High-Speed Locomotion With an Insect-Scale Legged Robot, in: IEEE Robotics and Automation Letters 2018; Misaki, D./Murakami, Y.: Development of a multi-leg type micro rescue robot for disaster victim search, in: IEEE, 2011; Sahai, R. et al.: Towards a 3g crawling robot through the integration of microrobot technologies, in: 2006; Asamura, K./Nagasawa, S.: A micro hexapod robot for swarm applications assembled from a single FPC sheet, in: Japanese Journal of Applied Physics 2021

[183] Full/Koditschek: Templates and anchors: neuromechanical hypotheses of legged locomotion on land. (see n. 112, p. 21).

as cockroaches which primarily rely on self-stabilization mechanism with zero-delay responses of an intelligent mechanical design (Section 1.2). Running gaits are thereby defined by an in-phase fluctuation (zero phase shift[184]) of the gravitational potential energy and the horizontal kinetic energy and not by the presence of an aerial phase. Based on this definition, Full/Tu[185] and Reinhardt/Blickhan[186] concluded for cockroaches and ants, respectively, that they run for a wide range of speeds, or more precisely, that they perform grounded running[187]. This is not a trivial result, because other than a (grounded) running ostrich[188] for instance, which does not have the attachment capabilities of small insects, the detachment processes of the feet in insects from the ground could have phase shifted those two energy forms. That is because sticky feet in insects could dissipate energy, which should subsequently increase their cost of transport. Thus, to explain how ants are able to run despite their adhesion capabilities, one has to evaluate the attachment and detachment mechanism of the feet with respect to the global body dynamics.

Linking the attachment characteristics and contact forces to the whole-body geometry and motion

Thus, the attachment system of the Hexapoda must have special features which still enables them to run despite their impressive (voluntary) adhering capabilities during climbing[189]. Relating to adhesion studies it was found out, for instance, that passive mechanical reactions of the various pretarsal morphologies[190] such as their direction-dependency[191], or their ability to vary the contact area and therewith the contact strength[192], contribute to the animals' capability for a "strong and

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[184] Full, R. J./Tu, M. S.: Mechanics of six-legged runners, in: Journal of Experimental Biology 1990.

[185] Ibid.

[186] Reinhardt/Blickhan: Level locomotion in wood ants (see n. 178, p. 31).

[187] Rubenson, J. et al.: Gait selection in the ostrich: mechanical and metabolic characteristics of walking and running with and without an aerial phase, in: Proceedings of the Royal Society of London. Series B: Biological Sciences 2004.

[188] Ibid.

[189] e.g. Goldman et al.: Dynamics of rapid vertical climbing in cockroaches reveals a template (see n. 178, p. 30)

[190] e.g. Endlein, T./Federle, W.: Walking on smooth or rough ground: passive control of pretarsal attachment in ants, in: Journal of Comparative Physiology A 2008

[191] e.g. Clemente/Federle: Pushing versus pulling: division of labour between tarsal attachment pads in cockroaches (see n. 180, p. 31); Bullock, J. M. R./Drechsler, P./Federle, W.: Comparison of smooth and hairy attachment pads in insects: friction, adhesion and mechanisms for direction-dependence, in: Journal of Experimental Biology 2008

[192] Federle/Labonte: Dynamic biological adhesion: mechanisms for controlling attachment during locomotion (see n. 180, p. 31); Federle, W./Endlein, T.: Locomotion and adhesion: dynamic control of adhesive surface contact in ants, in: Arthropod Structure & Development 2004.

reliable" attachment and a "fast and effortless" detachment[193]. Federle/Labonte[194] summarize and reveal in this context the biomechanical functions of the sprawled posture of climbing arthropods and vertebrates and link, therewith, the attachment characteristics to the whole-body geometry and motion:

> "Such gradual contact area adjustments can be made actively, i.e. via the contraction of muscles pulling feet inwards (or pushing them outwards), but they can also arise passively. Because of the sprawled posture of climbing arthropods and vertebrates, legs are pulled inwards automatically by the animal's body weight during inverted climbing (or pushed outwards during horizontal locomotion); during vertical climbing, legs above the body centre of gravity (CoG) will be pulled automatically, whereas those below will be pushed. External forces resulting from wind, rain or from carrying loads, further add to the shear force arising from the animal's own body weight."[195]

In summary, to describe the leg functions of locomoting animals mechanically and to link the attachment mechanism with the whole body dynamics, the contact forces between the animal's feet and the ground have to be measured. Within the next section, I enumerate studies which published ground reaction forces on Hexapoda to identify relevant but unanswered questions to motivate the studies of this dissertation more specifically.

1.4.2 Which leg is the main drive or brake on inclined and declined slopes, respectively?

As elaborated in the preceding section, the contact forces between the animal's feet and the ground have to be quantified together with the dynamics of the whole segmented chain to explain the locomotion and attachment mechanisms of the legged animals mechanically. Thus, in this section I first aim to (i) enumerate studies which measured the ground reaction forces on Hexapoda and (ii) reason thereafter why impulses are an additional necessary measure to identify, for instance, the main accelerating (driving) or decelerating (braking) leg in legged locomotion.

Functions of attachment structures, postures and leg actions

Studies which measure the ground reaction forces on ants together with their kinematics operate on the current lower size-limit in quantifying the locomotion

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[193] Labonte, D./Federle, W.: Biomechanics of shear-sensitive adhesion in climbing animals: peeling, pre-tension and sliding-induced changes in interface strength, in: Journal of The Royal Society Interface 2016.

[194] Federle/Labonte: Dynamic biological adhesion: mechanisms for controlling attachment during locomotion (see n. 180, p. 31).

[195] Ibid.

of freely walking legged animals. For instance, Endlein/Federle[196] explain how *Oecophylla smaragdina* ants (average mass of $8.2 \pm 2.1\,\mathrm{mg}(sd)$) engage their tarsal structures to climb vertically and invertedly on smooth and rough surfaces (Table 1). Thereby, kinematic measures such as the leg orientation and the tarsus angle were linked to morphological descriptions and to 2-dimensional individual leg contact force measurements. With this complex analysis the authors could quantify the functions and the obstacle-dependent engagement of different attachment structures (Figure 1 exemplifies common obstacles for locomoting terrestrial animals). For instance, they provided evidence that friction of the tarsi "increased with normal load as a result of the bending and increasing side contact of the tarsal hairs"[197], or that the "tarsal hairs generated higher friction forces in the pushing than in the pulling direction [on a rough sandpaper substrate], whereas the reverse effect was found on the smooth substrate"[198], or that "legs above the CoM [centre of mass] pulled and engaged the arolia ('toes'), whereas legs below the CoM pushed with the 3rd and 4th tarsomeres ('heels')"[199].

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[196] Endlein/Federle: On Heels and Toes: How Ants Climb with Adhesive Pads and Tarsal Friction Hair Arrays. (see n. 180, p. 31).

[197] Ibid.

[198] Ibid.

[199] Ibid.

Table 1: Literature review on studies which employed contact force measurements between the legs and the ground of *locomoting* Hexapoda.

Species and Reference	**Mass (mg)**	**Slope (deg)**	**Speed (cm)**	**Force**	**Selected conclusions**
Carausius morosus[a]	820 ± 160	0, 90, 180		3D	feeler functions of front legs on horizontal plane; simultaneous "braking and propulsive forces during part of each stride"; "front and middle legs actively resist the forward motion of the body, producing a 'lurching' type of locomotion"; propulsive function of hind legs on horizontal plane; supporting function of middle leg on horizontal plane; supporting function of all legs on inverted walking; propulsive function of middle leg on inverted walking; propulsive and supportive function alls legs on vertical climbing
Acheta domesticus[b]	435			1D	front leg more for balancing and searching than for progression
Blaberus discoidalis[c]	2600		8-66	2D	six-legged sum of the ground reaction forces "similar to to those found in two-, four- and eight-legged runners"
Blaberus discoidalis[d]	2100 ± 700	0	37.8 ± 7.5	3D	force vectors towards coxae (outward pushing), this minimizes (summed) joint moments, this minimizes (summed) muscle force
Periplaneta americana[e]	830 ± 80	0	44-150	3D	presence of aerial phases reject the "hypotheses that insects are confined to statically stable walking gaits"; hind legs as primary propulsive unit
Blaberus discoidalis[f]	4600 ± 260	0	22 ± 3	2D	inside legs do not contribute forces or torques to turn the body; inside legs push against the turn; legs farther away from center of rotation caused the body to turn; sprawled posture provide immediate options for maneuverability
Blaberus discoidalis[g]	2900.0 ± 1.0	90	19.5 ± 4.2	3D	front leg and middle leg pull laterally; hind legs push abdomen away from wall; front legs pull head toward wall; all legs pull the animal up
Formica polyctena[h]	10.3 ± 1.0	0	8.4 ± 2.0	3D	propulsive and braking function of the front and middle legs; propulsive function of the hind legs; supporting function of all legs;
Formica polyctena[i]	20.2 ± 3.0	0	10.9 ± 0.9	3D	propulsive function of the hind leg lateral outward pushing of middle and hind legs; negligible lateral outward pushing of front legs
Oecophylla smaragdina[j]	8.2 ± 2.1	0,90,180	2.14 ± 1.46 2.80 ± 1.25 2.17 ± 0.86	2D	legs above the CoG pull with arolia; legs below the CoG push with tarsal hairs; friction increase through bending of tarsal hair with increased side contact; direction-dependent friction of tarsal hair reversed on rough and smooth substrate; tarsal hair enable outward pushing
Carausius morsus[k]	800.0 ± 0.1	0	4.2 ± 1.0	3D	middle and hind leg propulsive force through torques about the coxa-trochanter joint rather than femur-tibia joint; small front leg propulsive force through torques about the femur-tibia joint
Carausius morsus[l]	900 ± 1	-45,0,45	2.3-8.5	3D	hind leg pulled inward on downslope hindleg pushed laterally outward on upslope; weight shifting towards do middle and front legs on downslope; hindleg propulsive function on upslope and braking function on declined slope;

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[a] Cruse, H.: The function of the legs in the free walking stick insect, Carausius morosus, in: Journal of Comparative Physiology 1976.

[b] Harris, J./Ghiradella, H.: The Forces Exerted on the Substrate by Walking and Stationary Crickets, in: Journal of Experimental Biology 1980.

[c] Full, R. J./Tu, M. S.: Mechanics of six-legged runners, in: Journal of Experimental Biology 1990.

[d] Full, R. J.: Animal motility and gravity, in: The Physiologist 1991.

[e] Full, R. J./Tu, M. S.: Mechanics of a rapid running insect: two-, four- and six-legged locomotion, in: Journal of Experimental Biology 1991.

[f] Jindrich, D. L./Full, R. J.: Many-legged maneuverability: dynamics of turning in hexapods, in: Journal of Experimental Biology 1999.

[g] Goldman, D. I. et al.: Dynamics of rapid vertical climbing in cockroaches reveals a template, in: Journal of Experimental Biology 2006.

[h] Reinhardt, L./Weihmann, T./Blickhan, R.: Dynamics and kinematics of ant locomotion: do wood ants climb on level surfaces?, in: Journal of Experimental Biology 2009.

[i] Reinhardt, L./Blickhan, R.: Level locomotion in wood ants: evidence for grounded running, in: Journal of Experimental Biology 2014.

[j] Endlein, T./Federle, W.: On Heels and Toes: How Ants Climb with Adhesive Pads and Tarsal Friction Hair Arrays. In: PLoS One 2015.

[k] Dallmann, C. J./Dürr, V./Schmitz, J.: Joint torques in a freely walking insect reveal distinct functions of leg joints in propulsion and posture control, in: Proceedings of the Royal Society B: Biological Sciences 2016.

[l] Dallmann, C. J./Dürr, V./Schmitz, J.: Motor control of an insect leg during level and incline walking, in: Journal of Experimental Biology 2019.

While such contact-force measurements in two dimensions (normal direction to the substrate and tangential fore-aft direction) were sufficient to quantify the directions-dependence of such micro-morphologies and the division of labor between distal and proximal attachment structures, it is not sufficient to describe, for instance, the dynamics of their (macro-morphological) crouched sprawled posture while in motion. On roughly 200 times heavier cockroaches *Blaberus discoidalis* AUDINET-SERVILLE, 1839, Full/Blickhan/Ting[200] found that large lateral forces of the sprawled posture help to direct the force vectors more towards the coxa joints and concluded that this minimizes joint moments and consequently the muscle force (Table 1). Moreover, they described with the help of their three-dimensional force measurements a preceding finding that "diverse leg designs can result in common whole body dynamics"[201]:

> "Whole-body dynamics common to two-, four-, six- and eight-legged runners is produced in six-legged runners by three pairs of legs that differ in orientation with respect to the body, generate unique ground reaction force patterns, but combine to function in the same way as one leg of a biped."[202]

Holmes et al.[203] summarize this finding similarly and link it to the minimum metabolic cost of locomotion (Section 1):

> "Insect legs push against one another, but force vectors are aligned approximately along the legs and directed largely toward joint centers of rotation, much as in upright-posture birds and mammals. Hence, sprawled posture locomotion of arthropods, amphibians, and reptiles does not necessarily result in large joint moments or muscle forces. This appears consistent with data showing that the minimum metabolic costs of locomotion in species that differ in posture can be similar.[204] [. . .] A sprawled posture bestows a wide base of support and low center of mass, both of which reduce overturning moments."[205]

Based on this observations, subsequent modeling and experimental studies concluded further that Hexapoda utilize their sprawled leg orientation to recover after

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[200] Full/Blickhan/Ting: Leg design in hexapedal runners (see n. 178, p. 30).

[201] Ibid.

[202] Ibid.

[203] Holmes, P. et al.: The Dynamics of Legged Locomotion: Models, Analyses, and Challenges, in: SIAM Review 2006, p. 238 f.

[204] Full, R. J.: Animal motility and gravity, in: The Physiologist 1991.

[205] Holmes, P. et al.: The Dynamics of Legged Locomotion: Models, Analyses, and Challenges, in: SIAM Review 2006, p. 238 f.

perturbations (lateral leg-spring model)[206] or to turn[207] (Table 1). In contrast to running cockroaches which employ their front legs mainly for their locomotion to establish bouncing gaits[208], crickets[209] and slowly walking stick insects[210] on horizontal planes seem to utilize (Table 1) their front legs more for feeling and balancing (e.g., lower normal forces of the front legs). It was also on walking stick insects, where first joint torques were calculated for Hexapoda based on force and kinematic measurements in synchronicity with electromyographic measurements to conclude that "stick insects adjust leg muscle activity on a step-by-step basis so as to maintain a similar kinematic pattern under different mechanical demands"[211]. With the help of this and its preceding study[212], the propulsive forces of the legs could be reasoned to the next smaller building blocks, the segment and joint level of the animals. It was found for instance, that middle and hind leg propulsive forces were mainly caused through torques about the coxa-trochanter joint rather than the femur-tibia joint.[213]

However, as elaborated on page 27 and in Figure 5, the leg actions of smaller animals such as ants may differ from the ones found in the approximately 50 to 200 heavier stick-insects or cockroaches (see Table 1). Surprisingly, compared to the running cockroaches[214], measurements of the three-dimensional ground reaction forces in wood ants *Formica* revealed similar patterns for their locomotion on a level surface: the weight seems to be equally distributed among the legs; front and middle legs work partially against the hind legs (antagonistic inter-leg action); middle legs accelerate and decelerate (antagonistic intra-leg actions); all legs push laterally outwards; and potential and horizontal kinetic energy are approximately in phase.

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[206] Schmitt, J. et al.: Dynamics and stability of legged locomotion in the horizontal plane: a test case using insects, in: Biological Cybernetics 2002.

[207] Jindrich, D. L./Full, R. J.: Many-legged maneuverability: dynamics of turning in hexapods, in: Journal of Experimental Biology 1999.

[208] Full, R. J.: Animal motility and gravity, in: The Physiologist 1991; Full, R. J./Tu, M. S.: Mechanics of a rapid running insect: two-, four- and six-legged locomotion, in: Journal of Experimental Biology 1991.

[209] Harris, J./Ghiradella, H.: The Forces Exerted on the Substrate by Walking and Stationary Crickets, in: Journal of Experimental Biology 1980.

[210] Cruse, H.: The function of the legs in the free walking stick insect, Carausius morosus, in: Journal of Comparative Physiology 1976.

[211] Dallmann, C. J./Dürr, V./Schmitz, J.: Motor control of an insect leg during level and incline walking, in: Journal of Experimental Biology 2019.

[212] Idem: Joint torques in a freely walking insect reveal distinct functions of leg joints in propulsion and posture control, in: Proceedings of the Royal Society B: Biological Sciences 2016.

[213] Idem: Joint torques in a freely walking insect reveal distinct functions of leg joints in propulsion and posture control, in: Proceedings of the Royal Society B: Biological Sciences 2016.

[214] Full, R. J./Blickhan, R./Ting, L. H.: Leg design in hexapedal runners, in: Journal of Experimental Biology 1991.

Thus, it may be concluded for the level locomotion of the referenced cockroach and ant samples that *miniaturization* from the gram to the milligram scale (including the morphological shape change of the species) neither changes notably their whole-body dynamics nor the shape of their ground reaction forces.

From contact force measurements to the evaluation of impulses

From this short literature review about the mechanical leg functions of locomoting Hexapoda, several new questions arise. First, if the middle legs, for instance, accelerate *and* decelerate the animals, do this contrary intra-leg actions cancel each other out over the duration of a ground contact/, or *do they operate effectively against the hind or middle leg? To answer this, one may calculate the average of the ground reaction forces* $\overline{F_{ij}(t)} = T_i^{-1} \cdot \int^{T_i} F_{ij}(t)\,\mathrm{d}t_i$ *of leg* /i in the direction j over the contact duration T_i and relate the sign to overall braking or propelling function of the leg. This averaging measure is closely related to the impulse $J_{ij(t)} = \int^{T_i} F_{ij}(t)\,\mathrm{d}t_i = \overline{F_{ij}(t)} \cdot T_i$ but very different in its explanatory power. For instance, if the contact time differs between the legs as measured on ants[215] or shown in the force-time-traces in the different figures in cockroaches[216], the force $F_{ij}(t)$ or average force $\overline{F_{ij}(t)}$ may not tell us *which* leg accelerates effectively the body the most per contact? To be more specific, it could be that one leg pushes with a high peak force but only for a very short time, whereas another leg pushes for a longer time but with lower forces. In this scenario, one cannot infer the “dominant” accelerating or decelerating leg without the calculation of the integral of the force over the contact time of the legs (impulse, or multiplying the average force with the contact duration). Of course, in the referenced studies for locomoting Hexapoda on plane surfaces one can estimate the main driving leg from the contrary signs in the force-traces, but without the quantification of the integral of the forces over time it would remain vague if the contact times differ and the signs are the same, or if the signs flip within one contact (e.g., middle legs). For instance, through the measurements of ground reaction forces on vertically climbing stick-insects[217], cockroaches[218] and ants[219], it became evident that each leg pair helped them to propel their body against gravity (same signs of the contact forces), but since the

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[215] Reinhardt, L./Blickhan, R.: Level locomotion in wood ants: evidence for grounded running, in: Journal of Experimental Biology 2014.

[216] Full, R. J./Blickhan, R./Ting, L. H.: Leg design in hexapedal runners, in: Journal of Experimental Biology 1991.

[217] Cruse, H.: The function of the legs in the free walking stick insect, Carausius morosus, in: Journal of Comparative Physiology 1976.

[218] Goldman, D. I. et al.: Dynamics of rapid vertical climbing in cockroaches reveals a template, in: Journal of Experimental Biology 2006.

[219] Endlein, T./Federle, W.: On Heels and Toes: How Ants Climb with Adhesive Pads and Tarsal Friction Hair Arrays. In: PLoS One 2015.

contact time may differ among the legs it is necessary to measure the impulses to evaluate their main driving or braking leg.

Research question and working hypothesis

This is the point where I step in with a specific research question for the first article, which asks for the main driving or braking leg pair in Hexapoda in different scenarios. With a case study on desert ants *Cataglyphis*, I aim to (i) quantify how the leg impulses differ or equal among their three leg pairs and (ii) how it changes from level walking to inclined and declined climbing. As a working hypothesis, I claim that desert ants employ the legs above the center of gravity as the main drive on inclined slopes (highest positive impulse among the three leg pairs) and the legs below the center of gravity as the main brake on declined slopes (highest negative impulse among the three leg pairs). This working hypothesis is derived from the results of experiments with vertically climbing weaver ants (Table 1) by Endlein/Federle[220], who found out that the direction dependence of the attachment structures rules together with the surface roughness which leg pulls or pushes the most (See elaborations on page 34). They concluded, for instance, that legs above the center of gravity engaged the arolia and "carried a significantly larger proportion of the body weight than legs below"[221] the center of gravity. Moreover, pulling with the front legs may also help to righten their posture on inclines. In flat, dry and granular desert habitats, however, the arolia of *Cataglyphis* could be less functional compared to its employment for reliable attachment capabilities in climbing arboreal *Oecophylla*. Thus, pioneering measurements of the three-dimensional ground reaction forces and kinematics in freely locomoting *Cataglyphis* ants will provide first insights in how a "none-climber" adopts its locomotion behavior when faced with inclined and declined obstacles (see research article in Section 2.1).

In contrast to such a proposed front leg driven locomotion behavior, it could also be that the desert ants try to distribute the contact forces and impulses uniformly among their free legs to flatten peak values, or that they push mainly with their longer [222] and possibly stronger hind legs. A prevalent hind leg pushing, for instance, was measured for level locomotion in wood ants[223] and discoid cockroaches[224]. Following this observation, the functioning of the hind legs as the

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[220] Endlein/Federle: On Heels and Toes: How Ants Climb with Adhesive Pads and Tarsal Friction Hair Arrays. (see n. 219, p. 38).

[221] Ibid.

[222] Tibia and femur of the hind legs are the longest among the three leg pairs in *Cataglyphis* according to Figure 16 and 17 in: Wehner, R.: Taxonomie, Funktionsmorphologie und Zoogeographie der saharischen Wüstenameise Cataglyphis fortis (Forel 1902) stat. nov, in: Senckenb. Biol. 1983

[223] Reinhardt/Blickhan: Level locomotion in wood ants (see n. 215, p. 38).

[224] Full/Blickhan/Ting: Leg design in hexapedal runners (see n. 216, p. 38).

main drive on even terrain could also result from a stable neuro-muscular program, which may not change on slopes and lead to a strong hind leg pushing on slopes, too. Furthermore, to avoid tipping and slipping, the ants may also perform antagonistic leg actions which could, for example, increase shear loading mechanism among the tarsal structures of different feet and concentrate high forces and impulses on small areas to adjust friction and adhesion in response to the obstacle properties, or their current gait and posture.

In summary, their six-leg design together with their direction-dependent attachment capabilities enables numerous combinations of how they could engage their legs on slopes. Consequently, with our limited knowledge about the climbing behavior in Hexapoda it is yet not possible to predict their leg engagement on inclined or declined slopes. Thus, the research article in Section 2.1 will provide first results whether the forces and impulses among the six legs in climbing ants are equally distributed, or whether there is a tendency to relocate the main propulsive function to one of their leg pairs.

1.4.3 How do ants prevent themselves from toppling over on inclined slopes?

In the preceding section it was reasoned why contact forces and their integral (impulses) are necessary measures to compare the braking and driving function of individual legs. In this section I motivate to look into the contact forces and tipping torques, because they help to explain and classify tip-over prevention behaviors of climbing animals.

From stability margins to torques with respect to the critical tipping axis

From a preceding kinematic study in the lab of my dissertation supervisor it is known that ants of *Cataglyphis fortis* lower their body height on inclined and declined slopes[225]. It was suggested that this behavior could help the ants to keep their center of gravity “inside the supporting polygon in order to avoid instabilities when surmounting slopes”[226]. With respect to the question of how ants prevent toppling over on inclined slopes, this open question helped me to define an initial working hypothesis for the article in section: Ants keep their center of gravity inside their supporting polygon when climbing up steep slopes. However, it is insufficient to judge tip-over prevention behaviors only based on the relative location of the center of gravity to the boundary of the supporting polygon (geometric strategy, Figure 1 in Section 2.2). Since ants may also pull with their legs normally

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[225] Weihmann, T./Blickhan, R.: Comparing inclined locomotion in a ground-living and a climbing ant species: sagittal plane kinematics. In: Journal of Comparative Physiology A 2009.

[226] Ibid.

to the substrate[227] they could also right their posture to prevent toppling (adhesion strategy, Figure 1 in Section 2.2) despite a negative stability margin (center of gravity moves out of the support polygon). Thus, to evaluate different tip-over (toppling) prevention behaviors, one has to look into the geometry of the locomoting animals *and* the contact forces which both affect the torques with respect to the tipping axes formed by the boundary of the supporting polygon.

Research question and working hypothesis

Based on such an analysis of the quasi-static torques one can evaluate whether the animals employ a geometric strategy by lowering the body height or by changing the geometry of the supporting polygon, or whether they employ an adhesive strategy by pulling on the substrate with the legs opposing the critical tipping axis (boundary of the support pattern nearest to the vertical projection of the CoG in the substrate plane, Figure 1 in section 2.2), or both. Such a quasi-static analysis of the torques may then also explain the other distinct observation on wood ants *Formica pratensis* which did not lower their body height[228]. First, for the wood ants, it could be that the 60 degree inclined and declined slopes did not suffice to force them to lower down its center of gravity for keeping it inside the supporting polygon of their feet. Consequently, only at steeper slopes wood ants may show a similar behavior like desert ants. Second, another study showed for *Formica pratensis* and *Cataglyphis fortis* that "slope had only marginal influence on kinematic parameters"[229] if the effect of speed was removed. Thus, it should be unlikely that ants change the geometry of their supporting polygon on slopes, which would in turn affect the torque equations. Third, it could also be that the gaster tip, which often touches the ground in locomoting ants[230], changed the supporting polygon and helped them keep their center of gravity inside the extended geometric shape. Forth, the legs could counterbalance potentially destabilizing torques of the center of gravity (negative stability margin) by pulling on the substrate.

To take these four points into account, the case study in Section 2.2 will exemplify a detailed analysis for the three-feet contact duration of climbing *Cataglyphis* and *Formica* ants on a 60 degree upslope.

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[227] e.g., Endlein/Federle: On Heels and Toes: How Ants Climb with Adhesive Pads and Tarsal Friction Hair Arrays. (see n. 219, p. 38)

[228] Weihmann/Blickhan: Comparing inclined locomotion in a ground-living and a climbing ant species: sagittal plane kinematics. (see n. 225, p. 40).

[229] Seidl, T./Wehner, R.: Walking on inclines: how do desert ants monitor slope and step length, in: Frontiers in Zoology 2008.

[230] E.g., Weihmann/Blickhan: Comparing inclined locomotion in a ground-living and a climbing ant species: sagittal plane kinematics. (see n. 225, p. 40); Reinhardt, L./Weihmann, T./Blickhan, R.: Dynamics and kinematics of ant locomotion: do wood ants climb on level surfaces?, in: Journal of Experimental Biology 2009

In summary, to evaluate the combined effects of the supporting geometry, the body height and the contact forces on the tip-over prevention behavior in ants, the second working hypothesis is proposed in the following way: If the vertical projection of the center of gravity moves out of the supporting polygon, torques of the legs with respect to the critical tipping axis counterbalance the ants to prevent a tipping over (toppling).

1.4.4 How do cockroaches self-right from an upside-down orientation?

In the preceding section about climbing ants, I suggested classifying their tip-over prevention behaviors into a geometric and an adhesion strategy. Within this section, I justify looking into a related problem which occurs when the animals cannot balance their posture, turn over and end up in an upside-down orientation: From such a vulnerable situation they must turn back to survive. Relying only on passive roll backs induced by external forces from, for instance, wind and gravity, and optimized (monostatic) rigid shapes such as turtle shells[231], may not be as reliable and fast as active self-righting strategies. Thus, the majority of animals should be capable of initiating a roll back on various ground properties with their own actions. One aim of this introduction and the article in Section 2.3 is to exemplify how such diverse self-righting strategies may be classified and described with the help of potential energy landscape models.

From forces and torques to energy landscapes

Tip-over prevention behaviors aim to *stabilize* an (intended) posture. To self-right in contrast, the animals have to *destabilize* an unintended (upside-down) posture. If the equilibrium of such an inverted posture is critical, a small perturbation may suffice to ease the self-righting process. However, if the unintended posture is in stable equilibrium, the animals have to overcome (gravitational) potential energy barrier(s).

With respect to the preceding section about tip-over prevention behaviors, there are again basically two ways for the animals to handle their undesired upside-down situation: They may modify the energy barrier by changing their shape (geometric strategy), they may invest in and harvest their kinetic energy (dynamic strategy), or of course, they may combine the both strategies.

Since many animals are capable of changing their shape through relative motions of their segments (e.g., bending or twisting), they may first shift their center of gravity with respect to their supporting base. This in turn changes the torque equations which could already suffice to initiate tipping and subsequently a rolling

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[231] Domokos, G./Várkonyi, P. L.: Geometry and self-righting of turtles, in: Proceedings of the Royal Society B: Biological Sciences 2008.

motion (wandering tipping axis) to self-right. Moreover, if such a relocation of the center of gravity through shape changes does not actuate an ongoing self-righting action, it is likely to affect their minimum tilt angle and thus their (intrinsic) potential energy barrier (or their potential energy landscape for considering the three-dimensional shape of the animals). Subsequently, a relatively small force or torque acting on the animal should be enough to lift their center of gravity over the remaining height in their energy landscape and initiate a rolling back into an upside-up orientation (dynamic strategy).

Goals of the study

Several studies[232] indeed showed that animals use their appendages (e.g., legs, wings, tail, antennae) and their head to push, pull, grasp, pivot or to jump, and/or deformed their body to self-right. However, little is known of the success rate and the duration of the self-righting process with respect to the two proposed strategies. To study this, the following characteristics of three cockroach species, the wingless Madagascar hissing cockroach *Gromphadorhina portentosa* SCHAUM 1853, the American cockroach *Periplaneta americana* LINNAEUS 1758, and the discoid cockroach *Blaberus discoidalis* AUDINET-SERVILLE 1839, will be quantified and compared.

First, the self-righting performance will be determined based on the number of attempts to succeed, the self-righting probability for a successful first attempt, the total self-righting time and the self-righting time on the first attempt (Figure 3, Section 2.3). Second, the probability for employing a dynamic strategy will be quantified by observing whether the animals are still moving upwards despite a stop in pushing against the ground by body parts which are used for the self-righting action (Figure 5, Section 2.3). Third, locomotor transition ethograms will visualize the intra-individual diversity of righting behaviors, their transition probabilities and in particular the employment of their appendages versus shape-changing strategies (Figure 7, Section 2.3). Forth, with the help of morphological and kinematic measurements, the paths of the successful and failed self-righting strategies will be visualized in shape-specific potential energy landscapes for each cockroach species (Figure 7, Section 2.3).

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[232] See Introduction in section 2.3 for elaboration and literature review.

2 Research Articles

2.1 Propulsion in hexapod locomotion: How do desert ants traverse slopes?

The main goal of this study was to quantify the principal driving and braking set of leg in climbing Hexapoda. To study this, a working hypothesis was worked out based on a literature review (Section 1.4.2), which claims that desert ants utilize the legs above the center of gravity as the main drive on inclined slopes (highest positive impulse among the three leg pairs) and the legs below the center of gravity as the main brake on declined slopes (highest negative impulse among the three leg pairs). The research article was published with the title "Propulsion in hexapod locomotion: How do desert ants traverse slopes" on the 1st of May 2017 in the *Journal of Experimental Biology* by the authors T. Wöhrl, L. Reinhardt, and R. Blickhan.[233] The data and code for the figures in this article are archived on the Dryad Digital Repository.[234]

By measuring the ground reaction forces of single ant legs over time while the ants were freely walking, the calculation of the leg impulses, and the kinematic tracing of various points of interest on the ant's body, it was first found that the hindlimbs function as the primary brake on steep 60 deg declined slopes whereas the forelimbs function as the primary drive on steep 60 deg inclined slopes. Thus, the working hypothesis can be approved. From this can be concluded that the tarsi of the front legs could act as the main suspension point of the supporting tripod on the steep upslope, and that the tarsi of the hind legs could act as the main suspension point on the steep downslope, to prevent a downswing of the ants in the case of an unintended slipping.

Second, it was further found out that the normalized double support durations were prolonged on steep slopes, and discussed that this could enhance the effect of lateral shear loading between left and right legs with the presence of direction-dependent attachment structures.

Third, a transition from walking at moderate 30 deg inclined and declined slopes to climbing at steep 60 deg inclined and declined slopes was identified, whereby the legs above the center of gravity changed from pushing away from the midline (laterally outwards) to pulling towards the midline (laterally inwards). It was discussed that this notable directional change in the lateral ground reaction forces between the moderate and steep slopes occurred through the utilization of different coordination programs in the extensor – flexor system and incorporates the advantages of direction-dependent attachment structures.

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[233] doi:10.1242/jeb.137505

[234] doi:10.5061/dryad.j4594

Finally, pulling in the normal direction to the substrate (adhesion) was negligible and could not sufficiently be distinguished from a zero line. This inspired us to look into the tipping and righting moments of the center of gravity and the legs with respect to the critical tipping axis which has led to the successive research article about strategies of two ant species to prevent toppling on inclines.

I contributed to the article *Propulsion in hexapod locomotion: How do desert ants traverse slopes* mainly by performing the experiments, by curating, analyzing, synthesizing, and visualizing the data, and by writing the original draft, as well as its reviewing and editing.

The article has been published with the "Green Open Access options"[235] of the *Journal of Experimental Biology*, which include literally:

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[236] `https://journals.biologists.com/jeb/article/220/9/1618/19604/Propulsion-in-hexapod-locomotion-how-do-desert` (visited on 03/14/2022)

[237] `https://journals.biologists.com/jeb/pages/rights-permissions` (visited on 03/14/2022)

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RESEARCH ARTICLE

Propulsion in hexapod locomotion: how do desert ants traverse slopes?

Toni Wöhrl*, Lars Reinhardt and Reinhard Blickhan

ABSTRACT

The employment of an alternating tripod gait to traverse uneven terrains is a common characteristic shared among many Hexapoda. Because this could be one specific cause for their ecological success, we examined the alternating tripod gait of the desert ant *Cataglyphis fortis* together with their ground reaction forces and weight-specific leg impulses for level locomotion and on moderate (±30 deg) and steep (±60 deg) slopes in order to understand mechanical functions of individual legs during inclined locomotion. There were three main findings from the experimental data. (1) The hind legs acted as the main brake (negative weight-specific impulse in the direction of progression) on both the moderate and steep downslopes while the front legs became the main motor (positive weight-specific impulse in the direction of progression) on the steep upslope. In both cases, the primary motor or brake was found to be above the centre of mass. (2) Normalised double support durations were prolonged on steep slopes, which could enhance the effect of lateral shear loading between left and right legs with the presence of direction-dependent attachment structures. (3) The notable directional change in the lateral ground reaction forces between the moderate and steep slopes implied the utilisation of different coordination programs in the extensor–flexor system.

KEY WORDS: Alternating tripod gait, Attachment, Ground reaction force, Impulse, Navigation, Stability

INTRODUCTION

Ants possess a large set of motor skills, such as moving within confined spaces in the soil (Gravish et al., 2013), traversing slopes (Seidl and Wehner, 2008; Weihmann and Blickhan, 2009), climbing (Endlein and Federle, 2015), swimming (Bohn et al., 2012) and even gliding (Yanoviak et al., 2005). Despite their wide range of body masses, which varies approximately from 0.008 mg (Kaspari and Weiser, 1999) to 480 mg (Linsenmair and Pfeiffer, 1998), ants as a family have adopted a common motion system that enables the lightest species to manoeuvre in a surface-dominated micro-environment where molecular forces predominate, and the heaviest species to prevail in a volume-dominated macro-environment where gravitational forces exceed molecular forces (Went, 1968).

One of the primary characteristics of their motion system is the alternating tripod gait, which was identified to be a relatively robust locomotion pattern for Hexapoda in different settings (e.g. Seidl and Wehner, 2008; Wahl et al., 2015; Zollikofer, 1994a,b,c) and probably helped them to inhabit various habitats. Because traversing slopes and climbing belong to the very basic routine of many worker ants, previous studies have already described either their kinematics over different inclines or their kinematics and forces for level locomotion and vertical climbing. For example, a kinematic study on desert ants found that the ground contact durations changed with the inclination of the slope, whereas the positioning of the legs was independent of the slope (Seidl and Wehner, 2008). Other studies have combined kinematics and forces and observed that wood ants and other hexapods such as cockroaches and stick insects pushed with both their front and hind legs for level locomotion (Cruse, 1976; Full et al., 1991; Reinhardt and Blickhan, 2014a), and identified the influence of surface on interactions between (pre)tarsal structures of weaver ants for level locomotion (Endlein and Federle, 2008). A separate study on vertically climbing weaver ants on a smooth surface found that the legs above the centre of mass (CoM) mainly held their body weight (Endlein and Federle, 2015). In order to overcome gravity and climb upward, their front legs used more pulling forces than the pushing forces of the hind legs in the fore-aft direction, while in climbing downward, their hind legs used more pulling forces than the pushing forces of the front legs. It was then concluded that weaver ants mainly utilised the distal-located arolia for pulling and the more proximally located third and fourth tarsomeres for pushing (Endlein and Federle, 2015).

A modelling study for a three-point climber with cockroach geometry has predicted that the slope angle for the push-pull transition of the front legs in the normal direction of the substrate could be increased from around 40 to 70 deg by lowering the relative height (body height per body length) from 0.2 to 0.1 (Günther and Weihmann, 2012). However, the transition between the pushing of the front and hind legs on level locomotion and the pulling by legs above the CoM on vertical climbing has not yet been supported with experimental data for any kind of hexapod. Therefore, the present study firstly examined the changes in the alternating tripod gait and ground reaction forces (GRF) of *Cataglyphis fortis* (Forel 1902) on different slopes to describe the kinematics and forces of ants during inclined locomotion.

In addition, we calculated the weight-specific leg impulses, which are the integrals of GRF over the time of foot contacts normalised by the body weight for each leg and direction, to determine the impact of individual legs on propulsion and load over stride cycles. While kinematic and GRF data can identify leg actions such as pulling (GRF vector points from the tarsi away from the CoM) and pushing (GRF vector points from the tarsi towards the CoM) at every point of time, they might not be sufficient to determine which pair of legs pulls or pushes the animals the most within one stride cycle in multi-legged locomotion. This is because one leg could generate relatively high force peaks for a short time (high average force), but its pulling or pushing impact on propulsion and load could still be less than the other leg if the latter had lower forces for a longer time (low average force). In such cases,

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List of symbols and abbreviations

BW	body weight
CoM	centre of mass
GRF	ground reaction force
i	slope i={(±60 deg, steep), (±30 deg, moderate), (0 deg, level locomotion)}
J_{lk}	weight-specific leg impulse $J_{lk}=(m\boldsymbol{g})^{-1}\cdot F_{lk}(t)\mathrm{d}t$ [GRF F_{lk} integrated over the time of foot contact for each leg and direction divided by body weight (body mass m times the local acceleration of free fall $\boldsymbol{g}$=9.81 m s^{-2})]
k	direction k={(x, fore–aft, direction of progression), (y, lateral, left–right), (z, normal to the substrate)}
l	leg number l={(1, front), (2, middle), (3, hind)}
t_{ll}	normalised double support duration for each leg pair from the touchdown of one tripod composition (left front leg L1, right middle leg R2, left hind leg L3) to the subsequent lift-off of the other tripod composition (R1, L2, R3) normalised by the stride duration of the middle legs

calculating the weight-specific leg impulses becomes crucial in pinpointing mechanical functions of individual legs, where a positive weight-specific impulse in the direction of progression (fore–aft) indicates the function of a motor, and a negative weight-specific impulse indicates the function of a brake.

Thus, in order to study mechanical functions of individual hexapod legs over inclined locomotion, the present study has focused on how the alternating tripod gait, the GRF and the weight-specific leg impulses of the desert ant *C. fortis* changed on different slopes. Because the load carrying functions of the leg pairs have been studied for vertical climbing weaver ants on a smooth surface (Endlein and Federle, 2015), where the front legs used more pulling forces in climbing upward and the hind legs used more pulling forces in climbing downward, it was hypothesised that for the transition between level locomotion and vertical climbing, the front legs of *C. fortis* would exert pulling forces as the dominant motor on upslopes whereas the hind legs would exert pulling forces as the dominant brake on downslopes.

MATERIALS AND METHODS

Animals

A *C. fortis* colony with more than 600 ants from Tunisia near Menzel Chaker was housed in a formicarium. A 60 W daylight lamp was installed to illuminate one half of the formicarium from 07:00 h to 19:00 h. The temperature of the formicarium was kept at around 28°C. The ants were fed with honey, water and insects *ad libitum*. The experiments were performed between October 2012 and March 2013 at Friedrich Schiller University Jena.

Data acquisition

We used the same experimental setup and procedure as previously published by our work group (Reinhardt and Blickhan, 2014a,b). For each set of measurements, one ant was randomly taken from the formicarium with a plastic tube (diameter 12 mm, length 150 mm) and repeatedly placed at the start of a 90 mm long running track. The running track was covered with graph paper and confined to a width of 25 mm and a height of 30 mm.

A custom-built three-dimensional 4×4 mm force platform with resolvable forces F_x=5.4 µN, F_y=2.9 µN and F_z=10.8 µN (Reinhardt and Blickhan, 2014b) was fixed in the middle of the track and also covered with graph paper. It was designed based on PVC/semiconductor strain gauges KSP-3-120-F2-11 (Kyowa, Tokyo, Japan) and used to record the GRF of single steps of the moving ants. The signals received by the force platform were amplified by a data acquisition system (MGCplus, Hottinger Baldwin Messtechnik, Darmstadt, Germany) and collected by a computer with a sampling frequency of 1200 Hz. The natural frequencies of the force platform with the graph paper attached were measured to be f_x=380 Hz, f_y=279 Hz and f_z=201 Hz. The force data could not be used to identify the dragging length because the dragging forces were smaller than the resolvable forces and the ants could drag their legs off the force platform.

A Photron Fastcam SA3 (San Diego, CA, USA) camera with a frequency of 500 Hz was used to record the dorsal view of the ants. The sagittal view was captured by the same camera objective via glass prisms functioning as a 45 deg mirror. MATLAB R20015b (The MathWorks, Natick, MA, USA) and DigitizingTools 20160711 (Hedrick, 2008) were used for motion tracking.

The body masses of the ants were measured with a precision scale (±0.1 mg, ABS 80-4, Kern & Sohn, Germany) directly after each single leg force signal was recorded. After each set of measurements, the investigated ant was isolated in a separate box and only placed back into the formicarium at the end of every measurement day.

Data selection

A total of 893 trials with GRF measurements and video sequences were recorded. In the first round of data screening, we excluded trials in which the ants stopped, changed direction or touched the force platform with their gasters. Trials in which the ants dragged their hind legs were not excluded from the dataset.

Subsequently, we took the first 15 force and kinematic measurements for each set of legs (front legs, middle legs, hind legs) and slope (steep=±60 deg, moderate=±30, level locomotion=0 deg) for further data analysis. Altogether, 225 different strides from 225 different runs were selected.

Data analysis

MATLAB 8.6.0 R20015b and R 3.3.1 (R Foundation for Statistical Computing, Vienna, Austria) were used for data analysis. Petiole and tarsi trajectories and the GRF were calculated over one stride cycle, i.e. consecutive touchdowns of the same leg, and adjusted to the average direction of progression through rotational transformation in the frontal x–y plane. The force signals were smoothed with a Savitzky–Golay filter of polynomial order 0 and frame length 5. All signals were normalised to the body weight and the mean stepping pattern for every slope (45 strides per slope). The GRF are given as arithmetic means and standard deviations unless stated otherwise.

The GRF signals were extrapolated with the assumptions that: (1) the GRF did not change over multiple stride cycles, i.e. straight locomotion and constant speed; and (2) left and right leg GRF were mirrored in the lateral direction and equal in the normal and fore–aft direction, i.e. bilateral symmetry of GRF and tripod symmetry of the ant body. As a result, the GRF signals were periodic.

The weight-specific leg impulses were approximated numerically using the trapezoidal sum method with partitions of equal size Δt=1200^{-1} s of the GRF over the whole ground contact duration.

The Wilcoxon rank sum test with Bonferroni correction was used to compare the measurements.

RESULTS

Actuation on upslopes

On the moderate upslope, the primary motors of *C. fortis* (Fig. 1A, Table 1) were found to be the middle and hind legs as J_{1x}(30 deg) <J_{2x}(30 deg) and J_{1x}(30 deg)<J_{3x}(30 deg), where J is the weight-

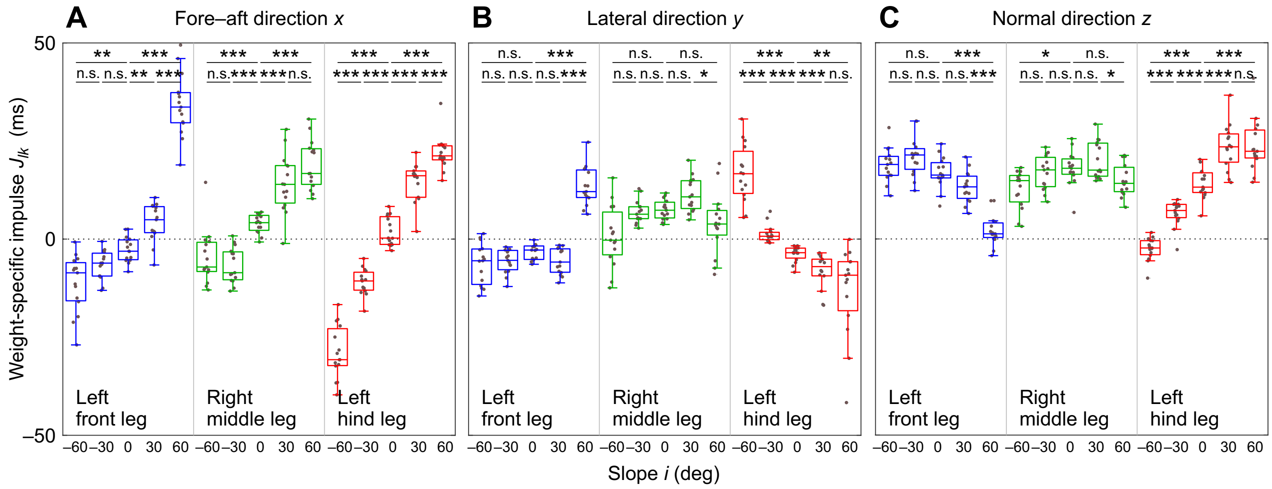

Fig. 1. Weight-specific leg impulses of *Cataglypis fortis* at different slopes. Results are grouped by the direction of the impulses [(A) fore–aft; (B) lateral; (C) normal] and by the type of leg (front, middle and hind leg). The central lines of the Tukey boxplots are the medians and the edges of the boxes are the 25th and 75th percentiles (N=15 strides for each subset). Asterisks indicate significant differences between slopes (*P≤0.05; **P≤0.01; ***P≤0.001; n.s., not significant; two-sided Wilcoxon rank sum test with Bonferroni correction).

specific leg impulse (both P<0.001). Pushing forces by the hind legs dominated over pulling forces by the front legs, where the CoM was mostly above the tarsi (Fig. 2D). On the steep upslope, the primary motor became the front legs as J_{1x}(60 deg)>J_{2x}(60 deg) and J_{1x}(60 deg)>J_{3x}(60 deg) (both P<0.001). Pulling forces by the front legs above the CoM dominated over pushing forces by the hind legs below the CoM (Fig. 2E). The front legs exhibited the highest amplitude of the mean GRF at approximately F_{1x}(60 deg)≈0.5 BW≈120 µN (Fig. 3A).

In the sagittal view (x–z plane), the mean GRF vectors of the hind legs pointed along the tibia axis towards the gaster on both the moderate and steep upslopes (Fig. 2D,E). In the dorsal view (x–y plane), they pointed into the area of the supporting tripod towards the CoM, whereas front and middle leg GRF vectors pointed out of the supporting tripod frame. All legs pushed outwards on the moderate upslope (Fig. 2D), but a directional change in the lateral GRF occurred for the front legs on the steep upslope as they started pulling inwards (Fig. 2E). The GRF standard deviations

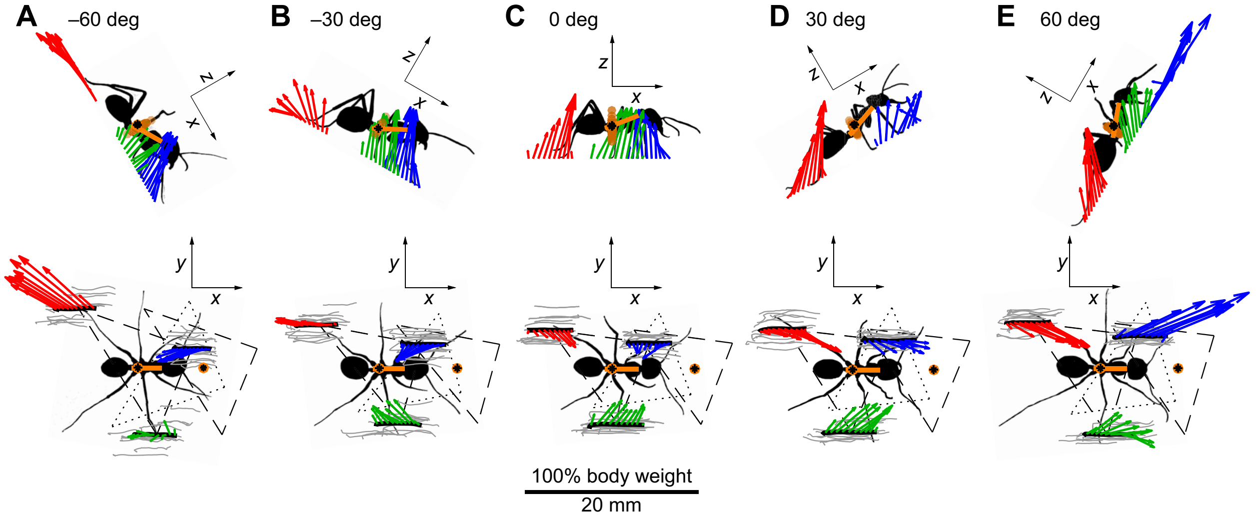

Fig. 2. Mean ground reaction force (GRF) vectors of *C. fortis* with mean stepping patterns at different slopes. (A) Steep downslope; (B) moderate downslope; (C) level locomotion; (D) moderate upslope; and (E) steep upslope. The direction of progression x is from left to right. Blue, green and red arrows indicate the mean GRF vectors of left front leg, right middle leg and left hind leg, respectively. GRF and tarsus trajectories are plotted in the sagittal (x–z plane) and dorsal views (x–y plane) in body-fixed coordinate systems with the origins in the centres of mass (CoM). The solid grey/black lines in the x–y plane represent the measured/mean tarsus trajectories during the ground contacts from touchdowns to lift-offs (tarsus motions from right to left). The dashed and dotted black triangles represent the mean area of the supporting tripods during the mean temporal mid-stance of the right and left middle legs, respectively. The orange lines in the x–z plane show the mean thorax length and orientation. The black asterisks represent the locations of the CoM, which were calculated near the thorax–petiole joint at 20% of the thorax length (McMeeking et al., 2012). The distance between the two asterisks represents the mean displacement of the ants for one stride cycle. The black contours represent individual sample ants on respective slopes during the temporal mid-stances of the right middle leg. All means were calculated from 15 strides per leg pair and slope, resulting in 225 strides in total.

Table 1. Inter-leg comparisons of the weight-specific leg impulses

Slope (deg)	k	N	N_m	N_d	N_1; N_2; N_3	$J_{1k} \overset{H_0}{=} J_{2k}$	$J_{1k} \overset{H_0}{=} J_{3k}$	$J_{2k} \overset{H_0}{=} J_{3k}$
–60	x	45	29	9	≤13; ≤9; ≤9	n.s.	***	***
	y	45	29	9	≤13; ≤9; ≤9	*	***	***
	z	45	29	9	≤13; ≤9; ≤9	**	***	***
–30	x	45	32	16	≤14; ≤10; ≤14	n.s.	**	*
	y	45	32	16	≤14; ≤10; ≤14	***	***	***
	z	45	32	16	≤14; ≤10; ≤14	n.s.	***	***
0	x	45	31	13	≤12; ≤9; ≤12	***	**	n.s.
	y	45	31	13	≤12; ≤9; ≤12	***	n.s.	***
	z	45	31	13	≤12; ≤9; ≤12	n.s.	n.s.	*
30	x	45	30	19	≤13; ≤12; ≤15	***	***	n.s.
	y	45	30	19	≤13; ≤12; ≤15	***	n.s.	***
	z	45	30	19	≤13; ≤12; ≤15	***	***	n.s.
60	x	45	25	8	≤10; ≤6; ≤8	***	***	n.s.
	y	45	25	8	≤10; ≤6; ≤8	***	***	***
	z	45	25	8	≤10; ≤6; ≤8	***	***	***

Tested with the two-sided Wilcoxon rank sum test with Bonferroni correction (N=15 strides for each subset). k: direction; N: number of different strides; N_m: number of unique masses ($\Delta m \geq 0.1$ mg); N_d: number of measurement days; N_1; N_2; N_3: number of different individuals for front, middle and hind leg measurements (individuals per nest ≥600). Asterisks indicate significant differences between weight-specific impulses (*$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$; n.s., not significant).

were observed to increase on the steep slopes for all leg pairs (Fig. 3A).

The shapes of the GRF over time changed remarkably from the moderate to steep upslope for the front and hind legs in the normal direction. Whereas front leg GRF diminished on the steep upslope, hind leg GRF changed from a triangular shape on the moderate upslope to a trapezoidal shape with longer double support durations on the steep upslope.

Braking on downslopes

Hind legs were used as the primary braking unit for both the moderate and steep downslopes as $J_{3x}(–30\ \mathrm{deg})<J_{2x}(–30\ \mathrm{deg})<0$ ($P<0.05$), $J_{3x}(–30\ \mathrm{deg})<J_{1x}(–30\ \mathrm{deg})<0$ ($P<0.01$), $J_{3x}(–60\ \mathrm{deg})<J_{2x}(–60\ \mathrm{deg})<0$ ($P<0.001$) and $J_{3x}(–60\ \mathrm{deg})<J_{1x}(–60\ \mathrm{deg})<0$ ($P<0.001$) (Fig. 1A, Table 1). Pulling forces by the hind legs above the CoM dominated over pushing forces by the front and middle legs below the CoM (Fig. 2A,B). The hind legs on the steep downslope had the strongest mean GRF at approximately $F_{3x}(–60\ \mathrm{deg})\approx–0.5\ \mathrm{BW}\approx–120\ \mu\mathrm{N}$ (Fig. 3A).

In the sagittal view, braking forces of the front legs pointed along the tibia axis towards the head (Fig. 2A,B). In the dorsal view, they pointed into the area of the supporting tripod towards the thorax.

Similar to the shift in direction in the lateral GRF of the front legs on the steep upslope, the hind legs started pulling strongly inwards on the steep downslope (Figs 1A, 2A).

Direction dependency

A comparison of impulses on the steep upslope against the steep downslope for the same leg pair revealed that front legs pulled more strongly on the steep upslope than they pushed on the steep downslope (Fig. 1A) as $|J_{1x}(60\ \mathrm{deg})|>|J_{1x}(–60\ \mathrm{deg})|$ ($P<0.001$). Similarly, hind leg pulling impulses were stronger on the steep downslope than pushing impulses on the steep upslope as $|J_{3x}(–60\ \mathrm{deg})|>|J_{3x}(60\ \mathrm{deg})|$ ($P<0.05$).

Front–hind leg symmetry

The GRF vectors of the front legs on upslopes (Fig. 4, dark blue arrows) were compared against those of the hind legs on downslopes (light red arrows). At the same time, the GRF vectors of the front legs on downslopes (light blue arrows) were also compared against those of the hind legs on upslopes (dark red arrows). Even though the starting points of the GRF vectors were more distal for the hind legs than for the front legs, it was observed that the GRF vectors of the front legs on the steep upslope and those of the hind legs on the steep downslope (Fig. 4A,B) had similar magnitudes but opposite directions along the body (x) axis, and vice versa. Such symmetry was also evident on moderate slopes (Fig. 4C,D), although there was slight deviation in the direction of the GRF vectors of the hind legs in the lateral direction on the moderate downslope.

In the fore–aft direction, front and hind legs exhibited supportive mechanical functions during inclined locomotion as $\mathrm{sgn}[J_{1x}(i)]=\mathrm{sgn}[J_{3x}(i)]$ for $i=\{\pm60\ \mathrm{deg},\ \pm30\ \mathrm{deg}\}$ and contrary mechanical functions for level locomotion as $\mathrm{sgn}[J_{1x}(0\ \mathrm{deg})]\neq\mathrm{sgn}[J_{3x}(0\ \mathrm{deg})]$. While the distribution of the body weight in the normal direction was nearly equal for level locomotion among the three leg pairs, it was shifted mostly to the hind leg on the steep upslope and to the front and middle legs on the steep downslope (Figs 1C, 2A–E).

Dragging hind leg

The hind legs were dragged behind the ants in numerous measurements. In order to distinguish aerial phases from dragging, we set the maximum height of uncertainty to 0.4 mm, which was twice the magnitude of the measuring accuracy. The number of lift-offs was counted and the dragging length for each slope was calculated (Fig. 5A, Table 2). The median dragging length ranged from 2.2 mm (moderate upslope) to 5.6 mm (steep downslope) and constituted 26% to 82% of the step length depending on the slope. Most of the dragging across the whole swing phase occurred on the steep downslope, which was observed in 67% of all steep downslope strides.

Total GRF over time

In order to ensure the validity of the measurements, the total GRF over time was calculated for all six legs on all slopes (Table 3). In the ideal case, the total GRF in the normal direction should oscillate at

Table 2. Dragging hind leg measurements

Slope (deg)	Strides	N_{LO}	l_3 (mm)	d_3 (mm)	l_{3n} (%)	h_3 (mm)
–60	15	5	6.8	5.6	82	0.4
–30	15	12	7.8	2.8	36	0.8
0	15	12	9.2	3.2	35	1.0
30	15	13	8.6	2.2	26	1.0
60	15	12	8.5	4.6	54	1.4

N_{LO}: number of lift-offs; l_3: step length; d_3: dragging length; $l_{3n}=d_3l_3^{-1}$: normalised dragging length; h_3: tarsus lift height (median).

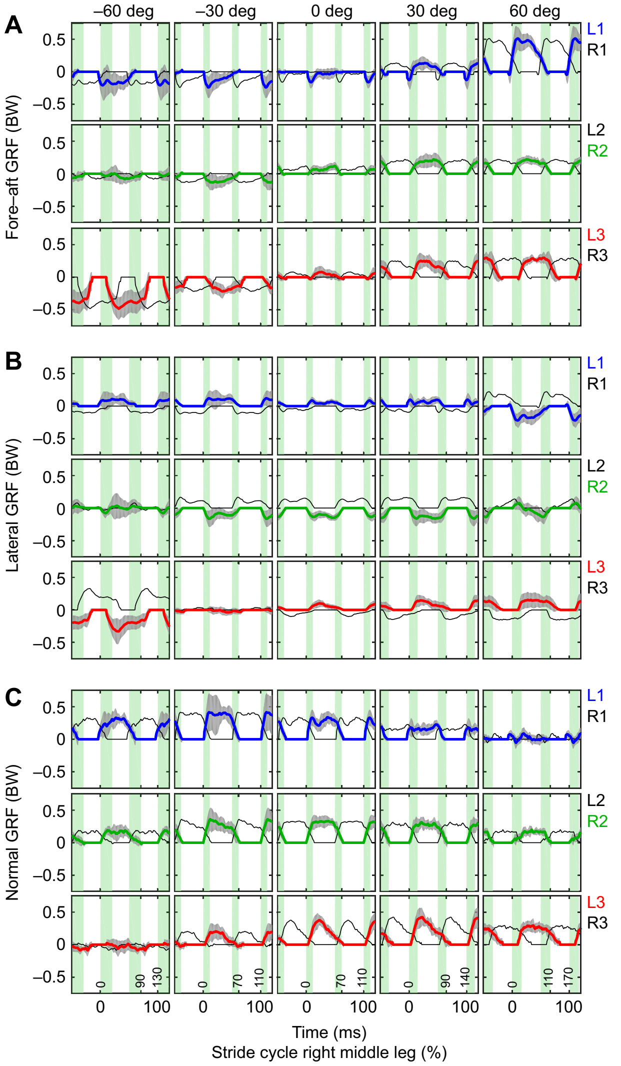

Fig. 3. GRF of *C. fortis* over time. (A) Fore–aft direction; (B) lateral direction; and (C) normal direction. Mean GRF with standard deviations (grey shaded areas) over time and percentage of the stride cycle of the middle legs (N=15 strides for each subset). The subplots are grouped by slope and leg pair (left front leg L1, right middle leg R2, left hind leg L3). The GRF signals are normalised to the mean stepping pattern of each slope (N=45 strides for each subset) and to the body weight (BW) (Table 3). The vertical green shaded areas mark the mean double support durations of the middle legs (Fig. 6).

around a mean of 1 BW for level locomotion, $\sqrt{3}\cdot 2^{-1}$ BW at ±30 deg slope, and 2^{-1} BW at ±60 deg slope. However, the calculated total GRF over multiple stride cycles was 0.03 BW (moderate downslope) to 0.10 BW (level locomotion) lower than the ideal case. This could be attributed to the dragging hind leg (Fig. 4, Table 2), which could have generated pulling or pushing forces during the dragging phase.

Kinematics

Temporal parameters such as ground contact duration and running speed were highly variable across all slopes (Table 4). For example, the standard deviations of the contact durations of the middle legs increased from 11 ms for level locomotion to 29 ms on the steep downslope. The mean speed ranged from 54±10 mm s^{-1} (steep upslope) to 87±17 mm s^{-1} (level locomotion). The duty factor of the middle legs lay between 62±9% (moderate downlsope) and 72±7% (steep downslope). The body height (CoM–substrate distance; Table 4, Fig. 5B) ranged from 2.4±0.4 mm (steep downslope) to 3.8±0.7 mm (level locomotion).

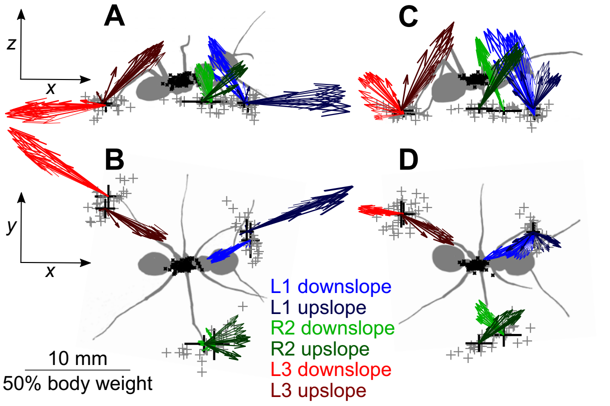

Fig. 4. Comparison of the mean GRF vectors on upslopes and downslopes in *C. fortis*. (A) Steep slopes, sagittal view; (B) steep slopes, dorsal view; (C) moderate slopes, sagittal view; and (D) moderate slopes, dorsal view. The mean GRF vectors (N=15 strides for each subset) are plotted in a space-fixed coordinate system for the left front legs (blue, L1), the right middle legs (green, R2) and the left hind legs (red, L3). Darker colours indicate the GRF on upslopes whereas lighter colours indicate the GRF on downslopes. The grey crosses represent the positions of the ground contacts of individual tarsi for all the strides (N=15 strides for each subset). The black crosses represent the mean positions with standard deviations of the grey crosses. The black dots illustrate the positions of petioles during temporal midstance of the right middle legs. The grey shaded contours represent sample ants during the temporal mid-stance of the right middle leg. The direction of progression is from left to right.

Touchdowns and lift-offs of the tripod composition occurred almost simultaneously on the moderate slopes and level locomotion. However, the tarsi of the left hind legs touched down and lifted off the ground later than the right middle legs and left front legs on the steep slopes, and vice versa (Fig. 3). The normalised double support durations (Fig. 6) increased significantly for the front (P<0.001) and hind legs (P<0.001) from level locomotion to the steep upslope and

Table 3. Mean of total GRF

Slope (deg)	*k*	Strides	BW (μN)	Mean total GRF (BW)	AE (BW)
–60	*x*	45	237±40	–0.77±0.10	–0.10±0.10
–60	*y*	45	237±40	0.00±0.13	0.00±0.13
–60	*z*	45	237±40	0.41±0.04	–0.09±0.04
–30	*x*	45	239±37	–0.45±0.08	–0.05±0.08
–30	*y*	45	239±37	0.00±0.02	0.00±0.02
–30	*z*	45	239±37	0.83±0.10	–0.03±0.10
0	*x*	45	249±35	0.06±0.08	0.06±0.08
0	*y*	45	249±35	0.00±0.02	0.00±0.02
0	*z*	45	249±35	0.90±0.08	–0.10±0.08
30	*x*	45	232±27	0.46±0.10	–0.04±0.10
30	*y*	45	232±27	0.00±0.05	0.00±0.05
30	*z*	45	232±27	0.79±0.07	–0.07±0.07
60	*x*	45	232±27	0.93±0.11	0.07±0.11
60	*y*	45	232±27	0.00±0.09	0.00±0.09
60	*z*	45	232±27	0.50±0.07	0.00±0.07

k: direction; BW: body weight; GRF: ground reaction force; AE: absolute error. Data are means±s.d.

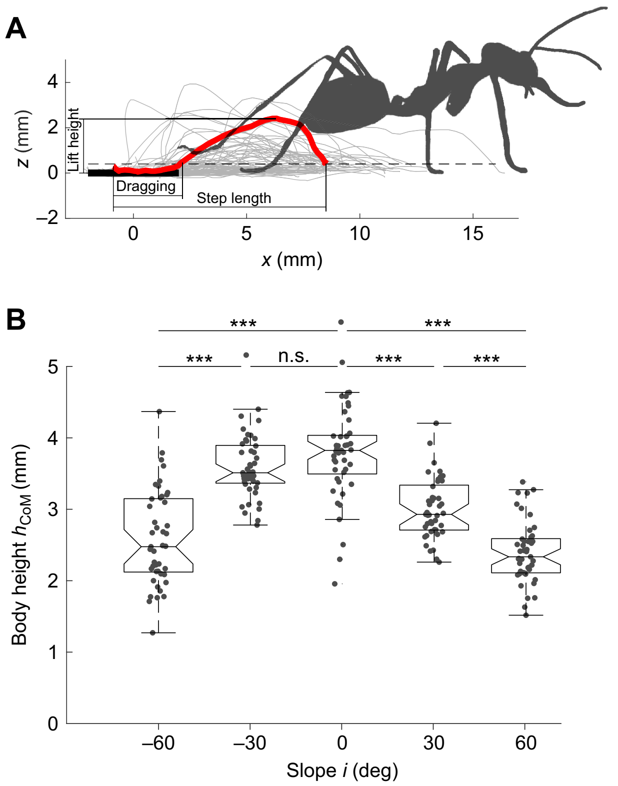

Fig. 5. Hind leg dragging and change of body height in *C. fortis*. (A) Dragging hind leg in the sagittal view. The dragging lengths are defined as the distances between the locations of touchdowns and the intersections of the hind leg tarsus trajectories (grey lines, N=75 strides) with the dashed horizontal line at twice the measurement accuracy z=2×0.2 mm. The red line highlights an example tarsus trajectory. The black bold horizontal line represents the location of the force plate. (B) Body height at different slopes. Body height was defined as the distance between the CoM and the substrate. The locations of the CoM were calculated near the thorax–petiole joint at 20% of the of the thorax length (McMeeking et al., 2012). Asterisks indicate significant differences between slopes (***$P \leq 0.001$; n.s., not significant; two-sided Wilcoxon rank sum test with Bonferroni correction; N=45 per subset).

Table 4. Kinematic parameters

Slope (deg)	t_{2s} (ms)	t_{2c} (ms)	t_{2d} (%)	v (mm s^{-1})	s (mm)	h_{CoM} (mm)
−60	128±30	93±29	72±7	64±25	7.7±1.9	2.6±0.7
−30	109±14	69±15	62±9	84±26	9.0±2.1	3.6±0.5
0	110±13	69±11	63±6	87±17	9.7±1.6	3.8±0.7
30	136±23	90±20	66±6	71±15	9.5±1.2	3.0±0.4
60	169±20	114±20	68±7	54±10	9.1±1.2	2.4±0.4

t_{2s}: stride duration of the middle legs; t_{2c}: contact duration of the middle legs; t_{2d}: duty factor of the middle legs; v: running speed; s: displacement of the CoM per stride; h_{CoM}: body height (CoM–substrate distance). Data are means±s.d.; N=45 strides for each subset.

for the middle legs from level locomotion to the steep slopes (P<0.01).

DISCUSSION

Motor and brake functions

Similar to the findings about vertically climbing weaver ants on a smooth surface, where a larger proportion of body weight was carried by the legs above the CoM (Endlein and Federle, 2015), our measurements showed that the front legs rose above the CoM and became the primary motor (positive weight-specific leg impulse in the direction of progression) on the steep upslope. The hind legs maintained their position above the CoM and kept their function as the primary braking leg pair (negative weight-specific leg impulse in the direction of progression) on both the moderate and steep downslopes. While the dominant braking function of the hind legs on downslopes corresponded with our hypothesis, the front legs did not act as the primary motor on the moderate upslope, probably because the tarsi did not rise above the CoM adequately (Fig. 2). Therefore, we deduced that the position of the tarsi relative to the CoM could be the main factor in determining the individual leg pairs as the primary motor or brake during inclined locomotion.

This suggested that the tarsi of the front legs could act as the main suspension point of the supporting tripod on the steep upslope and the tarsi of the hind legs could act as the main suspension point on downslopes. If the hind legs were used as the primary motor on the steep upslope, the main suspension point would be below the CoM, thereby causing instability. Further stability could be achieved by the dragging hind leg. Under risky situations such as moving down the steep slope where most of the dragging across the whole swing phase was observed, the dragging leg could form a temporary quadrangle configuration or hook onto protruding objects for abrupt braking.

Direction dependency and shear loading

The front and hind legs also showed direction-dependent GRF and weight-specific impulses. For the front legs, the fore–aft pulling impulses (motor function) on the steep upslope were higher than their pushing impulses (brake function) on the steep downslope. For the hind legs, the fore–aft pulling impulses (brake function) on the steep downslope were higher than their pushing impulses (motor function) on the steep upslope. In the lateral direction, the front legs changed from pushing outwards to pulling inwards from the moderate to the steep upslope, whereas the hind legs changed from

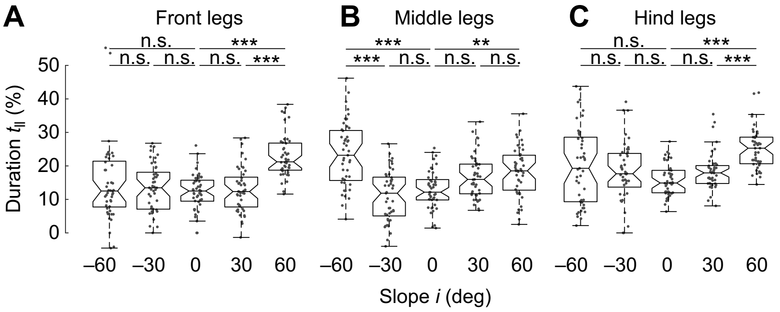

Fig. 6. Normalised double support durations for each leg pair at different slopes in *C. fortis*. The double support durations of the (A) front legs, (B) middle legs and (C) hind legs were normalised by the stride durations of the middle legs (N=45 strides for each subset). The central lines of the Tukey boxplots are the medians and the edges of the boxes are the 25th and 75th percentiles. Asterisks indicate significant differences between slopes (**$P \leq 0.01$; ***$P \leq 0.001$; n.s., not significant; two-sided Wilcoxon rank sum test with Bonferroni correction).

pushing outwards to pulling inwards from the moderate to the steep downslope.

Higher pulling forces over pushing forces were observed in other Hexapoda as well, including stick insects, cockroaches and ants (Bullock et al., 2008; Clemente and Federle, 2008; Endlein and Federle, 2015). Close examination of the silhouettes of the typical tarsus of *Cataglyphis*, hornets and weaver ants (Frantsevich and Gorb, 2004; Endlein and Federle, 2008) revealed that the claws of their front legs were curved against the direction of progression, but those of their hind legs were curved towards the direction of progression. As such, the action of pulling for both the front and hind legs would be able to help the ants interlock their claws better with the surface asperities of our substrate. This could be of special importance for *Cataglyphis* considering the granular surface of their desert habitat.

The presence of direction-dependent attachment structures could also enhance shear loading of the opposing tarsi of the ants. Just as shear loading of the opposing toes or legs enabled geckos to hang from the ceiling (Autumn, 2006) and spiders to make use of the collective effect of their hairy foot pads (Wohlfart et al., 2014), it could also help the ants to move on steep surfaces. The increase in the normalised durations of double support phases from level locomotion to steep slopes in the experiment implied that the forces in the lateral direction acted longer against each other on steep slopes (Fig. 3B). Thus, by changing their temporal gait kinematics, the ants could engage their opposing tarsal hair structures and probably adjust their whole-body adhesion force to move on steep surfaces.

Coordination and navigation

The changes in the weight-specific leg impulses as well as the changes of the magnitudes and directions of the GRF over time and different slopes could imply that the ants employed different coordination programs in their extensor–flexor system on different slopes. For example, the front legs switched from pushing to pulling laterally between the moderate and steep upslope, whereas the hind legs switched from pushing to pulling laterally between the moderate and steep downslope. This showed that the participating muscles and their interactions could have changed with the slope.

Such changes could further provide insights into the mechanisms behind hexapod navigation. *Cataglyphis* were found to employ odometry during inclined locomotion (Wittlinger et al., 2006; Wohlgemuth et al., 2001), and it has been suggested that both odometry and gravity perception could play a key role in their three-dimensional path integration. However, the primary receptors in gravity perception for *Formica,* the hair fields located on the body joints (Markl, 1962, 1974), were not necessary for path integration of *Cataglyphis* (Wittlinger et al., 2007), neither was the monitoring of the thorax–coxae joint angles. Instead, force sensors such as muscular strain sensors and campaniform sensilla could provide idiothetic cues for three-dimensional path integration (Seidl and Wehner, 2008). Such sense organs exhibited orientation-dependent directional sensitivity (Zill and Moran, 1981) and have been observed in other hexapods such as cockroaches (e.g. McIver, 1975; Moran et al., 1971; Pringle, 1938; Ridgel et al., 2000) and stick insects (e.g. Schmitz, 1993; Zill et al., 2013).

Even though we could not verify the involvement of proprioceptors in path integration directly from the results, it was clear that the strain on the attachment structures and leg segments has changed on different slopes because of the changes in the magnitudes and directions of the GRF. If similar patterns of GRF changes could be observed on a different substrate or with another ant species, it would be possible to hypothesise that ants triggered a relatively consistent motor program with respect to the angle of the slope, where the cuticular structures were affected more by the slope of the substrate than its roughness or stiffness. As such, the bending of leg segments or tarsi during inclined locomotion could probably be discussed together with odometry in three-dimensional path integration of *C. fortis*.

Conclusions

In the analysis of mechanical functions of the individual legs of desert ants on different slopes, our experimental data showed that the tarsi of the hind legs were above the CoM and acted as the main brake on both the moderate and steep downslopes, whereas the main motor changed from the middle and hind legs at the moderate upslope to the front legs at the steep upslope after the tarsi of the front legs rose above the CoM. This suggested that the need to maintain stability during inclined locomotion always constituted the shift of the main motor/brake towards the leg pair above the CoM. This finding varied slightly from our hypothesis about the mechanical function of the front legs, which we initially surmised to be the main motor on both the moderate and steep upslopes.

The increased double support durations on steep slopes probably enhanced shear loading of the opposing tarsal hair structures to ensure better adhesion on steep surfaces. In addition, the notable change of the weight-specific leg impulses from pushing laterally on the moderate slopes to pulling laterally on the steep slopes illustrated the flexibility of the extensor–flexor system, which could serve as another potential mechanism for the path integration of the desert ants.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
T.W. made substantial contributions to the execution and interpretation of the findings being published, as well as the drafting and revision of the article. L.R. and R.B. made substantial contributions to the design and execution of the findings being published.

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Data availability
Data are available from the Dryad Digital Repository (Wöhrl et al., 2017): http://dx.doi.org/10.5061/dryad.j4594.

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2.2 Comparative analysis of a geometric and an adhesive righting strategy against toppling in inclined hexapedal locomotion

The aim of this study was to quantify and evaluate how ants prevent tipping over by either changing their sprawled posture to adjust their body height and/or their supporting polygon (geometric strategy), or by pulling with their legs on the substrate (adhesion strategy), or both. To study this and to extend the established concept of the stability margin, the following working hypothesis was proposed: If the vertical projection of the center of gravity moves out of the supporting polygon, torques of the legs with respect to the critical tipping axis counterbalance the ants to prevent a tipping over (toppling).

The research article was published with the title “Comparative analysis of a geometric and an adhesive righting strategy against toppling in inclined hexapedal locomotion” on the 3rd of August in 2021 in the *Journal of Experimental Biology* by the authors Toni Wöhrl, Adrian Richter, Shihui Guo, Lars Reinhardt, Manuela Nowotny, and Reinhard Blickhan.[238] The data for the figures in this article have been archived on the Dryad Digital Repository[239] and the code and the electron micrographs have been uploaded to Zenodo[240] according to the recommended publisher guidelines.

Other than the first article which examined one species, the current article compares two species, the salt flat inhabiting desert ant *Cataglyphis fortis* with the mound dwelling European red wood ants of the *Formica rufa* species group.

It was first found that the desert ants avoid toppling during the three-feet stance on steep inclined slopes by a geometric strategy which helps them to move their center of gravity into the vertical projection of their supporting polygon. Second, the geometric changes in desert ants on the steep upslope compared to their level locomotion were caused by a significant lowering of the center of gravity *and* by a significant increase of the supporting area. Third, the desert ants did not generate notable leg righting torques. Fourth, compared to the desert ants the wood ants did not employ the geometric righting strategy. Fith, the wood ants neither changed their body height, nor their supporting area, implying that a potential stepping pattern change did not offset a possible change in the body height. Sixth, the wood ants counterbalanced their center of gravity torques with leg righting torques to prevent a tipping over on steep slopes (adhesive strategy). Last, the desert ants pushed with a significantly flatter hind-leg impulse substrate angle against the ground compared to the wood ants .

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[238] doi:10.1242/jeb.242677

[239] doi:10.5061/dryad.sbcc2fr6d

[240] doi:https://zenodo.org/record/5138459

It was discussed that the adhesive strategy enables the ants to traverse steeper slopes. This is because (adhesive) leg righting torques can hold against potentially higher center of gravity toppling torques on growing slopes (prevention of tipping over despite a negative stability margin) and the ability to generate adhesive forces with the front feet can facilitate potentially larger compressive forces on the hind feet. The latter one ensures that higher friction forces can prevent slipping on steep slopes.

I contributed to this article mainly by performing the experiments, by curating, analyzing, synthesizing, and visualizing the data, and by writing the original draft, its reviewing and editing.

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RESEARCH ARTICLE

Comparative analysis of a geometric and an adhesive righting strategy against toppling in inclined hexapedal locomotion

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ABSTRACT

Animals are known to exhibit different walking behaviors in hilly habitats. For instance, cats, rats, squirrels, tree frogs, desert iguana, stick insects and desert ants were observed to lower their body height when traversing slopes, whereas mound-dwelling iguanas and wood ants tend to maintain constant walking kinematics regardless of the slope. This paper aims to understand and classify these distinct behaviors into two different strategies against toppling for climbing animals by looking into two factors: (i) the torque of the center of gravity (CoG) with respect to the critical tipping axis, and (ii) the torque of the legs, which has the potential to counterbalance the CoG torque. Our comparative locomotion analysis on level locomotion and inclined locomotion exhibited that primarily only one of the proposed two strategies was chosen for each of our sample species, despite the fact that a combined strategy could have reduced the animal's risk of toppling over even more. We found that *Cataglyphis* desert ants (species *Cataglyphis fortis*) maintained their upright posture primarily through the adjustment of their CoG torque (geometric strategy), and *Formica* wood ants (species *Formica rufa*), controlled their posture primarily by exerting leg torques (adhesive strategy). We further provide hints that the geometric strategy employed by *Cataglyphis* could increase the risk of slipping on slopes as the leg-impulse substrate angle of *Cataglyphis* hindlegs was lower than that of *Formica* hindlegs. In contrast, the adhesion strategy employed by *Formica* front legs not only decreased the risk of toppling but also explained the steeper leg-impulse substrate angle of *Formica* hindlegs which should relate to more bending of the tarsal structures and therefore to more microscopic contact points, potentially reducing the risk of hindleg slipping.

KEY WORDS: *Formica*, *Cataglyphis*, Stability margin, Torque, Tipping axis, Slipping

INTRODUCTION

Terrestrial animals live in complex habitats. Consequently, many of them encounter situations where they may topple over and fall unintentionally. How they maintain their upright posture while traversing hilly habitats is therefore of particular interest in integrative biology and provides important insights with respect to the design of legged machines and physics-based computer animations.

The concept of the static stability margin SSM=min(d_1,d_2,…,d_n), which is defined as the minimum directed 'distance of the vertical projection of the center of gravity [CoG] to the boundaries of the support pattern in the horizontal plane' (Song, 1984), has been used to quantify the static stability for a slow walking animal with non-grasping feet (McGhee and Frank, 1968) (Fig. 1A). For a (quasi) statically stable gait, the vertical projection of the CoG is kept within the support pattern for a full gait cycle (SSM≥0) and the animal can move without toppling from one step to the next. When the vertical projection of the CoG moves out of the support base (SSM<0), a positive CoG torque emerges ($M_{\mathrm{CoG}}=\mathrm{SSM}\cdot F_{\mathrm{CoG}}$, where F_{CoG} is the body weight and has a negative value) and the animal has a tendency to topple over the critical tipping axis, which is the boundary of the support pattern nearest to the vertical projection of the CoG in the substrate plane (red line in Fig. 1A,B). A negative SSM (positive CoG torque) was observed to happen to load-carrying ants where the CoG was shifted (Merienne et al., 2020; Moll et al., 2013), and during high speeds in certain lizard species (Irschick and Jayne, 1999) and cockroaches (Full and Tu, 1991), where the animals changed their support patterns during level locomotion. Furthermore, it could also happen on steep slopes, where the distance between the vertical projection of the CoG and the support boundary diminishes (Song, 1984). Obviously, a negative SSM often does not oblige the real animals to fall while in motion. These led us to the question, how can the concept of the SSM be extended to quantify the anti-toppling behaviors of locomoting animals with grasping abilities?

A necessary condition for static stability in general is that the net torque is zero. The demand that the projection of the COG falls within the support pattern (positive SSM) is neither a sufficient nor a necessary stability criterion; the net torque can be zero if the SSM is negative or positive, provided that some feet produce a counterbalancing torque by 'pulling' or 'pushing' on the substrate. Furthermore, whereas a zero net torque can be expected for the ideal quiet stance at every point in time, it will most probably not be achieved for the legged locomotion of an animal, because it changes speed and direction, or the stepping pattern, and it moves under the influence of the gravitational pull and inertial effects. Therefore, to not tip over and fall while locomoting, the legged animal should compensate for a possible non-zero net torque with the passage of time to approach a zero integral of the net torque (angular momentum) over a stride. Such a postponed correction can be achieved, for instance, while touching down or lifting off legs, which in turn provides a new scenario of the support pattern, the forces and the torques to neutralize unintended velocity changes over time which otherwise may lead to toppling.

Thus, to describe how the animal avoids the tendency to topple over within different phases of the gait cycle, one must look at the sign and the magnitude of the CoG torque and the possibly countering leg torque about the critical tipping axis with the passage of time. For instance, the CoG torque changes permanently

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List of symbols and abbreviations

A	area of the support pattern
BW	body weight
CoG	center of gravity
d_n	vertically projected stability margins
F_{CoG}	gravitational pull on the specimen
$F_{lz'}$	ground reaction force of the front leg in the normal direction z'
GRF	ground reaction force
h	body height
$J_\perp$	time integral of the normal ground reaction force (impulse)
$J_\parallel$	time integral of the tangential ground reaction force (impulse)
M_{CoG}	quasi-static torque of the center of gravity about the critical tipping axis
M_{leg}	quasi-static torque of the front leg about the critical tipping axis
r_l	effective righting lever arm length of the front leg
SSM	vertically projected minimum static stability margin: $\min(d_1,d_2,\ldots,d_n)$
x	direction of progression in the horizontal plane
x'	direction of progression in the substrate plane
y	left–right direction
z	normal to the horizontal plane
z'	normal to the substrate plane
φ_3	impulse substrate angle of the hindlegs

because of the relative movement between the CoG and the tipping axes during the animal's legged locomotion, with a possible change of sign while crossing the boundary of the support pattern. Then, if not fully balanced by the countering leg or legs, the magnitude of the CoG torque increases and accelerates the animal with some curvature along the gravitational field lines. After calculating the sum of the CoG torque and the countering leg torque for some time interval or gait phase, one can evaluate whether the animal has the tendency to tip away from the support pattern, which we term toppling (positive net torque), or towards the support pattern, which we term righting (negative net torque). Thus, while in motion, the net torque can be non-zero for a certain interval of the gait cycle (functional tipping). If the animal stops, the net torque should indeed approach zero to prevent unintended tipping.

Despite the potential to classify different locomotion behaviors and to describe functions of the gait phases based on the subsequent torque analysis, to our knowledge neither the CoG torque about the critical tipping axis on slopes nor the possibly countering leg torque has yet been quantified for climbing animals. Therefore, we propose two major strategies to not topple over in climbing animals, based on the behavior of (i) avoiding positive CoG torques by changing the geometry (keeping the SSM positive) or (ii) engaging negative leg-righting torques by grasping feet. We compared level and climbing locomotion on a 60 deg upslope in the desert ants *Cataglyphis* Förster 1850 and the wood ants *Formica* Linnaeus 1758, as the results can be related to past inclined locomotion studies in ants (Seidl and Wehner, 2008; Weihmann and Blickhan, 2009; Wöhrl et al., 2017a).

Based on the definition of SSM, positive CoG torque on slopes can be avoided through geometric changes, such as posture changes, which shift the position of the CoG. Many animals have been found to lower their body height on inclines, such as cats (Carlson-Kuhta et al., 1998; Smith et al., 1998), rats and squirrels (Schmidt and Fischer, 2011), white tree frogs (Endlein et al., 2013), stick insects (Diederich et al., 2002), as well as desert iguanas (Jayne and Irschick, 1999) and the desert ants *Catalyptis fortis* (Weihmann and Blickhan, 2009; Wöhrl et al., 2017a). However, this behavior was not observed in mound-dwelling iguanas (Higham and Jayne, 2004) and the wood ants *Formica pratensis* (Weihmann and Blickhan, 2009).

Another possibility to improve SSM – or avoid a positive CoG torque – is through stepping pattern changes, which modify the geometry of the support pattern and thus the orientation or/and the number of tipping axes. Changes in the anterior and posterior extreme positions of the legs have been observed in Colorado potato beetles on wood panels (Pelletier and Caissie, 2001) and ants on granular media (Humeau et al., 2019) during sloped locomotion. However, neither *Cataglyphis fortis* nor *Formica pratensis* was observed to implement significant inclination-dependent changes of

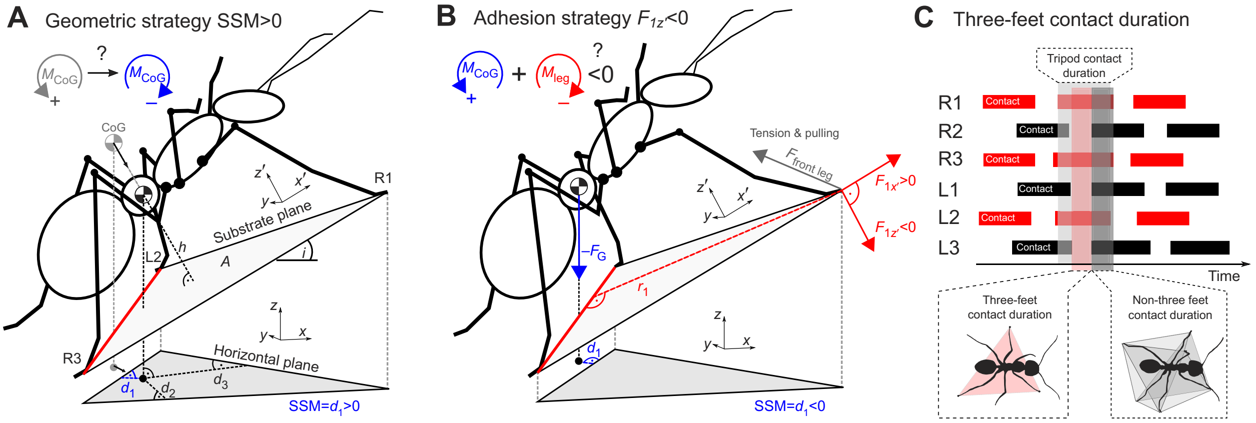

Fig. 1. Schematic illustration of an ant balancing on a slope of inclination *i* during the three-feet contact stance. d_1, d_2 and d_3 are static stability margins, or the distances between the vertical projections of the center of gravity (CoG) and the support pattern of the area A formed by the right front leg R1, the left middle leg L2 and the right hindleg R3 in the horizontal plane, whereas the shortest distance among them, d_1, is the minimum static stability margin (SSM). The support boundary nearest to the CoG is the critical tipping axis and is highlighted in red. (A) Geometric strategy: the vertical projection of the CoG remains within the support pattern (positive SSM) by changing the body height h and/or the supporting geometry. The resulting CoG torque M_{CoG} is negative and has a righting effect on the ant. (B) Adhesion strategy: the front leg pulls normally to the substrate with a negative ground reaction force (GRF) $F_{lz'}$ and the effective lever arm r_l to generate a negative leg torque $M_{\mathrm{leg}}=r_l{\cdot}F_{lz'}$ so as to counter the positive M_{CoG} and achieve a negative overall torque $M_{\mathrm{leg}}+M_{\mathrm{CoG}}<0$ (righting). (C) Three-feet contact duration: the duration highlighted by the vertical red bar, which is part of the tripod phase where only three feet are touching the ground simultaneously, is the focus of our present study.

the step length and footfall geometry with respect to the CoG on solid surfaces (Seidl and Wehner, 2008).

The destabilizing effect of the positive CoG toppling torques could be countered through strategy ii, the generation of negative leg-righting torques $M_{\mathrm{leg}}=r_l \cdot F_{lz'}$, where r_l is the effective lever arm length, or the shortest distance between the critical tipping axis and its opposing leg-surface contact point, and $F_{lz'}$ is the ground reaction force (GRF) of leg l in the normal direction to the substrate (see Fig. 1B for the front leg with l=1). This implies that at least three points are simultaneously touching the ground, that the support pattern has at least three sides, and that the feet have grasping abilities to employ adhesive forces. In the case of a triangular support pattern, only the leg which opposes the critical tipping axis can generate a leg torque about that axis, because the two remaining legs are forming the bearing for the critical tipping axis and have therefore no lever arm. Of course, the middle leg, for instance, can also employ leg torques about the line in the support plane that passes through the front leg and the hindleg and so forth. For a four-point contact scenario, the number of possible tipping axes increases accordingly, and the toppling analysis becomes even costlier. To evaluate the complete anti-toppling dynamics, one must measure the GRFs and the kinematics of each contact point over the full gait cycle. First, we could not achieve this with our current setup, because the forces of several legs could not be recorded simultaneously and independently. Second, for a three-point contact stance, this is not necessary if we are only interested in how toppling caused by the CoG can be avoided or countered.

Our proposed simplified version of this complex analysis extends the previous concept of the SSM sufficiently to distinguish between the two proposed strategies to avoid toppling: the (i) geometric strategy and the (ii) adhesive strategy. We exemplify our analysis on the simplest case, a triangular support pattern. First, to decide which leg torque should be considered for the further analysis, the identification of the critical tipping axis – which is the line where the animal would tip over, if the gravitational pull were the only force acting on the animal – must be identified. For instance, for a hexapod walking upslope along the gradient, the critical tipping axis for the three-point contact duration is most likely the axis between the hindleg and the middle leg and the countering leg would therefore be the front leg. It probably changes if the animal walks downwards or sidewards along the slope. Then, after calculating the quasi-static CoG torque and the countering leg torque for a fraction of time, one can evaluate, whether the animal has the tendency to employ the geometric strategy (i) by keeping the CoG torque negative (CoG righting), or the adhesive strategy (ii) by keeping the leg torques negative (leg righting).

During our previous study on the forces and impulses of ants (Wöhrl et al., 2017a), we found out that *Cataglyphis* did not employ notable pulling forces ($F_{lz'}<0$) normally to the substrate with their front legs on steep upslopes. This implies that *Cataglyphis* lacks the ability to generate negative leg torques to counter the possibly positive CoG torques and relies therefore on the geometric strategy. In contrast, if *Formica* could exert (adhesive) leg pulling forces, it is possible that *Formica* could generate sufficient negative leg torques to counterbalance the possibly positive CoG torques (adhesion strategy) without the need to adjust its body height or gait pattern. As the 'normal forces that prevent the foot from lifting' (Ramdya et al., 2017), adhesion mechanisms have been studied in a variety of animals such as geckos, frogs, beetles, stick insects, cockroaches, ants, spiders and mites (e.g. Endlein and Federle, 2015; Federle and Labonte, 2019; Gorb, 2008; Labonte and Federle, 2015), but they have not been used to calculate the leg torques with respect to the critical tipping axes. However, to evaluate the possible counterbalancing function of the legs, the leg torques must be quantified and contrasted to the CoG torques. We provide these data in our present study.

Previous observations (Seidl and Wehner, 2008; Weihmann and Blickhan, 2009) on the climbing behavior of desert and wood ants left a few open questions, which formed the basis for our present study. First, as certain animals in general, and *Cataglyphis* in particular, lower their body height on inclines (part of geometric strategy i), how effective is this strategy in helping it to achieve positive SSM (Fig. 1A)? A previous study discussed that *Cataglyphis* may hold its CoG inside the supporting polygon (Weihmann and Blickhan, 2009); however, actual quantification of the SSM is missing. Second, if *Formica* did not employ either of the geometric strategies (i), as suggested by the previous observations, does it experience positive CoG torques (negative SSM) on steep slopes, and if that is the case, does it counter the possibly positive CoG torques by employing negative leg torques (adhesive strategy ii)? To answer these questions, we analyzed the SSM, the height of the CoG, the effective lever arms, the area of the support pattern, the CoG and leg torques on level locomotion (control group) and on a 60 deg upslope for *Cataglyphis* and *Formica*. Finally, we examined and compared the tarsal structures of the legs to relate their morphological structures to their differing climbing strategies.

MATERIALS AND METHODS

Animals

Individual worker ants of the genus *Formica*, belonging to the *Formica* Linnaeus 1761 species group, were randomly collected from the outside area of their nest close to the village Golmsdorf (Germany) in autumn 2012. In total about 60 individuals were used for the measurements on level locomotion and the 60 deg upslope and sheltered in a formicarium with soil and materials from their natural habitat. The ants were released back into the field after the measurements. A colony of ants of the genus *Cataglyphis*, belonging to the species *Cataglyphis fortis* (Forel 1902) (identified using Wehner, 1983), from Menzel Chakar (Tunisia) with more than 600 ants, was borrowed from C. Bühlmann (Max Planck Institute for Chemical Ecology, Jena) from October 2012 to March 2013. Both ant species were fed with honey, water and insects *ad libitum*. One half of each formicarium was illuminated with a 60 W daylight lamp at around 28°C from 07:00 h to 19:00 h.

The two ant species in our measurements are comparable in body mass, size and temporal measures. The studied *Cataglyphis* ants (N=37) had a body mass of m=24.5±3.5 mg (mean±s.d.) and a thorax length (altitrunk including petiole) of l=3.9±0.3 mm, as compared with *Formica* ants (N=29), m=20.2±2.5 mg and l=3.6±0.2 mm. Of the analyzed *Cataglyphis* and *Formica* ants in our experiment, 97% walked by definition, as their mean duty factor of the front, middle and hindlegs was above 0.5.

Experimental setup

We used the same experimental setup and procedure for both ant species and conducted the experiments in our indoor laboratory between 2012 and 2013. Related data of the locomotion experiments and further details of the setup can be found in previous publications (Reinhardt and Blickhan, 2014a,b; Wöhrl et al., 2017a,b).

To carry out the experiments, an ant was randomly taken with a plastic tube and placed at the beginning of a 90 mm (length), 25 mm (width) and 30 mm (height) confined running track covered with ordinary millimeter paper. A three-dimensional 4×4 mm force platform was custom built in the center of the track and covered with the same millimeter paper. It used PVC/semiconductor strain gauges (KSP-3-120-F2-11, Kyowa, Tokyo, Japan) and resolved forces in the running direction F_x=5.4 µN, lateral direction F_y=2.9 µN and normal direction F_z=10.8 µN with natural frequencies of f_x=380 Hz, f_y=279 Hz and f_z=201 Hz (Reinhardt and Blickhan, 2014b). A data acquisition system (MGCplus, 1200 Hz, Hottinger Baldwin Messtechnik, Darmstadt, Germany) sampled the signals received by the force platform and amplified them.

One top-view Photron Fastcam SA3 (San Diego, CA, USA) captured the animals at 500 Hz dorsally and laterally through the right-angle glass prisms which were assembled at one side of the tunnel and functioned as mirrors. The kinematic data were obtained semi-automatically with DigitizingTools 20160711 (Hedrick, 2008) and MATLAB R2015b (The MathWorks, Natick, MA, USA). The body mass of each ant was measured with a precision scale (±0.1 mg, ABS 80-4, Kern & Sohn) immediately after it stepped on the force platform. The measured ants were kept separated from the ants in the formicaries and returned to the formicaries at the end of every daily series of measurements.

Data selection and analysis

In total, 753 individual leg force measurements of the two ant species on level locomotion and 60 deg upslope were recorded. In the first round of data screening, we excluded trials in which the ants stopped on the force plate or touched it with their gasters. As we could only measure the force of one leg from each run, the tipping behavior of the gait phase where more than three legs were touching the ground could not be analyzed. Therefore, we focused our analysis on the three-feet-only contact durations, which is not the same as the tripod duration (Fig. 1C), and excluded trials where no three-feet (only) contact stance was captured. As the ants were returned to the formicaries at the end of every measurement day, there was the chance of randomized pseudoreplications. To minimize bias by these pseudoreplications, we further reduced the dataset and chose only the first measurement per ant per leg per day for the force, torque and impulse data (detailed sample size statistics are given in Table 1) and maximum one measurement per ant per slope per day for the SSM data (sample size statistics are given in Table 2). However, a preceding study relativized the effects of possible pseudoreplications in force and kinematic measurements in *Formica* (Reinhardt and Blickhan, 2014a).

Table 1. Sample size statistics for individual leg force measurements on the 60 deg upslope

Species	Leg	*N*	*n*	*d*(*n*)
Cataglyphis	Front	>600	7	5
	Middle	>600	5	5
	Hind	>600	8	7
Formica	Front	>60	11	7
	Middle	>60	7	6
	Hind	>60	7	5

N, number of individual ants kept in one of the two formicaries; *n*, number of strides included in the force-related data, with a maximum of one stride per individual per day (maximum possible number of individual ants included in the statistics); *d*(*n*), number of measurement days covering the included stride measurements. One individual leg measurement was included if an ant did not stop during the force measurement, if it had not been measured successfully with the same leg on the same day before and if an alternating tripod gait with a three-feet-only contact duration of at least 8 ms could be detected.

Table 2. Sample size statistics for the geometric data of level and upslope locomotion

Species	Slope (deg)	*N*	*n*	*d*(*n*)
Cataglyphis	0	>600	25	13
	60	>600	11	8
Formica	0	>60	11	7
	60	>60	18	10

N, number of individual ants kept in one of the two formicaries; *n*, number of strides included in the static stability margin (SSM) data (subset of Table 1 with maximum one measurement per ant per slope per day); *d*(*n*), number of measurement days covering the included stride measurements.

The time series data of the measured ground reaction forces and calculated torques were time normalized with linear interpolation to the durations of the three-feet contacts. The mean three-feet contact duration on the 60 deg upslope was 15±9 ms for *Cataglyphis* and 24±7 ms for *Formica.*

As the slope-dependent changes of the gaster angle are relatively small for both ant species (Weihmann and Blickhan, 2009), the CoG was calculated according to previous studies at a distance of 20% of the thorax length cranially from the thorax–petiole joint for *Cataglyphis* (McMeeking et al., 2012) and 0.3 mm cranially from the same joint for *Formica* (Reinhardt and Blickhan, 2014a). The CoG and the support pattern formed by the three-feet contact were vertically projected into the horizontal plane to obtain the SSM (Figs 1 and 2).

MATLAB 9.6.0 R2019a and R 4.0.2 (http://www.R-project.org/) were used for data analysis. Estimation graphics (Ho et al., 2019) with median differences (Δ), 5000 bootstrap resampled distributions and bias-corrected 95% confidence intervals (CI) (R package dabestr v0.3.0) were used to quantify the total effect of slope or species.

Scanning electron microscope micrographs

One specimen of each species, *Cataglyphis fortis* and *Formica rufa*, was fixed in 70% ethanol. The legs were removed with fine forceps, dehydrated in a rising ethanol series (80%, 90%, 96%, 100%) and transferred to acetone for 1 h, with the acetone exchanged every 20 min. The samples were dried at the critical point in liquid CO_2 subsequently with an Emitech K 850 Critical Point Dryer (Sample Preparation Division, Quorum Technologies Ltd, Ashford, UK). The dried samples were glued on needles and sputter coated with gold in an Emitech K 500 (Sample Preparation Division, Quorum Technologies Ltd) and attached to a rotatable specimen holder (Pohl, 2010).

The scanning electron microscope (SEM) micrographs were taken with a Philips ESEM XL30 (Philips, Amsterdam, The Netherlands) equipped with Scandium FIVE software (Olympus, Münster, Germany). The SEM micrographs were assembled as an image plate using Adobe Photoshop® CS6 (Adobe System Incorporated, San Jose, CA, USA) and labeled in Adobe Illustrator® CS6 (Adobe Systems Incorporated).

RESULTS

Geometric strategy

To identify whether the ants employed the geometric strategy on steep upslopes, we first plotted the vertical projection of the CoG in relation to the support pattern and deduced the location of the critical tipping axis (Fig. 2A). For *Cataglyphis*, the vertical projections of the CoG fluctuated around the vertical projection of the critical tipping axis at the point in time where the SSM reached

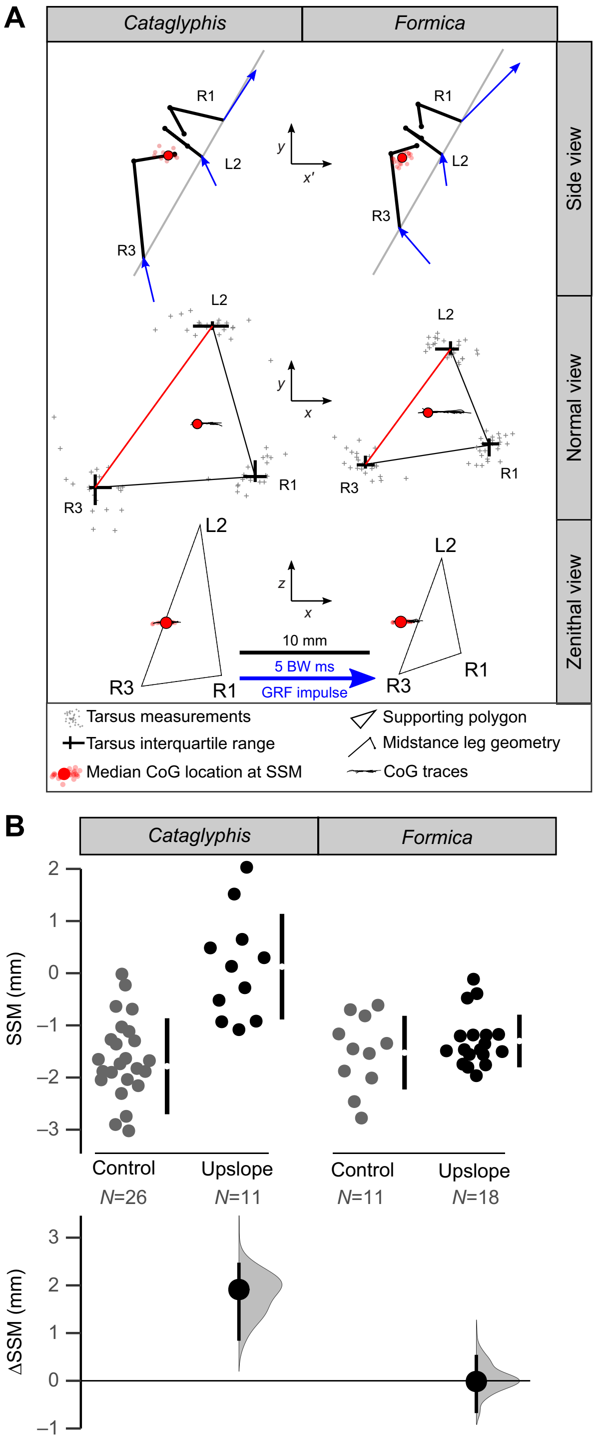

Fig. 2. Effects of slope on the SSM. (A) Measurements on the 60 deg upslope for *Cataglyphis* and *Formica*. The light red dots in the different views show the individual measurements and the large red dots visualize the median measurements of the CoG location where the distance to the boundary of the support pattern is at a minimum over each three-feet contact duration. The blue vectors in the side view show the time-integrated GRFs over the three-feet contact duration (impulses) for each leg divided by the body weight BW (for sample size statistics, see Table 1). The impulse vectors of the front legs pointed away from the substrate, indicating more pulling forces normal to the substrate (adhesion) than pushing forces. The normal view shows the CoG traces (black traces) with respect to the three-feet contact locations (gray crosses) and the support pattern. In the zenithal view, the median CoG location, where the distance to the boundaries of the support pattern is at a minimum over each three-feet contact duration, is vertically projected into the horizontal plane (red dots). Whereas for *Cataglyphis*, the red dots hovered around the projected line between the middle leg and the hindleg, they were clearly outside of the projected support pattern for *Formica* (negative minimum SSM). (B) Unpaired would-be SSM values (circles, with bars indicating 95% confidence intervals, CI) projected from 0 deg level locomotion measurements (Control) compared with actual SSM values from the 60 deg upslope measurements (Upslope). For *Cataglyphis*, the total effect of slope on the SSM (ΔSSM, median difference) was an improvement of +1.9 mm with a 95% CI that ranged from 0.8 to 2.5 mm (for sample size statistics, see Table 2). As the 95% CI does not overlap with zero, this can be interpreted as a significant change at an alpha level of 0.05. For the *Formica* sample, there was no conclusive evidence for a total effect of slope on the SSM.

its minimum (Fig. 2A, zenithal view). The critical tipping axis is the red line in Fig. 2A (normal view) formed by the middle leg and the hindleg for all upslope measurements and both ant species. For *Formica*, the vertical projections of the CoG were outside of the support pattern for the entire three-point contact duration.

To validate the first hypothesis, we first took the level locomotion geometry measurements of the ants and calculated their would-be SSM values for a hypothetical 60 deg upslope by rotating the level locomotion geometry around the y-axis by 60 deg (Fig. 2B, control group). Then we compared the would-be median SSM values with the actual median SSM values calculated from the geometric measurements on a 60 deg upslope. We expected that by changing its geometry, *Cataglyphis* could improve its SSM from a negative would-be SSM to a positive actual SSM. Vice versa, if *Formica* did not change its geometry, the actual SSM on the upslope should not differ from the would-be SSM estimated from the level locomotion measurements.

For *Cataglyphis*, the measured total effect of slope on the SSM was an improvement of +1.9 mm with a 95% CI that ranged from 0.8 to 2.5 mm. This can be interpreted as a significant change at an alpha level of 0.05 as the 95% CI does not overlap with zero (Fig. 2B). For the *Formica* sample, there was no significant difference at an alpha level of 0.05 between the level locomotion and the upslope measurements.

The change of the SSM of *Cataglyphis* was effected by a lowered CoG of −1.7 mm [95% CI −1.9, −0.7] and by an increased area of the support pattern of +17 mm² [95% CI 9, 29] (Fig. 3). The effective lever arm, as a link between the geometric and the adhesive strategy, did not change for both species significantly on an alpha level of 0.05. For *Formica*, none of the analyzed geometric parameters in Fig. 3 changed, implying that a potential stepping pattern change did not offset a possible change in the body height.

Adhesive strategy

To test the second hypothesis, we calculated the quasi-static CoG torques from the product of SSM and body weight $M_{\mathrm{CoG}}=\mathrm{SSM}\cdot F_{\mathrm{CoG}}$, as well as the quasi-static torques of the front legs M_{leg}. The leg torques were calculated from the product of the effective front leg lever arm r_l and the front leg GRF $F_{lz'}$ (Fig. 4A) in the normal direction $M_{\mathrm{leg}}=r_l\cdot F_{lz'}$. Thereby, *Formica* should exert negative front leg torques over a longer period and/or with higher magnitudes if our hypothesis holds. Furthermore, the sum of the two torques $M=M_{\mathrm{CoG}}+M_{\mathrm{leg}}$, as a measure of their tendency to tip

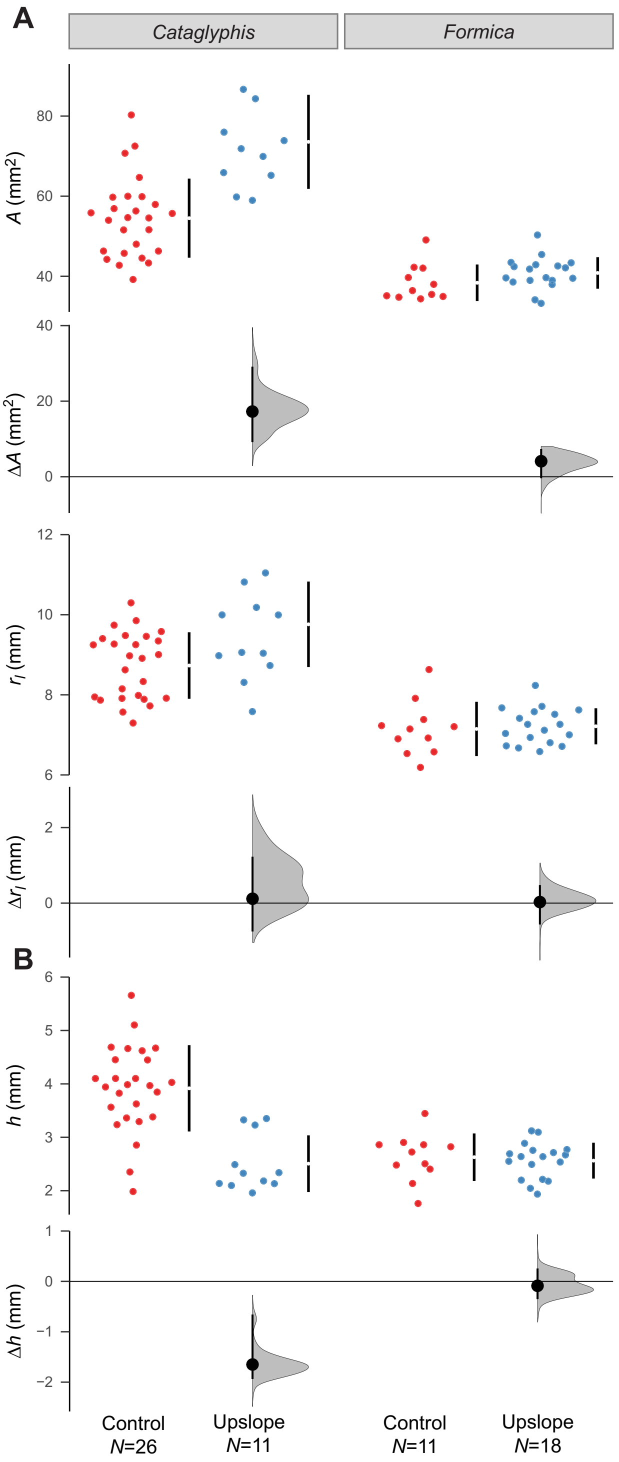

Fig. 3. Effect of slope on the geometric parameter. Unpaired measurements of the three-point contact area A and the front leg effective lever arm r_l (stepping pattern change, A), and the height of the center of gravity h (center of gravity change, B), on 0 deg level locomotion (Control) and on 60 deg upslope for *Cataglyphis* and *Formica*. Significant changes (upslope minus control measurements) at an alpha level of 0.05 occurred for *Cataglyphis* with an increased three-point contact area ΔA of +17 mm² [95% CI 9, 29] and a lowered body height Δh of −1.7 mm [95% CI−1.9, −0.7] on the upslope compared with level locomotion. For *Formica*, slope did not have a significant total impact on this geometric parameter, implying that a potential stepping pattern change did not offset a possible change in body height with respect to the SSM.

outwards (toppling) or inwards (righting) with respect to the supporting triangle, should not be greater than zero if the leg torques are sufficient to counter the possibly positive CoG torques.

The single leg force measurements indicated that *Formica* pulled stronger and longer with their front legs on the substrate ($F_{lz'}$<0) than *Cataglyphis* (Fig. 4A). *Cataglyphis* could hardly employ any negative leg torques over the whole three-feet contact duration (blue line in Fig. 4B) because of the negligible pulling forces of the front legs. In contrast, *Formica* pulled normally to the substrate with its front legs throughout the entire three-feet contact duration (Fig. 4A) and generated negative leg torques (leg righting) to counter the positive CoG torques (Fig. 4B).

For *Cataglyphis*, both M_{CoG} and the sum $M_{\mathrm{CoG}}+M_{\mathrm{leg}}$ were negative throughout the three-feet contact duration (geometric strategy), whereas M_{leg} was close to zero (Fig. 4B). This implies that *Cataglyphis* employed its geometric strategy successfully to avoid tipping backwards (toppling). *Formica* experienced the risk of positive M_{CoG} for the entire three-feet contact duration, but the overall static torque M was also kept below zero because of the presence of relatively high and continuous negative leg torque M_{leg} (Fig. 4B). This implies that *Formica* obviously tolerated the risk of toppling backwards by countering the positive CoG torques by negative leg torques (adhesive strategy).

Leg tarsal structures

Our scanning electron microscope micrographs of the front legs (Fig. 5) indicated that arolium, claws, spines, and long and short setae are present on the tarsomeres of both ants. The main differences are the size of the arolium, the width of the tarsomeres, as well as the number, distribution and length of the setae. The *Formica* sample has much wider tarsomeres and many fine short setae, while the *Cataglyphis* sample has a substantial reduction of the arolium and distinctly fewer short setae. A less conspicuous difference is the presence of tiny folds in the surface of the arolium in *Formica*, whereas the arolium is completely smooth in *Cataglyphis* (Fig. 5, insets).

DISCUSSION

Two distinct stabilizing strategies

In order to compare and explain distinct hexapedal locomotion behaviors for traversing steep slopes, we quantified SSM as well as CoG torques and leg torques over the three-feet contact duration for *Cataglyphis* and for *Formica* on a solid 60 deg upslope covered with millimeter paper. The results revealed that *Cataglyphis* primarily engaged in geometric changes (strategy i) to improve its SSM (Fig. 2B). Subsequently, it did not experience any positive CoG torques (toppling backwards) during the three-feet contact (Fig. 4B). The normal pulling and pushing forces of the front legs were negligible (Fig. 4A) and did not contribute notably to the righting (negative torques) nor did it enforce the overall toppling risk (positive torques) (Fig. 4B).

In contrast, *Formica*'s front legs were able to pull relatively strongly (Fig. 4A), which contributed to stronger negative leg torques (Fig. 4B). These were sufficient to counterbalance the positive CoG torques (Fig. 4B). In other words, *Formica* tolerated a higher risk of toppling backwards on upslopes. Instead of changing the geometry to improve its SSM, it chose to pull more strongly on the substrate with its front legs opposite the critical tipping axis (adhesion strategy ii).

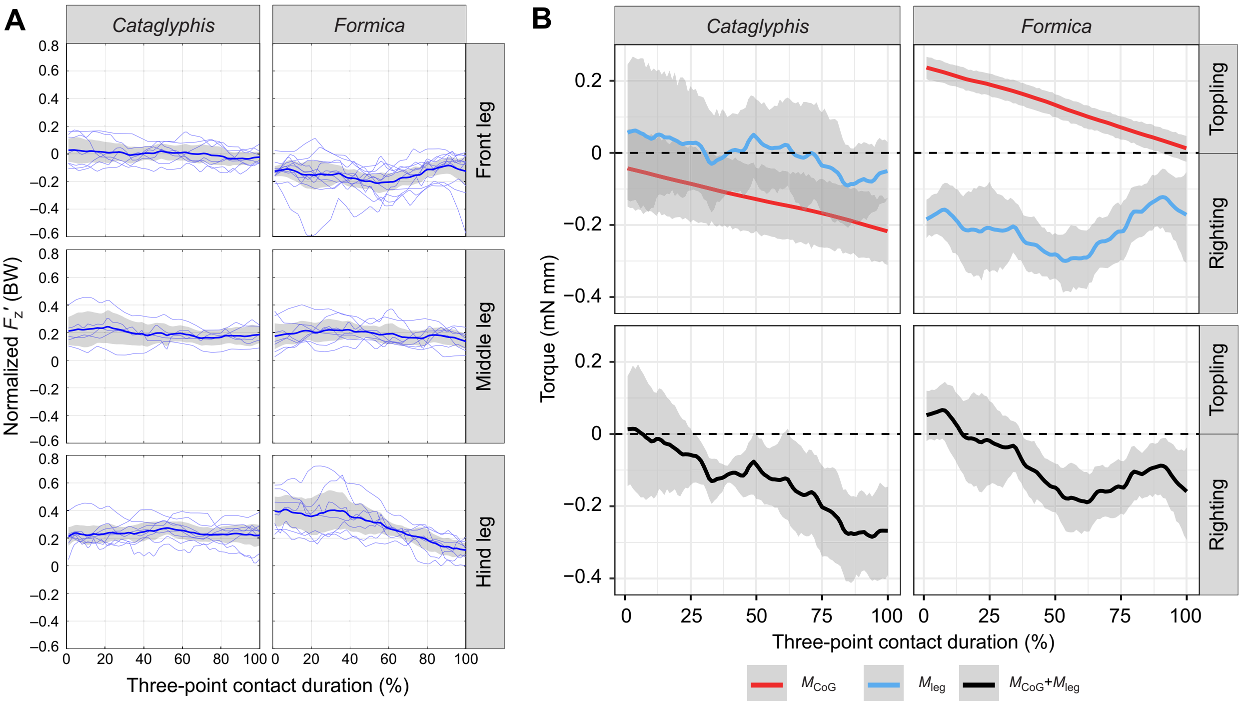

Fig. 4. Evidence for the geometric strategy in *Cataglyphis* and the adhesive strategy in *Formica*. (A) Time-normalized (linear interpolation) GRFs in the normal direction z' divided by the body weight BW for the front leg, middle leg and hindleg of *Cataglyphis* and *Formica* on a 60 deg upslope over the three-feet contact duration. Negative values imply leg pulling (adhesion) whereas positive values imply leg pushing in the normal direction to the substrate (for sample size statistics, see Table 1). The bold lines show the mean traces of the individual measurements (for sample size statistics, see Table 1) with 95% CI (gray shading). (B) Mean traces of the CoG torque M_{CoG}, front leg torque M_{leg} and net quasi-static torque $M=M_{\mathrm{CoG}}+M_{\mathrm{leg}}$ with 95% CI (gray shading) over the three-feet contact duration. For the entire three-feet contact duration, *Cataglyphis* exhibited negative CoG torque (geometric strategy) and negative overall static torque, whereas its front leg torque was close to zero. *Formica*, in contrast, experienced positive CoG torque and exerted relatively strong negative front leg torque (adhesion strategy). Its net quasi-static torque was also negative, implying that the righting torque was greater than the toppling torque.

Advantage of the adhesion strategy

As two common results, the sum of the quasi-static torques $M_{\mathrm{CoG}}+M_{\mathrm{leg}}$, remained negative for almost the entire three-feet contact for both ants (Fig. 4B), and the critical tipping axis was in all measurements the line that travels through the middle leg and hindleg tarsi. These imply that the ants experienced tipping torques towards the supporting area during their three-feet stance (righting). To not collapse under the observed negative net torques – which accelerated the ants towards the substrate above the critical tipping axis – the remaining three feet of the current swing phase should counterbalance the ants' posture later on by their following touch down with a new scenario of the support pattern, the forces and the torques. Furthermore, an impactful touch down could have advantages for the required load (positive normal force) on their tarsi to improve traction (Labonte and Federle, 2013).

Despite this, we observed qualitatively that *Formica* traversed steeper and even vertical inclines seemingly effortlessly, whereas *Cataglyphis* showed difficulties in traversing the 60 deg upslope. This is most probably attributed to the physical limitation of the geometric strategy, because the SSM cannot be maintained at a positive value once the slope crosses a certain steepness related to the geometry of the ant. In contrast, the adhesive locomotion enables climbing on a larger range of slopes, including vertical or inverted substrates (e.g. Federle and Endlein, 2004; Gorb et al., 2007), which is impossible on the basis of the geometric strategy.

Another advantage of the adhesion strategy is that it decreases the risk of slipping on steep slopes. As the slope becomes steeper, the ratio between the normal forces and the associated downhill or tangential forces decreases for quasi-static model assumptions. As the frictional forces are proportional to the normal forces according to Amontons' laws of friction, the frictional forces also become smaller and the risk for slipping becomes greater. To reduce the risk of slipping, the animal can increase the frictional force by pressing against the substrate with the hindlegs (increasing the normal pushing force) while pulling more strongly with its front legs. In contrast, with a lowered CoG of the geometric strategy (i), the tangential forces on the legs could be even further increased, which could easily surpass the maximum possible frictional force per leg and cause slipping. *Formica* does not reduce its CoG height, such that the time integral over the normal forces as a measure of the effective force applied during the three-point contact, or the impulse surface angle, remained relatively high compared with the time integral of the tangential forces (Fig. 6A). Furthermore, by exerting stronger pulling forces with its front legs, *Formica* might also push more strongly in the normal direction with at least one of the remaining legs to partly counter this impact. In particular, the stronger normal forces over time exerted by *Formica* can result in more bending of its many extremely fine setae (Endlein and Federle, 2015) (Fig. 6B). Subsequently, the bending of the setae can lead to more microscopic contact points (Gorb et al., 2007) and stronger nanoscopic attractive normal forces such as electrostatic forces (Izadi et al., 2014), van der Waals forces (Autumn et al., 2000) or capillary forces (Gorb et al., 2007). The increased number of contact points should hence result in higher maximal friction forces and a

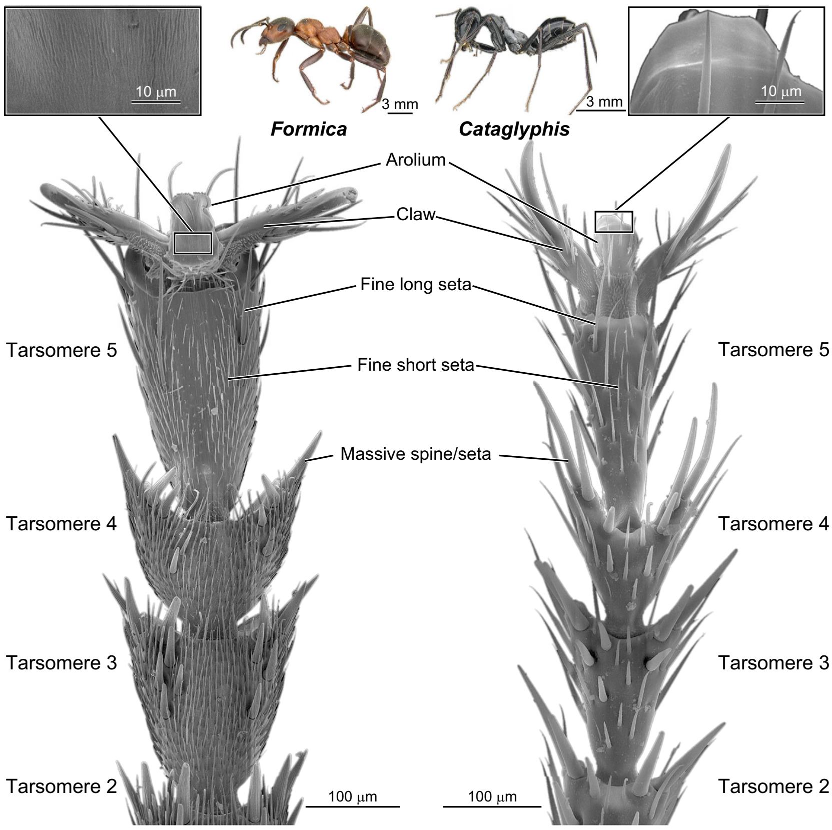

Fig. 5. Front leg tarsomere scanning electron microscope micrographs in the ventral view. All the structural elements are present in both ants, but there are distinct differences in the size and the fine structure (see insets) of the arolium, the tarsomere width, and the distribution and the length of setae. *Formica* have a dense cover of short fine setae, the arolium is bigger in size and shows fine micro-folds. *Cataglyphis* have a sparser cover of overall longer hairs and the surface of the arolium is completely smooth. Note that the claws and arolium in *Formica* are bent downwards. *Formica rufa* photo credit: Erin Prado, from www.antweb.org (https://www.antweb.org/bigPicture.do?name=casent0179909&shot=p&number=1 CASENT0179909). *Cataglyphis fortis* photo credit: Estella Ortega, from www.antweb.org (https://www.antweb.org/bigPicture.do?name=casent0906296&shot=p&number=1 CASENT0906296).

better performance in accelerating or traction. This was also observed in another climbing ant, *Oecophylla*, which pressed its dense tarsal hair against the substrate to intensify the friction forces (Endlein and Federle, 2015). Therefore, the upright body posture, the intensified pushing onto the substrate with the hindlegs (Fig. 4A) plus the presence of more fine tarsal hairs in *Formica* (Figs 5 and 6B) should explain its higher gradeability (the highest inclination an animal can ascend) and faster mean climbing speed (93±30 mm s^{-1} compared with 60±22 mm s^{-1} for *Cataglyphis*).

Reasons for limited pulling in *Cataglyphis*

Despite the advantages of the adhesion strategy with respect to the gradeability, *Cataglyphis* did not exert strong pulling forces with its front legs. Our microscopic examination revealed that its front legs (Fig. 5), like the hindlegs (Fig. 6B), had a smaller arolium, slimmer tarsomere and fewer fine short setae compared with those of *Formica*. In addition, the surface of the arolium was completely smooth in *Cataglyphis* but *Formica* had fine micro-folds in the arolium. Differences in the tarsal structures are well documented as varying factors between ground-dwelling and climbing species (Billen et al., 2017; Orivel et al., 2001). For example, the ground-dwelling ants *Brachyponera senaarensis* lack fine hair on the ventral tarsal surface and the arolium gland is very small compared with that of the climbing arboreal ant *Daceton armigerum* (Billen et al., 2017). Thus, unlike *Formica*, the ground-dwelling *Cataglyphis* might not have the ability to exploit sufficiently the adherence capabilities of their tarsal and pre-tarsal structures on the millimeter paper and is therefore forced to avoid the toppling risk by lowering its CoG. Moreover, in salt pan habitats with their dry, hot and granular ground, a large arolium may not benefit *Cataglyphis* as much as *Formica* in its surroundings, with probably more stimuli to climb up vertically or inverted on plant components with solid, smoother and colder surfaces. A potential wet adhesive functionality of the *Cataglyphis* arolium could also lead to faster dehydration in desert environments and to dust adherence to their tarsal structures. In addition, a larger arolium gland or the potentially attached dust particles may hamper the required fast swing-leg retraction time for their fast running. In contrast, the claws may still help *Cataglyphis* to generate traction or climb in their nest on the granular material.

Although fine dense hair on the tarsal euplantulae ('heel') and a prominent pre-tarsal arolium ('toe') are advantageous for climbing hexapoda (Bullock et al., 2008; Clemente and Federle, 2008; Labonte and Federle, 2013), the associated energetic cost of locomotion may be disadvantageous for ground-dwelling species. Furthermore, the longer spines on the tarsi of *Cataglyphis* could possibly function to store and release elastic energy for its well-known fast running capability (Wehner, 1983) better than shorter and finer setae. Apart from these differences in their tarsal structures, *Cataglyphis* may not yet be accustomed to utilizing their neuromuscular–adhesive system fully to switch from a 'pushing' gait to an adhesive 'pulling' gait on our slopes, which were covered with millimeter paper.

Conclusion

Based on the approach to calculate torque data with respect to the critical tipping axis, we were able to classify two different locomotion behaviors – a geometric strategy of the desert ants and an adhesive strategy of the wood ants – to avoid toppling when

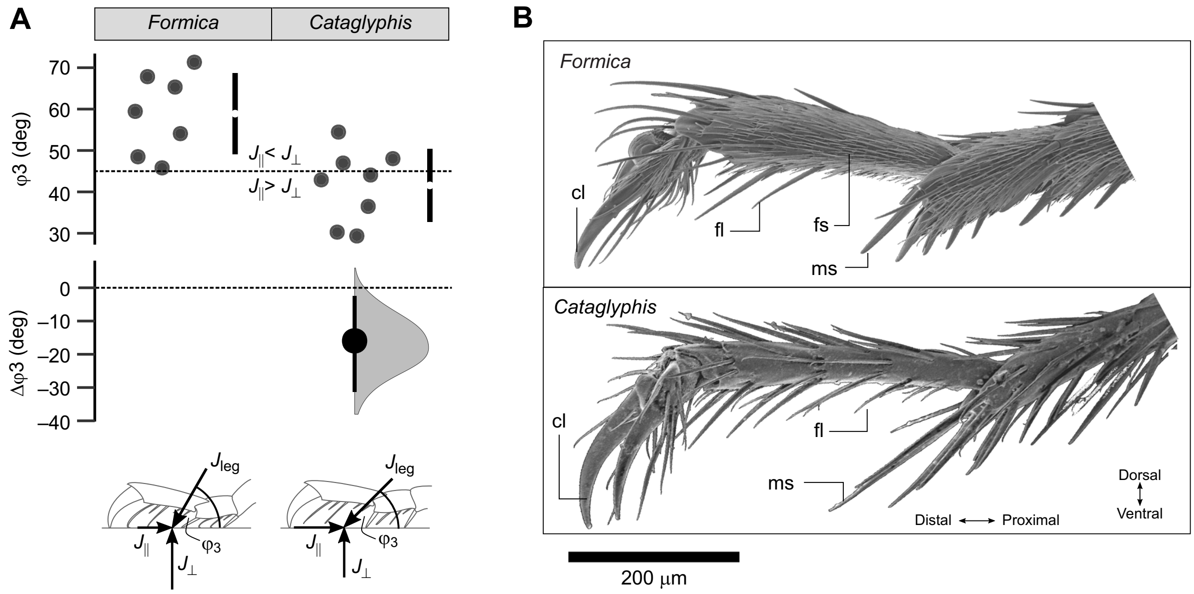

Fig. 6. Effect of leg impulse substrate angle on the risk of slipping on a 60 deg upslope. (A) Impulse substrate angle of the hindlegs φ_3 (with 95% CI), $\Delta\varphi_3$ (median difference) and possible effect of impulse J on hindleg tarsal structures. *Formica* hindlegs pushed with a median φ_3 of 60 deg more normally to the substrate than tangentially during the three-feet contact duration. This implies that the integral of the absolute values of the tangential GRFs (impulses) $J_{\parallel}$ was smaller than the impulses $J_{\perp}$ in the normal direction of the substrate. The dashed line at 45 deg denotes the equality of $J_{\parallel}$ and $J_{\perp}$. *Cataglyphis* ants pushed with a median φ_3 of 44 deg, about −16 deg flatter against the substrate. This implies that (1) *Cataglyphis* must employ relatively higher tangential friction impulses to counter the tangential leg impulses to not slip away and that (2) the fine tarsal structures of *Formica* should be pressed with higher magnitudes and/or longer periods against the substrate (for sample size statistics, see Table 1). Therefore, the tarsal hair should bend and buckle stronger with an augmented side contact (Endlein and Federle, 2015), which possibly increases traction (Labonte and Federle, 2013). Furthermore, the chance of microscopic contact points between the tarsal hair and the substrate should increase, which in turn could improve the overall strength of attachments (Gorb et al., 2007) by attractive forces such as electrostatic forces (Izadi et al., 2014), van der Waals forces (Autumn et al., 2000) or capillary forces (Gorb et al., 2007). (B) SEM images of the hindleg tarsomere 4–5 in the lateral view. *Formica* has more setae than *Cataglyphis*, which increases the number of possible microscopic contact points and therefore potentially the contact strength. cl, claw; fl, fine long setae; fs, fine short setae; ms, massive spine/setae.

climbing up steep slopes. This helped us to evaluate the effectiveness and the limitations of the body height adjustment by *Cataglyphis* to maintain its upright posture in inclined locomotion and to identify the righting behavior of *Formica* on steep slopes. The results showed that *Cataglyphis* desert ants turned potentially positive CoG torques (toppling) to negative ones (righting) with their geometric strategy but exhibited difficulties in traversing slopes steeper than 60 deg with this strategy. *Formica* wood ants tended to ignore the increasing influence of the positive CoG torques on the steep upslope and instead engaged an adhesive leg-righting strategy by pulling with their front legs on the substrate. The latter strategy is more advantageous for climbing with respect to the gradeability. Furthermore, its associated relatively steep leg impulse substrate angles do not increase the risk of slipping as much as relatively flat leg impulse substrate angles do. This strategy is thus able to exploit the capabilities of the sophisticated adhesive system of the tarsal structures by maintaining a relatively high normal force on the setae. Therefore, *Formica* benefits probably more from employing only one strategy instead of two, because the maintenance of its geometry keeps the normal load relatively high on its hindleg against slipping compared with a change of its geometry to reduce the risk of toppling.

Outlook

Our analysis exemplifies how the concept of the SSM could be extended for inclined locomotion with grasping feet to distinguish between a geometric and an adhesive locomotion behavior to prevent toppling. This biomechanical analysis may be linked to several adjacent physiological topics. For instance, a problem of potential general interest may link metabolic rate with the locomotion of animals in their habitats in terms of which strategy is energetically costlier, or in the end more relevant for survival in their ecological niche. A potential conflict between adhesion and locomotion would favor the geometric strategy energetically. In contrast, the lowered posture with its larger supporting area could also increase metabolic rate as a result of the varied operation of the muscles, or the possibly costlier adhesion strategy could increase the gradeability and subsequently enable steeper environments to be inhabited. A comparative analysis, based on the methods of a study on climbing *Camponotus* ants, for instance (Lipp et al., 2005), could relate the CO_2 release to the geometric and adhesive climbing behavior to approach this question.

Last but not least, our analysis relies on two main simplifications, which could be addressed in further studies with an advanced setup to gain elaborated insight into the tipping dynamics and behavior of the full gait cycle. First, we narrowed our analysis to the three-feet stance duration, because we could not measure the force of several legs simultaneously and independently. To expand and verify the results further to the complete gait cycle, one must record all the GRFs for at least one full cycle. Thereby, the time integral of the net torques (net angular momentum) of the transitions between the three-feet stances should counter the remaining negative net angular momentum from the three-feet stance (Fig. 4B). Second, our analysis ignored the existence of inertial effects, because the calculation of the inertial torques relies on a higher spatial resolution of the tracked points compared with what we could have provided with our data to present reliable results on the inertial torques. Theoretically, the inertial effects could also help the animals either to right their posture (negative inertial torques) or to enforce the risk of toppling over (positive inertial torques) during sudden changes of their speed or direction (Raibert et al., 1995). However, our results imply that no negative inertial torques were required to not topple over the critical tipping axis, and possibly positive inertial torques did not constrain the animals to a backward movement.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: T.W., L.R., M.N., R.B.; Methodology: T.W., A.R., L.R., R.B.; Software: T.W., S.G.; Validation: T.W., A.R., L.R., M.N., R.B.; Formal analysis: T.W., S.G.; Investigation: T.W., A.R., L.R.; Resources: T.W., A.R., L.R., R.B.; Data curation: T.W.; Writing - original draft: T.W., A.R., M.N., R.B.; Writing - review & editing: T.W., A.R., M.N., R.B.; Visualization: T.W., A.R.; Supervision: M.N., R.B.; Project administration: T.W., R.B.; Funding acquisition: L.R., R.B.

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Data availability
Data are available from the Dryad Digital Repository (Wöhrl et al., 2021): https://doi.org/10.5061/dryad.sbcc2fr6d.

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2.3 Cockroaches use diverse strategies to self-right on the ground

While the previous research article quantified how two ant species, as potential representatives for Hexapoda on the milligram scale, prevent toppling (postural stabilizing) during climbing on a steep inclined slope, the article *Cockroaches use diverse strategies to self-right on the ground* evaluated what is likely to happen after Hexapoda have toppled over: To survive, the overturned animals must *destabilize* their potentially vulnerable upside-down orientation to self-right.

To exemplify and compare such righting behaviors in Hexapoda, and to introduce concepts for the quantitative description of such behaviors, the wingless Madagascar hissing cockroach *Gromphadorhina portentosa* SCHAUM 1853, the American cockroach *Periplaneta americana* LINNAEUS 1758 and the discoid cockroach *Blaberus discoidalis* AUDINET-SERVILLE 1839 have been investigated. In particular, different performance measures such as the self-righting success and time were quantified. Furthermore, the probability for employing a dynamic strategy was evaluated, and locomotor transition ethograms visualized the intra-individual diversity and of righting behaviors and their transition probabilities. Last but not least, with the help of morphological and kinematic measurements, the paths of the successful and failed righting strategies were visualized in shape-specific potential energy landscapes for each cockroach species. The article was published on 9th of August in 2019 in the *Journal of Experimental Biology* and authored by Chen Li, Toni Wöhrl, Han K. Lam, Robert J. Full.[244]

It was first found out that all three species could self-right with a probability of 97 % within a given time of 30 s. Thus, it can be concluded that they all employ successful self-righting strategies.

Second, in 63 % of the righting attempts they could self-right on the first attempt, and on that attempt in less than one second. The fastest attempts took 0.46 s for the Madagascar hissing cockroach, 0.31 s for the discoid cockroach and 0.14 s for the American cockroach, whereas the median total time to achieve self-righting including failed attempts was 1.6 s, 1.1 s and 0.6 s, respectively. In conclusion, their righting attempts are not only successful but also fast.

Third, whereas the American cockroaches used their legs (93 %) and the discoid cockroaches used their wings (46 %) or their legs (49 %) to self-right, the Madagascar hissing cockroaches used its legs only in the final stage of its righting action and relied primarily on the arching of its body which together led in 98 % of their attempts to success. Thus, whereas all species used legs to assist their self-righting actions, only two species pushed with their appendages against the ground to initiate the righting action (dynamic strategy). The dynamic strategy

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[244] doi:10.1242/jeb.186080

for the American cockroach and the discoid cockroach could further be verified by observing upward motions of the animals' body in 63 % and 78 % of all attempts, respectively, after the pushing of their appendages had stopped. The Madagascar hissing cockroaches, in contrast, relied mainly on its shape changing (geometric) strategy.

I contributed to this study mainly through performing the experiments and working on the setup during my research visit at Professor Full's Poly-PEDAL lab at the University of California Berkeley between January and May in 2014 (bilateral exchange programme between the University of California, Berkeley and the Friedrich Schiller University Jena).

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RESEARCH ARTICLE

Cockroaches use diverse strategies to self-right on the ground

Chen Li[1,2,*], Toni Wöhrl[3], Han K. Lam[2] and Robert J. Full[2]

ABSTRACT

Terrestrial animals often must self-right from an upside-down orientation on the ground to survive. Here, we compared self-righting strategies of the Madagascar hissing, American and discoid cockroaches on a challenging flat, rigid, low-friction surface to quantify the mechanical principles. All three species almost always self-righted (97% probability) when given time (30 s), frequently self-righted (63%) on the first attempt, and on that attempt did so in 1 s or less. When successful, two of the three species gained and used pitch and/or roll rotational kinetic energy to overcome potential energy barriers (American 63% of all attempts and discoid 78%). By contrast, the largest, heaviest, wingless cockroach (Madagascar hissing) relied far less on the energy of motion and was the slowest to self-right. Two of the three species used rolling strategies to overcome low potential energy barriers. Successful righting attempts had greater rolling rotation than failed attempts as the center of mass rose to the highest position. Madagascar hissing cockroaches rolled using body deformation (98% of all trials) and the American cockroach rolled using leg forces (93%). By contrast, the discoid cockroach overcame higher and a wider range of potential energy barriers with simultaneous pitching and rolling using the wings (46% of all trials) and legs (49%) equally to self-right. Our quantification revealed the performance advantages of using rotational kinetic energy to overcome the potential energy barrier and rolling more to lower it, while maintaining diverse strategies for ground-based self-righting.

KEY WORDS: Locomotion, Potential energy barrier, Insects, *Periplaneta americana*, *Blaberus discoidalis*, *Gromphadorhina portentosa*

INTRODUCTION

Righting oneself from upside down on the ground is a prevalent locomotor transition that many animals must perform to survive. Even on flat, level ground with high friction, legged locomotion can induce large pitch and roll moments (Ting et al., 1994) that can result in overturning. During locomotion in complex terrain with inclinations (Minetti et al., 2002), uneven topology (Chiari et al., 2017; Daley and Biewener, 2006; Sponberg and Full, 2008), low friction (Clark and Higham, 2011), uncertain contact (Spagna et al., 2007), flowable ground (Li et al., 2012) and cluttered obstacles (Li et al., 2015, 2017), overturning is even more likely. Other forms of terrestrial locomotion such as jumping (Faisal and Matheson, 2001; Libby et al., 2012) and climbing (Jusufi et al., 2008), as well as flying (Faisal and Matheson, 2001) and swimming (Vosatka, 1970), can suffer instability and loss of body control resulting in overturning. Non-locomotor behaviors such as fighting and courtship can also produce overturning (Mann et al., 2006; Willemsen and Hailey, 2003). Under these circumstances, animals must be able to self-right promptly to avoid predation, starvation and dehydration, as well as to sense, locomote and reproduce.

Small animals like insects are particularly susceptible to overturning, because they are more sensitive to perturbations resulting from small body inertia (Walter and Carrier, 2002) and terrain irregularities that are negligible to larger animals (Kaspari and Weiser, 1999). Ground-based self-righting has been studied in many insect species, including beetles (Evans, 1973; Frantsevich, 2004; Frantsevich and Mokrushov, 1980), cockroaches (Camhi, 1977; Delcomyn, 1987; Full et al., 1995; Reingold and Camhi, 1977; Sherman et al., 1977; Zill, 1986), stick insects (Graham, 1979), locusts (Faisal and Matheson, 2001) and springtails (Brackenbury, 1990). Many self-righting strategies have been described (Brackenbury, 1990; Camhi, 1977; Evans, 1973; Faisal and Matheson, 2001; Frantsevich, 2004; Full et al., 1995; Zill, 1986), including: (1) using appendages (legs, wings, tail and antennae) and head to grasp, pivot, push or pull; (2) deforming the body; and (3) jumping with elastic energy storage and release. Some insects use multiple strategies and transition among them to self-right (Frantsevich, 2004). In addition, insects can use diverse body rotation including pitching, diagonal rotations (simultaneous pitching and rolling) and rolling (Brackenbury, 1990; Camhi, 1977; Delcomyn, 1987; Evans, 1973; Frantsevich, 2004; Frantsevich and Mokrushov, 1980; Full et al., 1995; Reingold and Camhi, 1977; Sherman et al., 1977; Zill, 1986). Furthermore, neural control and motor patterns of self-righting have been investigated in a variety of insect species (Camhi, 1977; Delcomyn, 1987; Faisal and Matheson, 2001; Frantsevich and Mokrushov, 1980; Graham, 1979; Reingold and Camhi, 1977; Sherman et al., 1977; Zill, 1986). Although these strategies have been well described, the mechanical principles of ground-based self-righting of small animals remain less understood. Here, we quantified the performance and body rotation of self-righting cockroaches and modeled the mechanical challenges to gain insight into what governs a small animal's use of various strategies and body rotation.

Previous observations and modeling in turtles have provided insight into the mechanics of how body and appendage morphology affects ground-based self-righting of larger animals (Ashe, 1970; Domokos and Várkonyi, 2008). Ground-based self-righting is the change of body orientation during which the body overcomes gravitational potential energy barriers (Domokos and Várkonyi, 2008). Based on this concept, a planar geometric model explained how shell shape and appendage length together determine whether turtles use active or passive strategies to self-right in the transverse plane (Domokos and Várkonyi, 2008). Turtles primarily rely on passive rotations of unstable shells and/or active, quasi-static pushing of their necks and legs to overcome large, primary potential energy barriers. To assist self-righting, turtles also use head and leg bobbing

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to gain modest amounts of rotational kinetic energy to overcome small, secondary potential energy barriers (Domokos and Várkonyi, 2008). In addition, the dependence of potential energy barriers on body rotation explained why many turtles almost always self-right via body rolling in the transverse plane on level, flat surfaces (Domokos and Várkonyi, 2008; Malashichev, 2016; Rubin et al., 2018; Stancher et al., 2006). Turtles have shells longer in the fore–aft than in the lateral direction, so body pitching overcomes higher potential energy barriers than body rolling does. Because turtles cannot gain sufficient body rotational kinetic energy to overcome the large potential energy barriers required for self-righting using pitching, they roll to self-right.

Here, inspired by these insights, we took the next step in understanding the mechanical principles of ground-based self-righting of small animals. First, we hypothesized that small insects' self-righting strategies can be dynamic, being able to gain and use pitch and/or roll rotational kinetic energy to overcome primary potential energy barriers. Dynamic behavior is plausible because many insects like cockroaches and beetles are capable of rapid locomotion and generating large impulses relative to body weight (Koditschek et al., 2004; Sponberg and Full, 2008; Ting et al., 1994; Zurek and Gilbert, 2014). Second, we hypothesized that, given the diverse three-dimensional body rotations possible, insects roll more when they succeed in self-righting than when they fail because increased rolling lowers potential energy barriers.

To test our hypotheses, we studied self-righting on a flat, rigid, low-friction surface of three species of cockroaches, the Madagascar hissing cockroach [*Gromphadorhina portentosa* (Schaum 1853)], the American cockroach [*Periplaneta americana* (Linnaeus 1758)] and the discoid cockroach (*Blaberus discoidalis* Audinet-Serville 1839), which differ in body size, body shape, leg length and availability of wings (Fig. 1). The selection of multiple species (Chiari et al., 2017; Domokos and Várkonyi, 2008) from a common super order (Dictyoptera) (Bell et al., 2007) enabled us to observe a greater number of strategies and body rotations, but with phylogenetic control that allows comparison. We used high-speed imaging to measure the animals' self-righting performance and body rotation. We used a locomotor transition ethogram analysis to quantify probability distribution of and transitions between self-righting strategies. We developed a simple geometric model to examine how the animal body moved to overcome barriers on a potential energy landscape. We compared successful and failed attempts to reveal what factors among body deformation and body and appendage behaviors contributed to successful self-righting (Rubin et al., 2018).

MATERIALS AND METHODS

Animals

We used six Madagascar hissing cockroaches, seven American cockroaches and seven discoid cockroaches. We used adult males because females were often gravid and under different load-bearing conditions. Prior to experiments, we kept the cockroaches in individual plastic containers at room temperature (28°C) on a 12 h:12 h light:dark cycle and provided water and food (fruit and dog chow) *ad libitum*. See Table 1 for animal body mass and body and leg dimensions.

The Madagascar hissing and American cockroaches are both relatively elongate and have similar body aspect ratios (body length versus body width versus body thickness) (Table 1, Fig. 1A,B). By contrast, the discoid cockroach is less elongate (ANOVA, $P<0.05$) and flatter (ANOVA, $P<0.05$) (Table 1, Fig. 1C). The American and discoid cockroaches have wings, whereas the Madagascar hissing cockroaches are wingless.

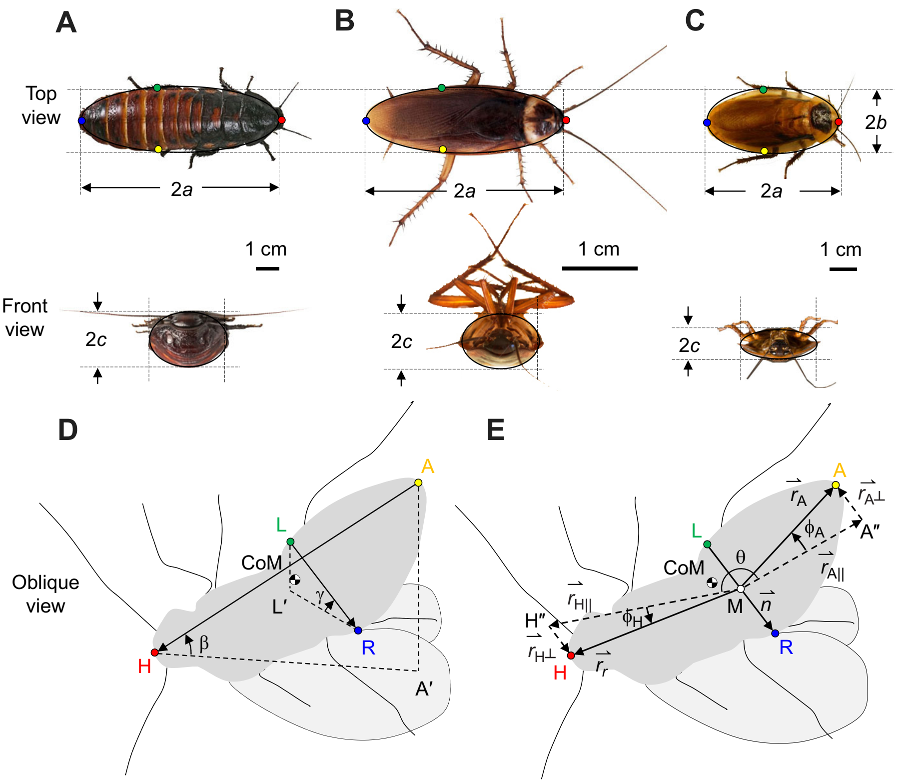

Fig. 1. Interspecies comparison of body and appendage morphology and definition of digitized markers and variables. (A) Madagascar hissing cockroach. (B) American cockroach. (C) Discoid cockroach. The animals are scaled to the same width in top and front views to illustrate differences in body elongation and flatness (Table 1). The body shape of each species is well approximated by an ellipsoid, with length, width and thickness of $2a$, $2b$ and $2c$, respectively. The four colored points in the top view are the four digitized markers. (D,E) Schematic diagrams of a self-righting animal, showing the four digitized markers – head (H), abdomen (A), left (L), right (R) – and definitions of body pitch (β), body roll (γ), body flexion (θ), head twisting (ϕ_H) and abdomen twisting (ϕ_A). A′ and L′ are downward projections of A and L to the same height levels of H and R, respectively. M is a point midway between L and R. $\vec{n}$ is the plane normal of the estimated sagittal plane. H″ and A″ are projections of H and A into the sagittal plane. In the example shown (discoid cockroach using wings), the body is flexing, the head is twisting to the right and the abdomen is twisting to the left.

Table 1. Sample size and morphological measurements

Species	Madagascar	American	Discoid
No. of individuals	6	7	7
No. of trials	55	59	61
No. of successful trials within 30 s	54	56	58
No. of failed trials within 30 s	1	3	3
No. of successful trials on first attempt	41	40	29
No. of successful trials needing more than one attempt	13	16	29
No. of attempts	78	95	205
No. of successful attempts	54	56	58
No. of failed attempts	24	39	147
Mass (g)	7.44±1.17	0.66±0.05	2.14±0.15
Body length 2*a* (cm)	6.03±0.42	3.34±0.14	4.98±0.17
Body width 2*b* (cm)	2.24±0.10	1.19±0.07	2.38±0.11
Body thickness 2*c* (cm)	1.32±0.10	0.70±0.01	0.96±0.02
Front leg length (cm)	2.08±0.08	1.62±0.03	1.91±0.10
Mid-leg length (cm)	2.93±0.03	2.20±0.09	2.67±0.06
Hindleg length (cm)	3.65±0.10	3.12±0.03	3.60±0.00
Body elongation (body length/body width)	2.69±0.22	2.81±0.20	2.09±0.12

Morphological measurements are means±1 s.d.

Experimental setup and protocol

We used a low-friction, level, flat, rigid surface as the righting arena. The surface was covered with low-friction cardstock, with static friction coefficient μ=0.10±0.01 (mean±1 s.d.) between the ground and dorsal surface of the animal body (measured by the inclined plane method). Side walls around the arena prevented animals from escaping. Four 500 W work lights above and three fluorescent lights around the righting arena provided lighting for the high-speed cameras. The temperature during experiments was 36.5°C. Two webcams (Logitech C920) recorded the entire duration of the experiments from top and side views at 30 frames s^{-1}. Four synchronized high-speed cameras (AOS and Fastec) recorded up to 30 s of each trial from four sides of the arena at 250 frames s^{-1} and 800×600 resolution.

For every trial, we held the animal in an upside-down orientation by grasping the edges of its pronotum and gently released it from a small height (<0.5 cm) above the center of the area. The small drop was to ensure that the animal did not begin leg searching, a common strategy used for self-righting, before it was set upside down on the ground. From high-speed videos, we verified that kinetic energy from the small drop dissipated so that the animal was stationary before it initiated the self-righting response. If the animal did not right within 30 s, it was picked up and placed back into its container to rest. We tested all individuals of all three species by alternating individuals and species to ensure sufficient time (>10 min) for each individual to rest between trials to minimize the effect of fatigue (Camhi, 1977).

Sample size

Excluding trials in which the animals touched the side walls when attempting to self-right, we collected a total of 176 trials from a total of 20 individuals from the three species of cockroaches, with approximately 9 trials from each individual. Because the animal often needed more than one attempt to self-right, from the 176 trials, we identified a total of 378 attempts (see definition below), including 168 successful attempts and 210 failed attempts. See Table 1 for details of sample size.

Definition of attempts

Because the animal was allowed up to 30 s for each trial, much longer than the duration of a typical self-righting attempt (Fig. S1A), the animal could make more than one attempt in a trial. Thus, for each trial, we observed the videos to record how many attempts the animal made and whether each attempt was successful, and measured the duration of each attempt.

We defined an attempt as the entire process during which the animal moved its body and appendages to eventually generate a pitching and/or rolling motion, because change in body yaw did not contribute to self-righting. We separated two consecutive attempts by when the animal returned to an upside-down orientation between the two pitching and/or rolling motions. By this definition, each failed attempt included not only the duration of the body pitching and/or rolling motion but also the duration prior to it during which the body and appendages moved to generate the attempt. We note that attempts by this definition may and often do include multiple movement cycles of wing opening/closing or leg pushing or flailing, which often occur at higher frequencies than body pitching and/or rolling motion. We did not use wing or leg motion to define attempts because they do not necessarily generate body pitching or rolling, which are defining features towards self-righting.

We then separated attempts into successful and failed ones depending on whether they resulted in self-righting. Each trial could have up to one successful attempt preceded by zero to several failed attempts.

Performance analysis

For each trial, we recorded whether the animal succeeded in self-righting within 30 s. We also recorded whether the animal succeeded in self-righting on the first attempt of each trial. For each successful trial, we recorded the total number of attempts it took the animal to self-right. We measured total self-righting time, defined as the duration from the instant the animal's dorsal surface touched the surface in an upside-down orientation to the instant when all its six legs touched the ground after the body became upright. We also measured successful attempt time, defined as the duration of the successful attempt of each successful trial. We calculated the probabilities of self-righting within 30 s and on the first attempt, as the ratio of their occurrence to the total number of trials for each species.

Strategy transition analysis

To quantify the transitions between strategies during self-righting, we performed a locomotor ethogram analysis for each trial (Li et al., 2015). For each species, we first recorded the sequence of locomotor strategies and the outcome (either successful self-righting or failure). We then calculated the animal's probabilities of entering various self-righting strategies, transitioning between them, and attaining a final outcome. The probability of each transition between nodes was defined as the ratio of the number of occurrences of that transition to the total number of trials of each species. To quantify the often-repeated failed attempts before the final successful attempt, we also counted for each trial the number of times the animal consecutively pitched and/or rolled using the same strategy. We then averaged this number across all trials of each species to obtain the probability of self-transitions.

Body rotation and deformation analysis

To quantify body rotation and deformation during self-righting, for each attempt, we digitized four markers on the animal's body (Fig. 1D,E) at the start and end of the attempt and when the body center of mass (CoM) was highest. The instance when the body CoM was highest was determined from high-speed videos by observing when the body stopped pitching and/or rolling upward and began pitching and/or rolling downward.

The four markers included: a head marker at the tip of the head (H), an abdomen marker at the tip of the abdomen (A), a left marker on the left side of the abdomen (L), and a right marker on the right side of the abdomen (R). Both the left and right markers were located at about 60% body length from the head, close to the fore–aft position of the CoM (Kram et al., 1997). Each marker was digitized in at least two high-speed videos from different views using DLTdv5 (Hedrick, 2008), which were used to reconstruct 3D positions using DLTcal5 (Hedrick, 2008) and a custom 27-point calibration object. The position midway (M) between the left and right markers was calculated.

We approximated the CoM position using the average position of all four markers. Using positions of the tips of the head (H) and abdomen (A), we calculated body pitch and body yaw relative to the ground. Using positions of the left (L) and right (R) points on the sides of the abdomen, we calculated body roll relative to the ground. In addition, we calculated body flexion θ as the angle within the sagittal plane formed between the in-plane components ($\vec{r}_{\mathrm{H}||}$ and $\vec{r}_{\mathrm{A}||}$) of two vectors $\vec{r}_{\mathrm{H}}$ and $\vec{r}_{\mathrm{A}}$, which started from the midway point (M) and pointed to the head (H) and abdomen (A) markers, respectively. $\vec{r}_{\mathrm{H}\perp}$ and $\vec{r}_{\mathrm{A}\perp}$ are components of $\vec{r}_{\mathrm{H}}$ and $\vec{r}_{\mathrm{A}}$ perpendicular to the sagittal plane. A negative body flexion meant body hyperextension. Further, we calculated head and abdomen twisting, ϕ_{H} and ϕ_{A}, as the angles between the sagittal plane and the vectors $\vec{r}_{\mathrm{H}}$ and $\vec{r}_{\mathrm{A}}$, respectively. Sagittal plane was approximated by a plane whose normal vector $\vec{n}$ was the vector from the left (L) to the right (R) marker. See Fig. 1D,E for details. Equations are summarized below.

CoM position:

$$x_{\mathrm{CoM}} = 1/4(x_{\mathrm{H}} + x_{\mathrm{A}} + x_{\mathrm{L}} + x_{\mathrm{R}}), \tag{1}$$

$$y_{\mathrm{CoM}} = 1/4(y_{\mathrm{H}} + y_{\mathrm{A}} + y_{\mathrm{L}} + y_{\mathrm{R}}), \tag{2}$$

$$z_{\mathrm{CoM}} = 1/4(z_{\mathrm{H}} + z_{\mathrm{A}} + z_{\mathrm{L}} + z_{\mathrm{R}}); \tag{3}$$

body orientation:

$$\text{pitch} = \tan^{-1}\left[(z_{\mathrm{A}} - z_{\mathrm{H}})/\sqrt{(x_{\mathrm{A}} - x_{\mathrm{H}})^2 + (y_{\mathrm{A}} - y_{\mathrm{H}})^2}\right], \tag{4}$$

$$\text{roll} = \tan^{-1}\left[(z_{\mathrm{L}} - z_{\mathrm{R}})/\sqrt{(x_{\mathrm{L}} - x_{\mathrm{R}})^2 + (y_{\mathrm{L}} - y_{\mathrm{R}})^2}\right], \tag{5}$$

$$\text{yaw} = \tan^{-1}[(y_{\mathrm{A}} - y_{\mathrm{H}})/(x_{\mathrm{A}} - x_{\mathrm{H}})]; \tag{6}$$

body flexion:

$$\theta = \cos^{-1}[(\vec{r}_{\mathrm{H}||} \cdot \vec{r}_{\mathrm{A}||})/(|\vec{r}_{\mathrm{H}||}|\,|\vec{r}_{\mathrm{A}||}|)]; \tag{7}$$

head twisting:

$$\phi_{\mathrm{H}} = \tan^{-1}\left(|\vec{r}_{\mathrm{H}\perp}|/|\vec{r}_{\mathrm{H}||}|\right); \tag{8}$$

abdomen twisting:

$$\phi_{\mathrm{A}} = \tan^{-1}\left(|\vec{r}_{\mathrm{A}\perp}|/|\vec{r}_{\mathrm{A}||}|\right); \tag{9}$$

where:

$$\vec{n} = (x_{\mathrm{R}}, y_{\mathrm{R}}, z_{\mathrm{R}}) - (x_{\mathrm{L}}, y_{\mathrm{L}}, z_{\mathrm{L}}), \tag{10}$$

$$\vec{r}_{\mathrm{H}\perp} = \vec{r}_{\mathrm{H}} \cdot \vec{n}, \tag{11}$$

$$\vec{r}_{\mathrm{H}||} = \vec{r}_{\mathrm{H}} - \vec{r}_{\mathrm{H}} \cdot \vec{n}, \tag{12}$$

$$\vec{r}_{\mathrm{A}\perp} = \vec{r}_{\mathrm{A}} \cdot \vec{n}, \tag{13}$$

$$\vec{r}_{\mathrm{A}||} = \vec{r}_{\mathrm{A}} - \vec{r}_{\mathrm{A}} \cdot \vec{n}. \tag{14}$$

To study how the animal moved in each attempt to self-right, we calculated the changes in these variables from the start of each attempt to when the body CoM was highest. When doing this, we used absolute values of pitch, roll and yaw considering symmetry of the animal's ellipsoidal body. We also set head and abdomen twisting at the start of the attempt to be always non-negative, considering lateral symmetry of the animal.

Body and appendage behavior analysis

To further identify what contributed to successful self-righting, for each attempt, we recorded the following events (or lack thereof) to quantify the animal's body and appendage behaviors. (1) Dynamic: whether the animal's body rotation was dynamic, being able to gain and use pitch and/or roll rotational kinetic energy to overcome potential energy barriers. Dynamic behavior was determined by observing whether the animal's body was still moving upward when its appendage (wings or legs) or arching body used for self-righting had stopped pushing against the ground. A wing stopped pushing against the ground when its distal section lifted off the ground as the body pitched and/or rolled. A leg stopped pushing against the ground when its distal segments, which engaged the surface for self-righting, slipped, reducing vertical force production (Full et al., 1995). An arching body stopped pushing against the ground when the body hyperextension began decreasing. When any of these occurred, the body could only continue to move upward if it still had rotational kinetic energy. (2) Body lift-off: whether the body lifted off from the surface. (3) Body hold: whether the body was held in the air after pitching up so that the abdomen remained raised, when using the wings to self-right. (4) Body sliding: whether the body slid on the ground as it pitched/rolled toward self-righting. (5) Leg assist: whether the legs assisted by pushing against the surface to generate body pitching and/or rolling towards self-righting, when using the wings to self-right. (6) Leg slip: whether the leg engaging the surface to self-right (as both the primary and assisting mechanisms) slipped on the surface. (7) Accelerate: whether the assisting leg accelerated body pitching and/or rolling motion towards self-righting. (8) Overshoot: whether there was any overshooting in body pitching and/or rolling motion beyond the upright orientation that must be corrected by the legs.

We calculated the probability of each of these body and appendage behaviors as the ratio of the occurrence of each to the total number of attempts for each strategy, separated by whether the attempt was successful or not.

All data analyses were performed using Microsoft Excel and MATLAB.

Statistics

Before pooling trials, for each species, we performed a mixed-design ANOVA (for continuous variables) or a chi-square test (for binomial variables), both with trial number as a fixed factor and individual as a random factor to account for individual variability. We found no effect of trial for any measurements relevant to a trial (P>0.05, ANOVA or P>0.05, chi-square test), including number of attempts to self-right, self-righting probabilities, righting times and transition probabilities. Thus, we pooled all trials from each individual to calculate their means and confidence intervals (for binomial variables) or standard deviations (for continuous variables).

Before pooling attempts, for each species, we performed a mixed-design ANOVA (for continuous variables) or a chi-square test (for binomial variables), both with attempt number as a fixed factor and individual as a random factor to account for individual variability. We found no effect of attempt for most (72 out of 84) measurements relevant to an attempt (P>0.05, ANOVA or P>0.05, chi-square test), including attempt time, changes in body pitch, roll and yaw, CoM height, body flexion, head and abdomen twisting, and body and leg behavior probabilities. Thus, we pooled all attempts for each of the self-righting strategies, separated by whether the attempt was successful or not, to calculate their means and confidence intervals (for binomial variables) or standard deviations (for continuous variables).

To test whether measurements relevant to an attempt differed between successful and failed attempts, for each species using each strategy, we used a mixed-design ANOVA (for continuous variables) or a chi-square test (for binomial variables), with the successful/failure record as a fixed factor and individual as a random factor to account for individual variability.

To test whether measurements relevant to the strategy used (winged or legged) differed between winged and legged attempts, for each species separated by whether the attempt was successful or not, we used a mixed-design ANOVA or a chi-square test (for binomial variables), with the strategy used as a fixed factor and individual as a random factor to account for individual variability.

To test whether measurements relevant to successful trials differed between species, we used a mixed-design ANOVA (for continuous variables) or a chi-square test (for binomial variables), with species as a fixed factor and individual as a nested, random factor to account for individual variability.

Wherever possible, we used Tukey's honestly significant difference test (HSD) to perform *post hoc* analysis. All the statistical tests followed McDonald (2009) and were performed using JMP.

Potential energy landscape model using simple body geometry

To visualize how the animal rotated during self-righting attempts and how this differed between strategies and species, we used a simple geometric model to calculate the potential energy landscape of the body (Fig. 2). Because the animal rarely lifted off the ground during self-righting for all three species (7 out of 378 attempts; Fig. S3B), as a first-order approximation, we considered the animal body as an ellipsoid with its lowest point in contact with a horizontal, flat surface (Fig. 2A–C). Ellipsoid length $2a$, width $2b$ and thickness $2c$ were body length, width and thickness from morphological measurements (Table 1). We approximated the CoM position with the ellipsoid's geometric center (Kram et al., 1997).

The simple geometric model allowed us to visualize the state of an ellipsoidal body on a potential energy landscape (Fig. 2D). For an elongate ellipsoid body, self-righting by pitching overcomes the highest potential energy barrier (Fig. 2A), whereas self-righting by rolling overcomes the lowest barrier (Fig. 2B). Self-righting by a diagonal body rotation (Frantsevich, 2004), with simultaneous pitching and rolling, overcomes an intermediate barrier (e.g. Fig. 2C, an ideal diagonal rotation about a fixed axis in the horizontal plane between pitch and roll axes). Body yawing did not affect CoM height or barrier height (yawing is relative to the world frame because we used the yaw–pitch–roll convention of Euler angles).

RESULTS

Self-righting attempts

For all three species, self-righting on a flat, rigid, low-friction surface was a challenging task and often required more than one attempt to succeed (Table 1, Fig. 3A; 24%, 29% and 48% of all trials had multiple attempts for the Madagascar hissing, American and discoid cockroaches, respectively). Repeated attempts were consistent with previous observations in the discoid cockroach

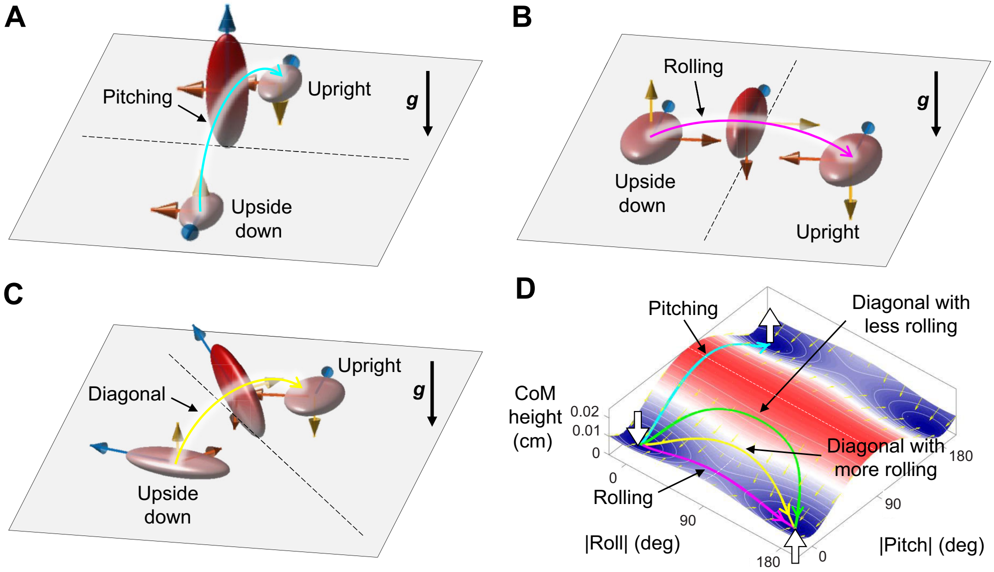

Fig. 2. Potential energy landscape from the simple geometric model. (A–C) An ellipsoid approximating the animal body in contact with the ground, pitching (A), rolling (B) or rotating diagonally (simultaneous pitching and rolling; C). Dashed line shows rotation axis. Diagonal rotation shown is about a fixed axis within the horizontal ground plane for simplicity; actual diagonal rotation of the animal may be about a time-varying axis. Red, blue and yellow arrows on each ellipsoidal body show its three major axes to illustrate body rotation. Vector ***g*** shows the direction of gravity. (D) Potential energy landscape, shown as center of mass (CoM) height as a function of body pitch and body roll (using Euler angles with yaw–pitch–roll convention), calculated from the geometric model. We used absolute values of body pitch and roll considering symmetry of the ellipsoid. Downward and upward arrows indicate an upside-down and upright body orientation, respectively. Cyan, green, yellow and magenta curves with arrows are representative trajectories for pure pitching, two different diagonal rotations and pure rolling, all about a fixed axis in the horizontal plane, to illustrate the fact that more body rolling decreases the potential energy barrier. White curves on the landscape are iso-height contours. Small yellow arrows on the landscape are gradients. Model results shown were obtained using the discoid cockroach's body dimensions as an example.

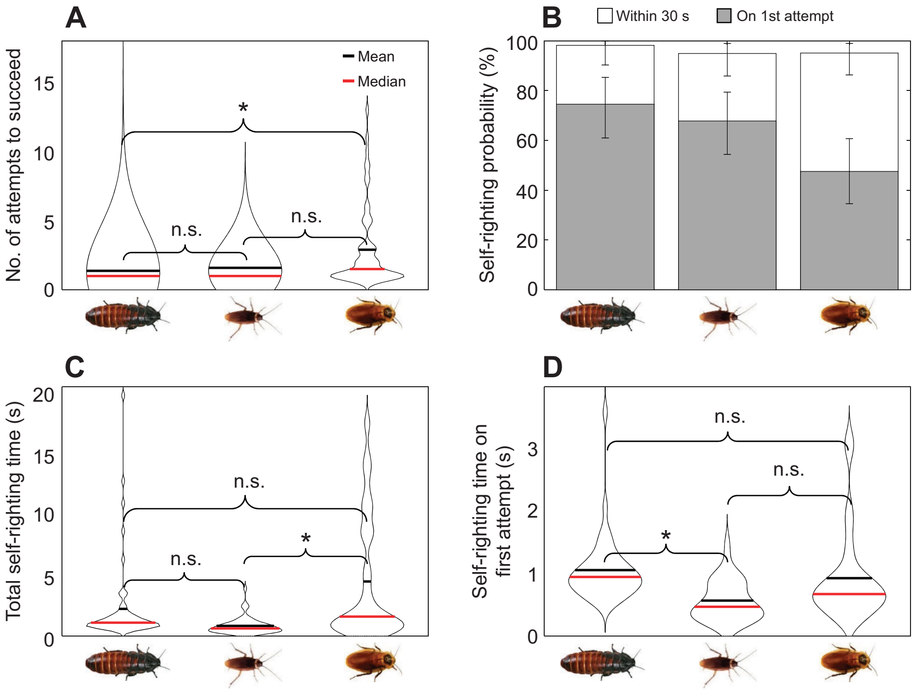

Fig. 3. Self-righting performance. (A) Number of attempts to achieve self-righting. (B) Self-righting probability within 30 s and on the first attempt. Error bars represent 95% confidence intervals. (C) Total time to achieve self-righting. (D) Time to achieve self-righting on the first attempt. From left to right: Madagascar hissing, American and discoid cockroaches. In A, C and D, data are shown using violin plots. Black and red lines show the mean and median, respectively. Width of graph shows the frequency of the data along the *y*-axis. Braces show whether there is a significant difference (**P*<0.05, ANOVA) or not (n.s.). See Table 1 for sample size.

(Full et al., 1995). The Madagascar hissing, American and discoid cockroaches needed an average of 1.3, 1.8 and 3.2 attempts to self-right. The difference was significant only between the Madagascar and discoid cockroaches ($P<0.05$, ANOVA, Tukey HSD).

For all three species, we found no dependence on trial number and only a few cases of dependence on attempt number (see Materials and Methods, ‘Statistics’). The lack of dependence on trial number showed that there was only a minor effect of history dependence, if any, on self-righting and that the animal’s motion and use of strategies was stochastic and unpredictable (Full et al., 1995) over consecutive attempts.

Self-righting probability

All three species self-righted with high probability when given time (30 s in our experiments; Fig. 3B, white bar; averaging 97% for all three species) and self-righted on the first attempt in over half of all trials (Fig. 3B, gray bar; averaging 63% for all species) with no significant difference across species ($P>0.05$, chi-square test).

Self-righting time

All three species were capable of self-righting rapidly. The fastest self-righting took only 0.14 s for the American cockroach, 0.31 s for the discoid cockroach and 0.46 s for the Madagascar hissing cockroach. The median total time to achieve self-righting including failed attempts was 1.1, 0.6 and 1.6 s for the Madagascar hissing, American and discoid cockroaches, respectively (Fig. 3C). The maximal time was 19.9, 3.9 and 17.7 s for the Madagascar hissing, American and discoid cockroaches, respectively. The difference was only significant between the American and discoid cockroaches ($P<0.05$, ANOVA, Tukey HSD). The mean self-righting time on the first attempt (Fig. 3D) was 1.0 s for the Madagascar hissing cockroach, longer than the American cockroach’s 0.6 s ($P<0.05$, ANOVA, Tukey HSD), although neither differed from the discoid cockroach’s 0.9 s.

Self-righting strategies

Body arching

The Madagascar hissing cockroach’s self-righting relied primarily on changing body shape assisted by the legs (Fig. 4A; Movie 1). When lying upside down (Fig. 4Ai), the animal hyperextended its body into an arch to raise the CoM (Fig. 4Aii) (Camhi, 1977), similar to some beetles (Frantsevich, 2004). The narrow base of support between the head and tip of the abdomen in contact with the ground and lateral perturbations from flailing legs induced the body to roll (Fig. 4Aiii). As the body fell onto one side, rolling stopped as a result of resistance from the legs and the metastable body shape in the transverse plane (Camhi, 1977), resembling that of medium-height turtle shells (Domokos and Várkonyi, 2008). Then, the legs on the lowered side kept pushing, resulting in skidding and yawing on the surface, while the body continued to hyperextend (Fig. 4Aiv). When a body arching attempt failed, the animal sometimes quickly flexed its body straight (occurring at a 25% probability per attempt) to reverse the direction of body rolling using rotational kinetic energy gained as a consequence of falling of the CoM to start another body arching attempt. When one of the pushing legs eventually managed to wedge under the body, its thrust rolled the body further over the protruding legs to overcome their secondary potential energy barriers to achieve self-righting (Fig. 4Av).

Wing use

Both the American and discoid cockroaches can self-right primarily using the wings (Fig. 4B,C; Movie 2). When lying upside down (Fig. 4Bi,Ci), the animal separated its wings laterally and pronated them so that their outer edges pushed against the surface while the head remained in contact as a pivot, which pitched the abdomen upward (Fig. 4Bii,Cii) and often resulted in additional body rolling. When a winged attempt failed, the animal closed its wings to pitch back downward and sometimes started the same process again in another attempt (occurring at a 3% probability per attempt for the American cockroach and an average of 1.1 times per attempt for

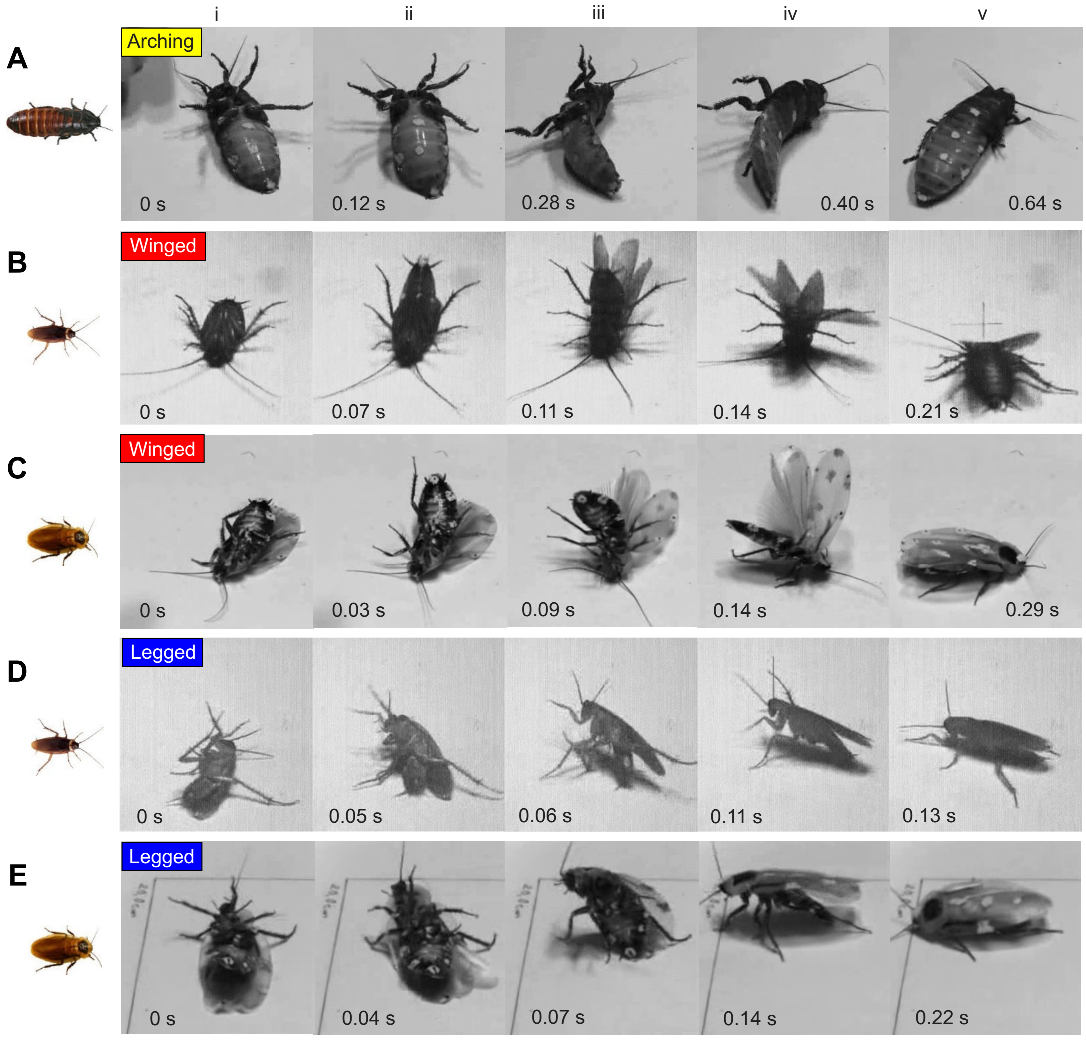

Fig. 4. Representative snapshots of self-righting strategies. (A) Madagascar hissing cockroach using body arching. (B) American cockroach using wings. (C) Discoid cockroach using wings. (D) American cockroach using legs. (E) Discoid cockroach using legs. i–v are five snapshots moving forward in time.

the discoid cockroaches). When a winged attempt succeeded, the animal fell with additional body pitching and/or rolling to become upright (Fig. 4Biii–v,Ciii–v). The legs flailed in this process, resulting in small lateral perturbations. Flailing legs frequently hit and pushed against the ground (91% of attempts), providing impulses to change body rotation.

Leg use

The American and discoid cockroaches can also self-right primarily using the legs (Fig. 4D,E; Movie 3). When lying upside down, these insects always continuously kicked their legs outward in an attempt to push against the ground (Reingold and Camhi, 1977; Zill, 1986). Frequent slipping of the legs (55% of attempts) as a result of the low friction of the surface resulted in continuous body sliding (41% of attempts). In failed attempts, body rolling and pitching induced by kicking the legs were not sufficient to achieve self-righting, and the animal started the same process in another attempt (occurring at a 51% and 21% probability per attempt for the American and discoid cockroaches, respectively). When a legged attempt succeeded (Fig. 4Di,Ei), two legs engaged the surface simultaneously (Fig. 4Dii,Eii), typically a hindleg and a contralateral middle leg (76% and 93% of attempts for the American and all attempts for the discoid cockroaches, respectively). The two legs pushed to thrust the body forward, pitched it head up, and rolled it such that the abdomen cleared the surface to self-right (Fig. 4Diii–v,Eiii–v).

Probability of dynamic self-righting

For both the American and discoid cockroaches using both wings and legs, self-righting attempts were often dynamic (Fig. 5; American: 67% of winged attempts, 55% of legged attempts, 56% of all attempts; discoid: 37% of winged attempts, 80% of legged attempts, 51% of all attempts), i.e. these two species of cockroach were able to gain and use pitch and/or roll rotational kinetic energy in an attempt to overcome potential energy barriers. By contrast, self-righting of the Madagascar hissing cockroach using body arching was never dynamic (0%; Fig. 5).

Self-righting transitions

All three species attempted more than one strategy and often transitioned between them to self-right, even though not all of them

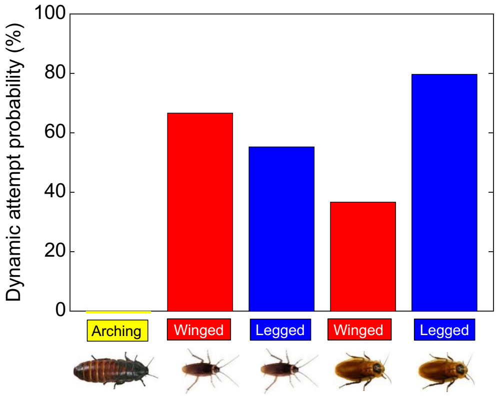

Fig. 5. Probability of self-righting dynamically. A dynamic attempt is one in which the animal is able to gain and use pitch and/or roll rotational kinetic energy in an attempt to overcome potential energy barriers, whether the attempt is successful or not. See Table 1 for sample size.

led to successful righting on the flat, rigid, low-friction surface (Fig. 6). Self-righting of both the Madagascar hissing and American cockroaches was more stereotypical and they primarily used one successful strategy, in contrast to the discoid cockroach, which used two successful strategies nearly equally.

The Madagascar hissing cockroach (Fig. 6A) most frequently used body arching to self-right (85% of all trials). When not successful, this cockroach always continued to use body arching, leading to a high probability of self-righting (98%). It occasionally used body twisting (13%) (Camhi, 1977), which never succeeded, after which it always transitioned to body arching (13%).

The American cockroach (Fig. 6B) frequently used its legs (93%) and occasionally used its wings (2%), despite being capable of self-righting using both strategies. When not successful, it often continued to use the same legged or winged strategy, but also occasionally transitioned between them. It also infrequently used flapping (2%), which never succeeded.

By contrast, the discoid cockroach (Fig. 6C) initially used either the wings (49%) or the legs (34%) to self-right. When unsuccessful, it continued to use the same legged or winged strategy, but also frequently transitioned between them, resulting in high probabilities of self-righting (46% or 49% eventually using wings or legs to self-right, respectively).

All three species occasionally entered a temporary quiescent mode (Camhi, 1977) without apparent body or appendage movement (2%, 3% and 16% for Madagascar hissing, American and discoid cockroaches, respectively).

Movement of body state on potential energy landscape

For all three species, because the body rarely lifted off the ground for all three species (7 out of 378 attempts; Fig. S3B), the measured state of the animal (body pitch, body roll and CoM height) lay on the surface of the potential energy landscape from the simple geometric model (Fig. 7). Being on the surface of the energy landscape allowed us to examine how the animal's body moved through three stages (start, highest CoM height and end) of an attempt to overcome potential energy barriers (or lack thereof).

For the Madagascar hissing cockroach using body arching and the American cockroach using the legs, body rotation was mainly rolling during both successful and failed attempts (Fig. 7A,C), which overcame the lowest potential energy barrier if successful

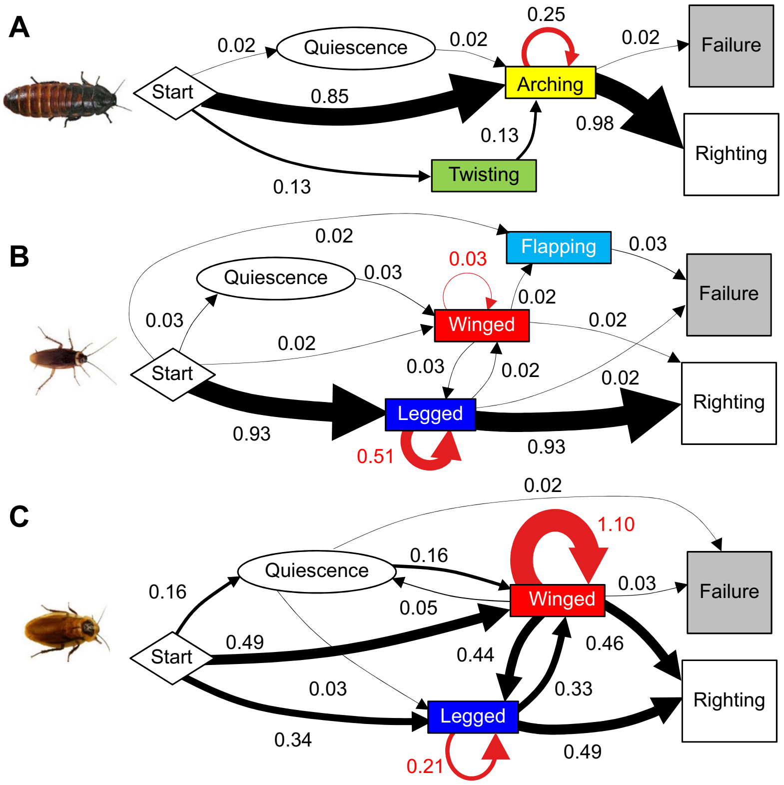

Fig. 6. Self-righting locomotor transition ethograms. (A) Madagascar hissing cockroach. (B) American cockroach. (C) Discoid cockroach. Arrow widths are proportional to transition probabilities between nodes, with probability values shown by numbers. Transition probabilities are defined as the ratio of the number of occurrences of each transition to the total number of trials for each species. Red arrows and numbers are for self-transition and represent the average number of times that cockroaches continued with the same strategy during each trial. A self-transition probability greater than one means that on average it occurred more than once for each trial. The sum of transition probabilities out of each node equals that into the node, except for the start with a total probability of 1 going out, and righting and failure with a total probability of 1 into both together. See Table 1 for sample size.

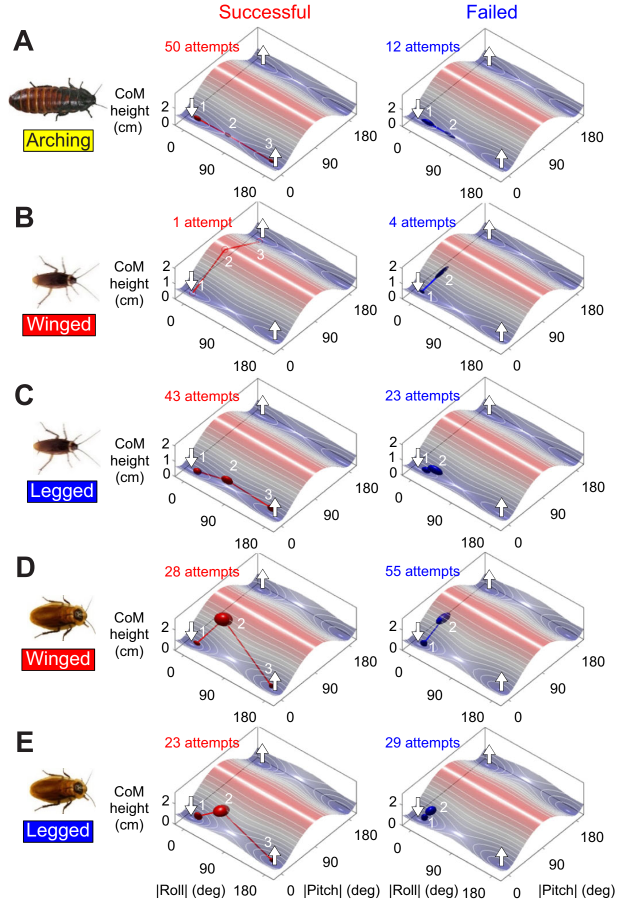

Fig. 7. Movement of body state on the potential energy landscape during successful versus failed righting attempts. (1) Start, (2) highest CoM position and (3) end of the attempt. (A) Madagascar hissing cockroach using body arching. (B) American cockroach using wings. (C) American cockroach using legs. (D) Discoid cockroach using wings. (E) Discoid cockroach using legs. Landscape is defined in Fig. 2D. On each landscape, the ellipsoids show means (center of ellipsoid) ±1 s.d. (principal semi-axis lengths of ellipsoid) of body pitch, body roll and CoM height at each stage of the attempt. For failed attempts, the end state (3) is not shown because it overlaps with the start state (1). The number of attempts in each case is shown. Note that the number of attempts shown combined for each species is slightly smaller than the total number of attempts, because in some attempts the animal markers were out of the field of view and could not be digitized.

(Fig. 7A, left). For the American cockroach using the wings, body rotation was mainly pitching during both successful and failed attempts (Fig. 7B), which overcame the highest potential energy barrier if successful (Fig. 7B, left). For the discoid cockroach using both wings and legs, body rotation involved simultaneous pitching and rolling during successful attempts (Fig. 7D,E, left), which overcame intermediate potential energy barriers, and body rotation was mainly pitching during failed attempts (Fig. 7D,E, right). In failed attempts, the animal was unable to overcome the potential energy barriers (Fig. 7A–E, right).

In addition, both the Madagascar hissing and American cockroaches had a large number of successful attempts (50 and 43, respectively) using strategies (body arching and legs, respectively) that overcame low potential energy barriers (Fig. 7A,C, left). The American cockroach had only one successful attempt using the wings which overcame high potential energy barriers (Fig. 7B, left). By contrast, the discoid cockroach had similar numbers of successful attempts to overcome potential energy barriers using the two self-righting strategies, wings (28) and legs (23) (Fig. 7D,E, left).

Body rotation and CoM height increase

Madagascar hissing cockroach

Using body arching to self-right, the Madagascar hissing cockroach pitched little towards 90 deg (Fig. 8Ai) but rolled substantially towards 90 deg (Fig. 8Bi) as the body attained its highest CoM position. Rolling resulted in a small CoM height increase relative to the highest potential energy barrier possible (*a*–*c*) (Fig. 8Ci). The body rolled more in successful than in failed attempts (Δ|roll|=69 deg versus 50 deg; $P<0.05$, ANOVA).

American cockroach

Using the wings to self-right, the American cockroach pitched substantially towards 90 deg (Fig. 8Aii) and rolled little towards 90 deg (Fig. 8Bii) as the body attained its highest CoM position. This resulted in a large CoM height increase relative to the highest potential energy barrier possible (*a*–*c*) (Fig. 8Cii).

Using the legs to self-right, the American cockroach pitched little towards 90 deg (Fig. 8Aiii) and rolled substantially towards 90 deg (Fig. 8Biii) as the body attained its highest CoM position. This resulted in a small CoM height increase relative to the highest potential energy barrier possible (*a*–*c*) (Fig. 8Ciii). The body rolled more in successful than in failed attempts (Δ|roll|=61 deg versus 20 deg; $P<0.05$, ANOVA).

For successful attempts, the American cockroach pitched more (Δ|pitch|=78 deg versus 5 deg; $P<0.05$, ANOVA) and rolled less (Δ|roll|=6 deg versus 61 deg; $P<0.05$, ANOVA), and its CoM height increased more (Δz_{CoM}=1.8 cm versus 0.7 cm; $P<0.05$, ANOVA) when using the wings than when using the legs (Fig. 8A–C, ii versus iii).

Discoid cockroach

Using the wings to self-right, the discoid cockroach pitched substantially towards 90 deg (Fig. 8Aiv) and rolled less towards 90 deg (Fig. 8Biv) as the body attained its highest CoM position. This resulted in a large CoM height increase relative to the highest potential energy barrier possible (*a*–*c*) (Fig. 8Civ). The body rolled more in successful than in failed attempts (Δ|roll|=17 deg versus 2 deg; $P<0.05$, ANOVA).

Using the legs to self-right, the discoid cockroach both pitched (Fig. 8Av) and rolled (Fig. 8Bv) a little towards 90 deg as the body attained its highest CoM position. This resulted in a small CoM height increase relative to the highest potential energy barrier possible (*a*–*c*) (Fig. 8Cv). The body rolled more in successful than in failed attempts (Δ|roll|=34 deg versus 5 deg; $P<0.05$, ANOVA).

For successful attempts, the discoid cockroach pitched more (Δ|pitch|=51 deg versus 21 deg, $P<0.05$, ANOVA) and rolled less (Δ|roll|=17 deg versus 34 deg, $P<0.05$, ANOVA), and its CoM height increased more (Δz_{CoM}=1.3 cm versus 0.8 cm, $P<0.05$, ANOVA) when using the wings than when using the legs (Fig. 8A–C, iv versus v).

All three species

For all three species, body rolling was the best predictor of whether an attempt succeeded or failed. Roll increase when the CoM was highest was greater in successful than in failed attempts for all cases ($P<0.05$, ANOVA; Fig. 8Bi,iii–v), except for the American cockroach using the wings (Fig. 8Bii) which had a small sample size (1 successful and 4 failed attempts).

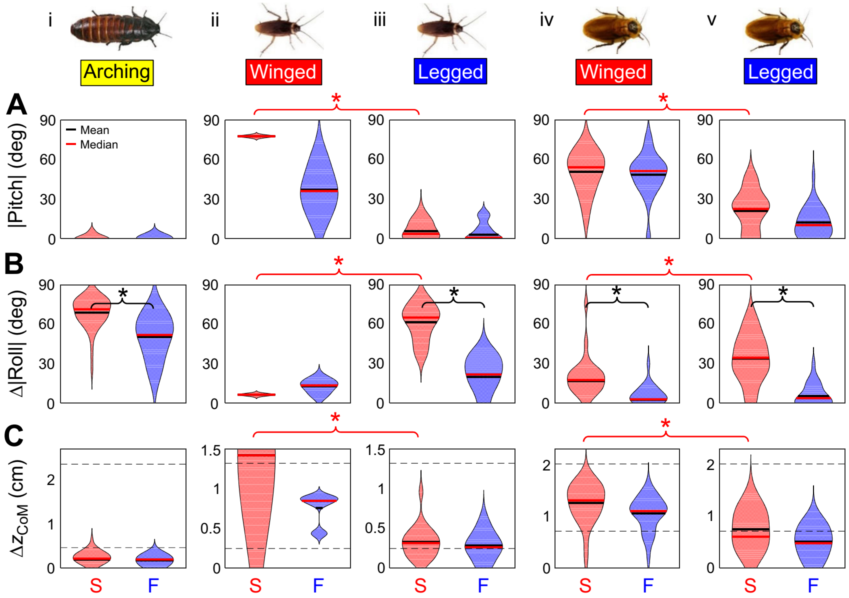

Fig. 8. Body rotation and CoM height increase. Body pitch increase (A), body roll increase (B) and CoM height increase (Δz_{CoM}; C) when the body was highest for successful (S, red) versus failed (F, blue) self-righting attempts. (i) Madagascar hissing cockroach using body arching. (ii) American cockroach using the wings. (iii) American cockroach using the legs. (iv) Discoid cockroach using the wings. (v) Discoid cockroach using the legs. We used absolute values of body pitch and roll considering symmetry of the ellipsoid representing the body. Data are shown using violin plots. Black and red lines indicate the mean and median. Width of graph indicates the frequency of the data along the *y*-axis. Black asterisks and braces indicate a significant difference between successful and failed attempts ($P<0.05$, ANOVA). Red asterisks and braces indicate a significant difference between winged and legged attempts for the same species ($P<0.05$, ANOVA). In C, the two horizontal dashed lines show the lowest and highest potential energy barriers from the ellipsoid model, *b*−*c* and *a*−*c*, for pure rolling and pure pitching, respectively. For successful attempts, CoM height increase is the measured potential energy barrier. For failed attempts, potential energy barrier was not measured because the animal did not overcome it. See Table 1 for sample size.

Because the CoM height increase was the measured potential energy barrier for successful attempts, both the American and discoid cockroaches overcame higher barriers when using the wings than when using the legs, and this difference was greater for the American cockroach.

Other factors contributing to successful self-righting

Besides body rolling, three factors were important in differentiating successful from failed attempts (Fig. S2). First, except for the American cockroach using the wings, leg slip was less frequent in successful attempts for all three species (Fig. S2Ai,iii–v; Madagascar arching, successful: 0%, failed: 100%; American legged, successful: 0%, failed: 90%; discoid winged, successful: 45%, failed: 97%; discoid legged, successful: 0%, failed: 100%; $P<0.05$, chi-square test). Second, for the American cockroach using the legs and the discoid cockroach using both wings and legs, the legs more frequently hit the ground in successful attempts to accelerate body rotation, after the wings or legs generated the initial body pitching and/or rolling (Fig. S2B iii–v; American legged, successful: 51%, failed: 10%; discoid winged, successful: 62%, failed: 5%; discoid legged, successful: 34%, failed: 0%; $P<0.05$, chi-square test). Third, for both the American and discoid cockroaches using the wings, the body was held in the air with the abdomen pitched upward less frequently in successful attempts (Fig. S2Cii,iv; American winged, successful: 0%, failed: 80%; discoid winged, successful: 52%, failed: 98%; $P<0.05$, chi-square test). Body holding was not observed in the legged and arching strategies.

We did not observe significant differences between successful and failed attempts that were consistent across species and strategies for all other measurements (Figs S1, S3), including attempt time, body yaw change, body flexion change, head and abdomen twisting changes, dynamic probability, body lift-off probability, body sliding probability, leg assist probability and overshoot probability. We did find significant differences between successful and failed attempts ($P<0.05$, ANOVA; $P<0.05$, chi-square test) in attempt time for the discoid cockroach using both wings and legs (Fig. S1Aiv,v), in body yaw change for the American cockroach using the wings (Fig. S1Bii), in both head and abdomen twisting change for the Madagascar hissing cockroach using body arching (Fig. S1Di,Ei), in the probability of dynamic self-righting for the discoid cockroach using the legs (Fig. S3Av), and in body sliding probability for the American cockroach using the wings (Fig. S3Cii).

DISCUSSION

Our study quantified self-righting attempts (Fig. 3A; Fig. S1A), performance (Fig. 3B–D), probability of using kinetic energy (Fig. 5), use of and transitions among strategies (Figs 4 and 6), body rotation (Figs 7 and 8; Fig. S1B) and deformation (Fig. S1C–E), and body and appendage behaviors (Figs S2, S3) in the context of a potential energy landscape (Figs 2 and 7).

Advantages of dynamic self-righting using rotational kinetic energy

As we hypothesized, self-righting strategies in insects like cockroaches can be dynamic. The ability to self-right dynamically (Fig. 5) by gaining and using pitch and/or roll rotational kinetic energy to overcome potential energy barriers offered the American and discoid cockroaches several performance advantages. First, with all else being equal and as confirmed using a physical model (Li et al., 2016, 2017), the larger its pitch and/or roll rotational kinetic energy, the faster the body pitched and/or rolled, and the shorter the time to self-right. In addition, although each dynamic attempt costs more energy, as our physical modeling demonstrated (Li et al., 2016, 2017), greater body rotational kinetic energy increased the chance of self-righting for each attempt and could save energy overall by reducing the number of failed attempts. Further, pitch and/or roll rotational kinetic energy allowed the animal to reach a broad range of body rotation states of higher potential energy on the landscape (Fig. 7B–E). This gives them the opportunity to overcome energy barriers using a greater number of self-righting strategies. Finally, on slippery surfaces or sand, where self-righting using quasi-static leg grasping may be difficult (see fig. 16B of Frantsevich, 2004), pushing appendages rapidly to gain body rotational kinetic energy to self-right can be more effective.

Successful attempts revealed three body and appendage behaviors favoring dynamic self-righting performance (Fig. S2). First, the animal's legs slipped less frequently in successful attempts (Fig. S2A). This was beneficial because leg slipping leads to body yawing, sliding and premature falling of the CoM, which either dissipates pitch and/or roll rotational kinetic energy or converts it into yaw rotational kinetic energy or horizontal translational kinetic energy that does not contribute to self-righting. Second, the animal's assisting leg(s) more frequently accelerated body rolling and/or pitching in successful attempts (Fig. S2B), adding pitch and/or roll rotational kinetic energy. Third, when using the wings to self-right, the animal's body was held during pitching less frequently in successful attempts (Fig. S2C), and therefore did not lose the pitch and/or roll rotational kinetic energy generated by prior wing pushing.

Body rolling facilitates self-righting by lowering potential energy barrier

As we hypothesized, for all but one strategy (Fig. 8B), cockroaches rolled their body more during successful than during failed attempts as the center of mass rose, because increased rolling lowers the potential energy barrier (Figs 2D, 7). This is important because ground-based self-righting is a strenuous task. For example, a single hindleg of the discoid cockroach may need to generate ground reaction forces during self-righting as large as 8 times those during high-speed running (at 8 body lengths s^{-1}) (Full et al., 1995). Using the potential energy landscape model (Fig. 2), if the discoid cockroach self-righted using wings with pure pitching, the mechanical work needed to overcome the highest potential energy barrier (420 μJ) would be 7 times that needed per stride during medium-speed running (at 5 body lengths s^{-1}) (Kram et al., 1997). Using the observed body rotation during winged self-righting with simultaneous pitching and rolling (Figs 7D, 8iv), this mechanical work is reduced by 40% (to 260 μJ). Consistent with this finding, winged self-righting of a cockroach-inspired physical model (Li et al., 2016, 2017) demonstrated that body rolling increased the chances of successful self-righting by lowering the potential energy barrier.

Both the American and discoid cockroaches are capable of self-righting using both the wings and legs. For both species, using the legs with greater body rolling and less pitching is more favorable because it overcomes a lower potential energy barrier than using the wings with greater body pitching and less rolling (Fig. 8A–C, ii versus iii, iv versus v, red). Given this, the American cockroach's successful self-righting is more stereotyped than the discoid cockroach's (Figs 6B versus C, 7B,C versus D,E) partly because the potential energy barrier difference between these two strategies is larger. For the American cockroach, the potential energy barrier is 1.7 cm for pitching versus 0.7 cm for rolling (Fig. 8C, ii versus iii, red). By contrast, for the discoid cockroach, the potential energy barrier is only 1.3 cm for pitching versus 0.8 cm for rolling (Fig. 8C, iv versus v, red).

Advantages of diverse self-righting strategies

The ability of cockroaches and other insects (Frantsevich, 2004) to use and transition among more than one strategy to self-right offers several possible performance advantages. First, if damaged or lost appendages (Fleming et al., 2007; Jayaram et al., 2011) preclude the use of one strategy, the animal still has the opportunity to self-right using an alternative strategy. Second, the observed unsuccessful strategies such as body twisting and wing flapping (Figs 4 and 6), as well as body yawing and deformation and various body and appendage behaviors (Figs S1, S3), which seemed not to be beneficial here, could allow the animal to self-right in novel ways in natural environments by interacting with slopes, uneven and deformable surfaces, or nearby objects (Golubovic et al., 2013; Peng et al., 2015; Sasaki and Nonaka, 2016). Third, even the seemingly stochastic and unpredictable motion over consecutive attempts may be an adaptation to heterogeneous, stochastic natural environments (Kaspari and Weiser, 1999).

More broadly, the use of and transitions among diverse self-righting strategies may be an adaptation for many animal species. Studies of ground-based self-righting of beetles (Frantsevich, 2004) and turtles (Ashe, 1970; Domokos and Várkonyi, 2008), and aquatic self-righting of marine invertebrates on underwater substrates (Vosatka, 1970; Young et al., 2006), also observed diverse strategies, including leg pivoting, head bobbing, tail pushing, body dorsiflexion, leg pushing, body flexion and tail bending.

Future work

Our quantification of motion on the potential energy landscape using a simple rigid body only offers initial insight into the mechanical principles of self-righting of small insects. Future work should expand the potential energy landscape by adding degrees of freedom to better understand how appendage motion and body deformation change energy barriers and stability (as well as injecting kinetic energy) to result in self-righting (Othayoth et al., 2017). Our quantification of self-righting on a flat, rigid, low-friction surface represents a very challenging scenario. Future experiments should test and model how animals interact with slopes, uneven and deformable surfaces, or nearby objects (Golubovic et al., 2013; Peng et al., 2015; Sasaki and Nonaka, 2016) using potential energy landscapes to reveal principles of self-righting in nature. In addition, given our finding that rolling facilitates self-righting by lowering the potential energy barrier, we speculate that searching to grasp the ground or nearby objects (Frantsevich, 2004; Sasaki and Nonaka, 2016), leg flailing (Othayoth et al., 2017) and body twisting during self-righting may induce lateral perturbations to increase rolling. Further, experiments (Rubin et al., 2018) and multi-body dynamics simulations (Xuan et al., 2019) to obtain three-dimensional ground reaction forces of the body and appendages in contact with the substrate will help elucidate the dynamics of self-righting. Finally, electromyography measurements will shed light on how animals control or coordinate (Xuan et al., 2019) their wings, legs and body deformation to self-right.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: C.L., R.J.F.; Methodology: C.L., T.W., H.K.L., R.J.F.; Software: C.L., T.W.; Validation: C.L., R.J.F.; Formal analysis: C.L., T.W.; Investigation: T.W.,

H.K.L.; Resources: C.L., R.J.F.; Data curation: C.L., T.W.; Writing - original draft: C.L.; Writing - review & editing: C.L., R.J.F.; Visualization: C.L.; Supervision: C.L., R.J.F.; Project administration: C.L.; Funding acquisition: C.L., T.W., R.J.F.

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Supplementary information

Supplementary information available online at
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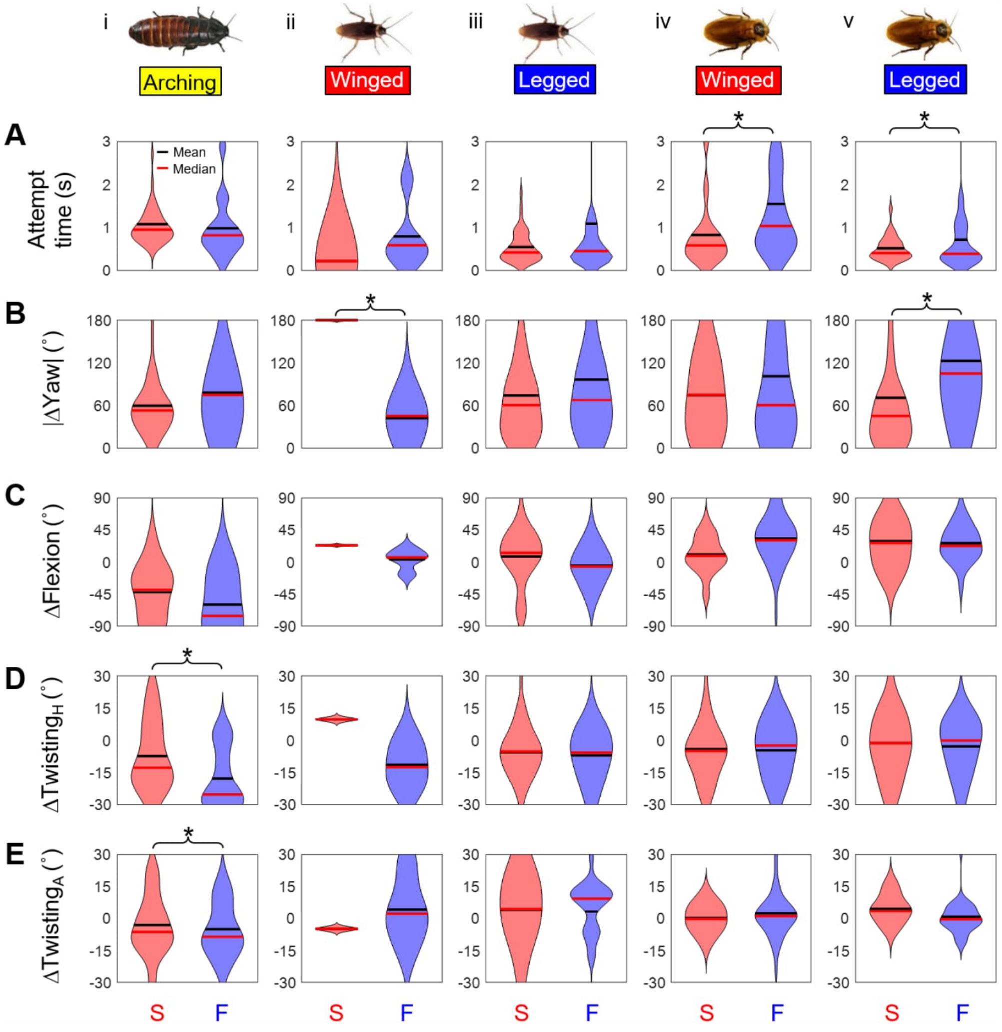


Fig. S1. Attempt time and body yaw and deformation. Attempt time (A), body yaw change (B), body flexion change (C), head twisting change (D), and abdomen twisting change (E) when the body was highest for successful (S, red) vs. failed (F, blue) self-righting attempts. (i) Madagascar hissing cockroach using body arching. (ii) American cockroach using the wings. (iii) American cockroach using the legs. (iv) Discoid cockroach using the wings. (v) Discoid cockroach using the legs. We used absolute values of body yaw considering rotational symmetry on the level, flat surface. Data are shown using violin plots. Black and red lines indicate the mean and median. Width of graph indicates the frequency of the data along the *y*-axis. Black asterisks and braces indicate a significant difference between successful and failed attempts ($P < 0.05$, ANOVA). In (C), negative flexion changes in (i) and positive flexion changes in (ii-v) mean increase in hyperextension and flexion, respectively. In (D,E), positive and negative changes in twisting mean increase and reduction in twisting, respectively. See Table 1 for sample size.

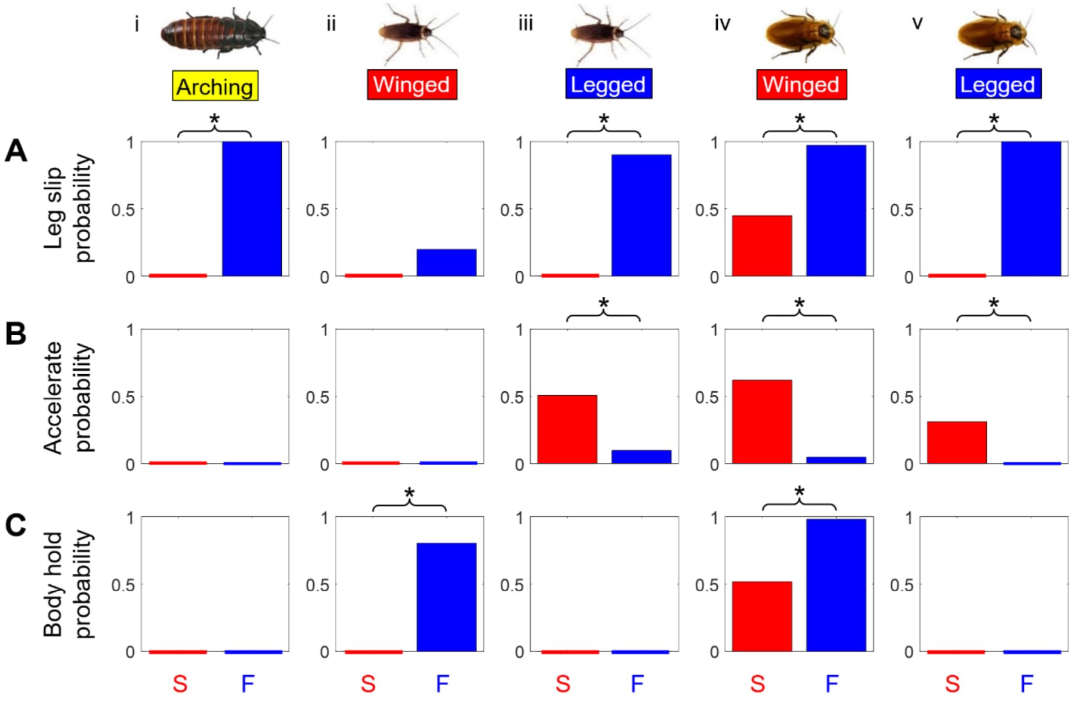


Fig. S2. Body and appendage behaviors that show a consistent difference between successful (S, red) and failed (F, blue) attempts. (A) Leg slip probability. (B) Accelerate probability. (C) Body hold probability. (i) Madagascar hissing cockroach using body arching. (ii) American cockroach using the wings. (iii) American cockroach using the legs. (iv) Discoid cockroach using the wings. (v) Discoid cockroach using the legs. Asterisks and braces indicate a significant difference between successful and failed attempts ($P < 0.05$, chi-square test). The large differences between successful and failed attempts in (A, ii-iv) are due to individual variation. See Table 1 for sample size.

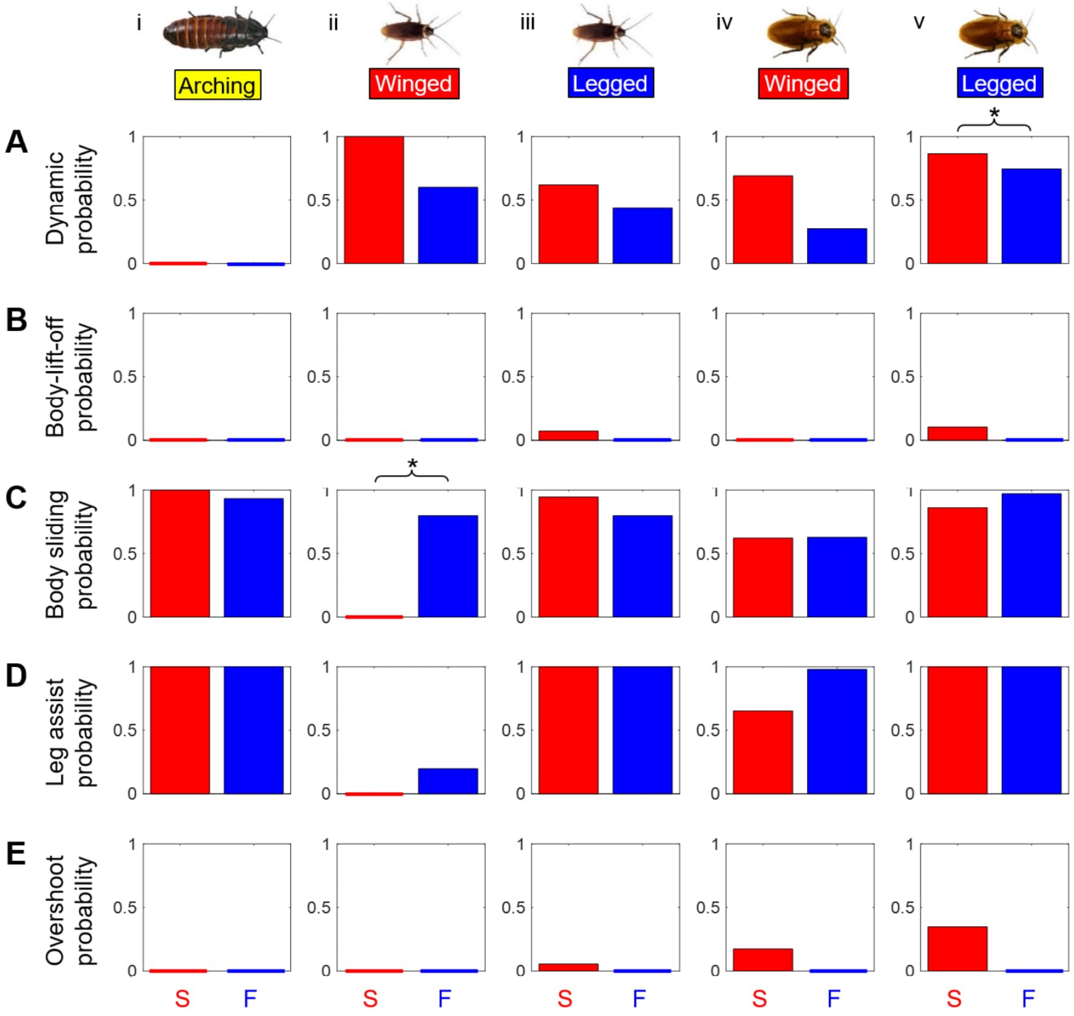
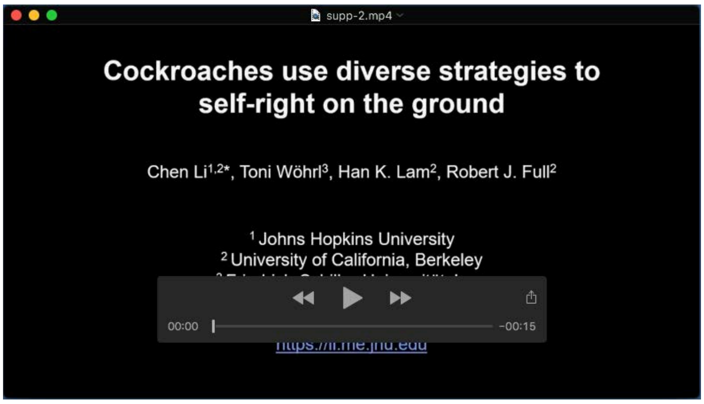


Fig. S3. Body and appendage behaviors that do not show a consistent difference between successful (S, red) and failed (F, blue) attempts. (A) Dynamic probability. (B) Body lift-off probability. (C) Body sliding probability. (D) Leg assist probability. (E) Overshoot probability. (i) Madagascar hissing cockroach using body arching. (ii) American cockroach using the wings. (iii) American cockroach using the legs. (iv) Discoid cockroach using the wings. (v) Discoid cockroach using the legs. Asterisk and braces indicate a significant difference between successful and failed attempts ($P < 0.05$, chi-square test). See Table 1 for sample size.



Cockroaches use diverse strategies to self-right on the ground

Chen Li[1,2*], Toni Wöhrl[3], Han K. Lam[2], Robert J. Full[2]

[1] Johns Hopkins University
[2] University of California, Berkeley

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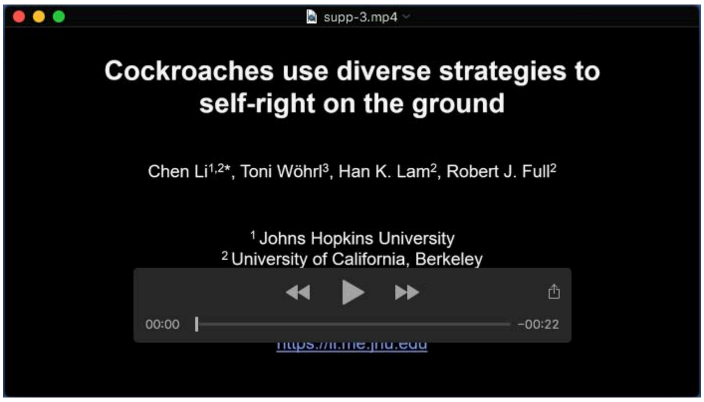
Movie 1: Madagascar hissing cockroach self-righting using body arching.



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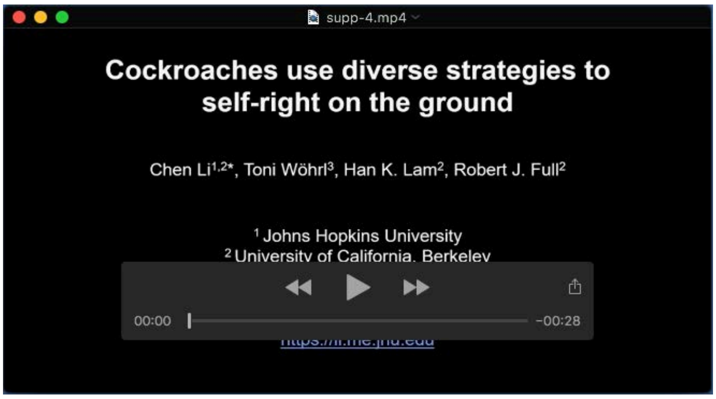
Movie 2: American and discoid cockroaches self-righting using wings.



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Movie 3: American and discoid cockroaches self-righting using legs.

3 Discussion

Ants and cockroaches are both known for their successful radiation into various habitats.[248] For initial movements into such unknown terrains and the ongoing threat by diverse obstacles, the survival of the ants and cockroaches – or organisms in general – relies to a large extent on their versatile locomotor system (Section 1.1). Moreover, their locomotion behaviors may be of significant ecological impact since, for instance, cockroaches function as "mobile fermentation tanks"[249], or ants service as "ecosystem engineers"[250]. Consequently, their role as a kind of model organism for studying the potential advantages of their locomotory morphologies and behaviors has been recognized widely. They have not only been studied extensively in biology, but also in adjacent fields such as robotics and recently in computer animation. However, throughout an elaborated evaluation of the available literature on the description of the very basic mechanical functions of the legs in Hexapoda (see Table 1), I could not find adequate answers of how Hexapoda engage their different leg pairs mechanically for very basic motion tasks such as propulsion and tip-over prevention (intended stabilization) on slopes, or self-righting after toppling (intended destabilization). This includes that the existing contact force measurements (see Table 1), a key in explaining the functioning of legs, do not suffice to explain how Hexapoda employ their legs to hurdle inclined and declined slopes and what happened if they fell and landed in an upside-down orientation.

I motivated further in the general introduction to study animals on the gram and milligram scale, because on such a size level they should be capable of exploiting inertial and gravitational forces as well as adhesion forces for their movements. Specifically the capability to climb could have helped various such small animals to radiate into complex habitats above and below ground, to ascend plants and eventually to become as ecologically dominant and evolutionary successful as they are. Moreover, an integrative study showed that the tripod gait is the optimal gait for fast climbing with adhesion[251], the manner how Hexapoda usually coordi-

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[248] See for instance: Wilson: Success and Dominance in Ecosystems (see n. 167, p. 29); Hölldobler, B./Wilson, E. O.: The Ants, 1st, Belknap Press, 1990; Lach, L./Parr, C./Abbott, K. (eds.): Ant Ecology, Oxford: Oxford University Press, 2009; Bell, W. J./Roth, L. M./Nalepa, C. A.: Cockroaches - Ecology, behavior, and natural history, with a forew. by Wilson, E. O., Baltimore: Johns Hopkins University Press, 2007

[249] Idem: Cockroaches - Ecology, behavior, and natural history (see n. 248), p. 166.

[250] Lach/Parr/Abbott (eds.): Ant Ecology (see n. 248), p. 153; Decaëns, T. et al.: Surface activity of soil ecosystem engineers and soil structure in contrasted land use systems of Colombia, in: European Journal of Soil Biology 2002; Folgarait, P. J.: Ant biodiversity and its relationship to ecosystem functioning: a review, in: Biodiversity & Conservation 1998

[251] Ramdya et al.: Climbing favours the tripod gait over alternative faster insect gaits (see n. 174, p. 30).

nate their legs on land to locomote despite their diverse morphologies and shapes. Thus, I worked out the following question as leitmotif through the three research articles and motivated to conduct the studies on ants or cockroaches:

- (i) Which set of legs among the three leg pairs in Hexapoda accelerates or brakes the animals the most on inclined or declined slopes, respectively (A1 in Figure 6)?
- (ii) How do Hexapoda prevent toppling over on slopes (A2 in Figure 6)?
- (iii) How do Hexapoda self-right from an upside-down orientation after toppling over (A3 in Figure 6)?

3.1 Propulsion

The main brake or drive on declined or inclined slopes, respectively, is above the center of gravity.

With a case study on desert ants *Cataglyphis fortis*, hereafter shortened to *Cataglyphis*, we aimed to identify the main drive and brake among their six legs and how it changes from level walking to inclined and declined locomotion. It was elaborated in Section 1.4.2, that the integral of the ground reaction forces over the contact time (impulses) has to be quantified to compare such accelerating and decelerating functions of the different leg pairs, because the contact time of the legs may differ. It was found that the front legs changed its functioning from the main brake on level locomotion to the main drive on the steep 60 deg upslope. In contrast, the hind legs changed from being the main drive on level locomotion to the main brake on the steep 60 deg downslope (Fig. 1 in Section 2.1).

In combination with kinematic measurements (Fig. 7 and Fig. 2 in the Research Article in Section 2.1) it could be concluded that desert ants utilize the legs above the center of gravity as the main drive on inclined slopes and the legs below the center of gravity as the main brake on declined slopes. The results are plausible when compared with similar experiments on vertically climbing weaver ants[252], because the legs above the center of gravity "carried a significantly larger proportion of the body weight"[253], too, when compared to the legs below the center of gravity.

However, as reasoned earlier, an exact comparison among the studies in labeling the legs with a *main drive* or *main brake* in the different species is vague, because

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[252] Endlein/Federle: On Heels and Toes: How Ants Climb with Adhesive Pads and Tarsal Friction Hair Arrays. (see n. 219, p. 38).

[253] Ibid.

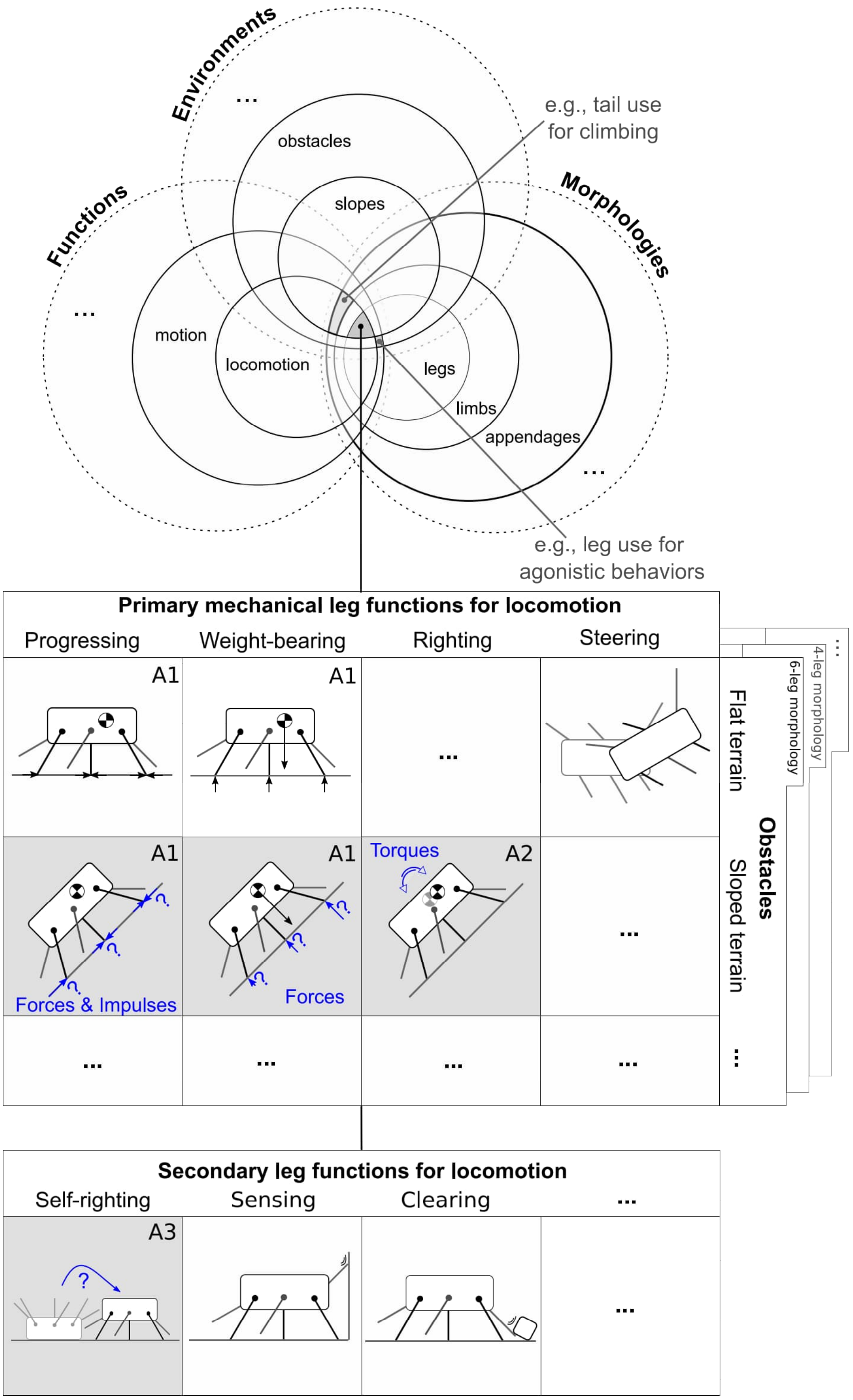

Figure 6: *Mosaic of research effort:* Novel questions (blue questionmarks in grey shaded squares) of the three research articles A1, A2 and A3 of this cummulative dissertation. While the articles A1 and A2 quantify the propulsive, weight-bearing and righting functions of the legs in ants with concepts such as impulses, forces or torques, article A3 analyzes how cockroaches self-right from an upside down orientation and how they employ their legs and body for this action. The figure illustrates further that the results of the three case studies depend highly on the context such as the functional morphology of the animals but also on the motion behavior such as walking, climbing or righting in their environment (obstacles).

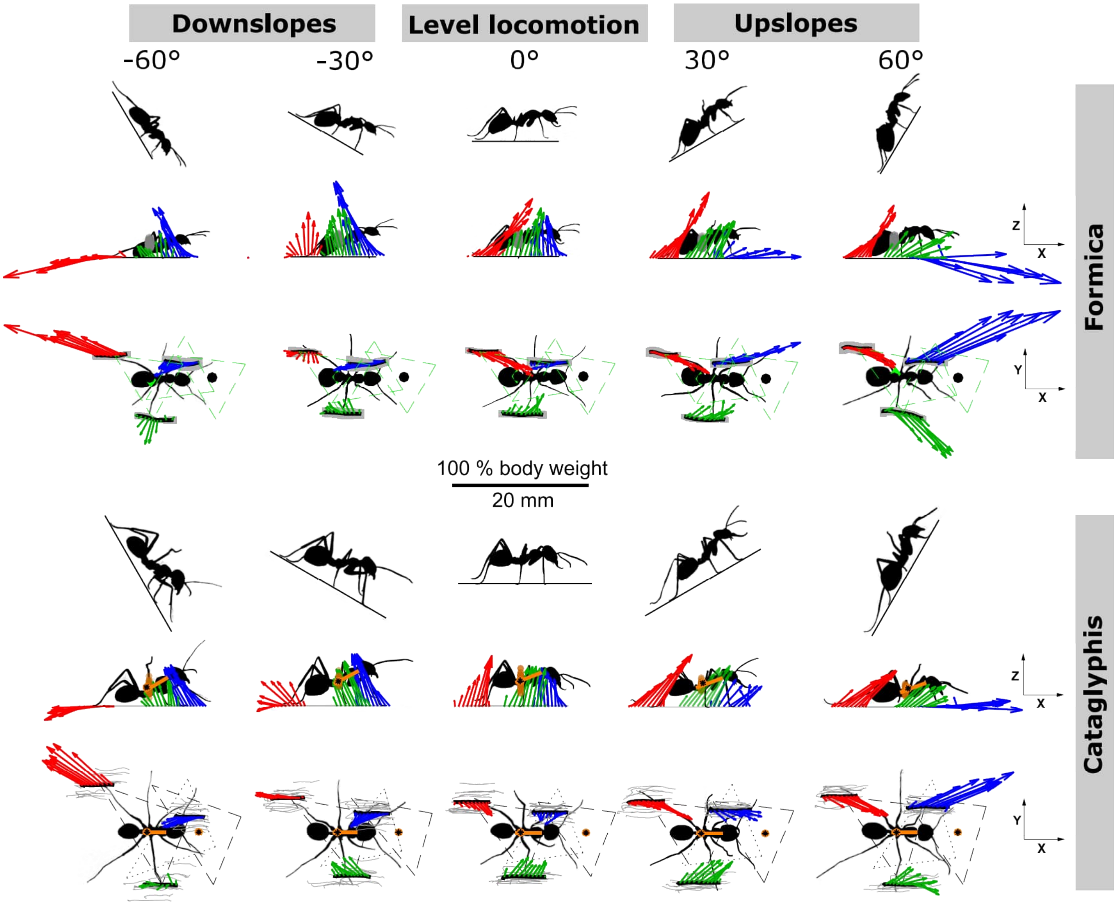

Figure 7: Mean ground reaction force vectors of *Formica* and *Cataglyphis* on -60 deg and -30 deg downslopes, 0 deg level locomotion, and 30 deg and 60 deg upslopes in side views (x-z plane) and normal (top) views (x-y plane). Arrows pointing away from the animals imply leg pulling forces (blue: front leg, green: middle leg, red: hind leg, 15 measurements per leg per species per slope). The triangles border the mean areas of the supporting polygons, and the black dots inside the triangles represent the locations of the center of gravity during mid-stance of the right and left middle legs. The subfigures for *Cataglyphis* were taken from the first publication in section 2.1, whereas the subfigures for *Formica* were presented at the *Motions Systems Perspectives Conference* on the 21st of July, 2016 in Jena.

the integrals of the ground reaction forces (impulses) were not calculated in any of the preceding studies. For instance, Reinhardt/Blickhan[254] showed that the middle legs in *Formica polyctena* (hereafter shortened to *Formica*) kept contact with the ground for about 53.0 ± 3.1 ms, whereas the front and hindlegs had with 44.7 ± 4.2 ms and 46.1 ± 2.6 ms, respectively, about 10 ms shorter contact times, which makes it necessary to either multiply the average force with the contact time

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[254] Reinhardt/Blickhan: Level locomotion in wood ants (see n. 215, p. 38).

or to calculate the integral of the force over the contact time to identify a drive or brake among the legs. I provide this missing link of the leg impulses of *Formica* in Figure 8, which upon the published force measurements by Reinhardt/Blickhan[255].

When the impulses of *Formica* in Figure 8 are compared to the ones of *Cataglyphis* (Figure 1 of Research Article in Section 2.2), the main difference becomes visible in the normal direction of the front legs on the steep upslope and in the lateral direction of the middle legs on the steep upslope. In both cases, the mound dwelling species *Formic* pulls effectively in the normal direction during the ground contact (adhering), whereas the ground dwelling *Cataglyphis* does not pull notably on the substrate. This observation encouraged us to calculate the tipping torques with respect to the critical tipping axis to approach the question of how ants prevent toppling over on inclines (Section 1.4.3 and 2.2).

In summary, as one important extension to earlier studies, the investigation on *Cataglyphis* provides the first quantification of the integrals of the ground reaction forces (impulses), which has led to the identification of the effective accelerating and decelerating function per leg per contact (main drive and main brake) in locomoting Hexapoda.

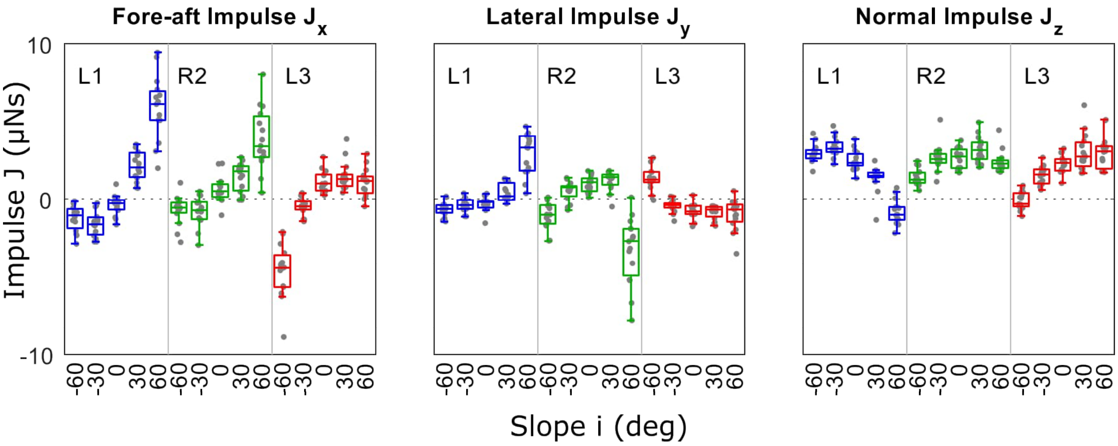

Figure 8: Accumulated forces from the ground on the ants' legs during the contact with the ground (integrals of the ground reaction forces, or impulse) for each leg of *Formica* on -60 deg or -30 deg downslopes, level locomotion, and 30 deg or 60 deg upslopes (15 measurements per leg per slope). The Figure was presented at the *Motions Systems Perspectives Conference* on the 21st of July, 2016 in Jena. Negative or positive signs imply an effective leg pulling or pushing, respectively. Figure 1 in Section 2.1 shows the published impulse data for *Cataglyphis*.

The change from pushing outwards on level locomotion to pulling inwards implies the employment of direction-dependent attachment structures

Furthermore, a transition from pushing away from the midline (laterally out-

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[255] Reinhardt/Blickhan: Level locomotion in wood ants (see n. 215, p. 38).

wards) to pulling towards the midline (laterally inwards) by the legs above the center of gravity was observed when the leg actions on moderate up- and downslopes were compared to the steep up- and downslopes (Figure 7). It was discussed that this notable directional change in the lateral ground reaction forces should incorporate the advantages of direction-dependent attachment structures (e.g., employing the arolia or the claws instead of tarsal hair structures).

Coplanar contact forces during prolonged double support phases enhance shear loading mechanisms

Moreover, with the prolonged double support durations on steep slopes (Table 4 of the Research Article in Section 2.1 and Figure 9) the lateral inwards pulling of the front legs could enhance the effect of "lateral shear loading"[256] (see Figure 10). A notable difference between the desert ant *Cataglyphis* and the wood ant *Formica* occured when the force vectors of the front legs are compared with the ones from the middle legs: Their coplanarity in *Formica* indicate lateral shear loading between the different leg pairs (L1-R2), and their same direction in *Cataglyphis* implies that no shear loading contact forces were employed between the front and the middle leg (see Figure 10).

3.2 Tip-over prevention

3.2.1 Geometry

Cataglyphis prevents tipping-over on slopes by keeping its center of gravity inside the supporting polygon

The prevention of tipping over is another primary mechanical function of the legs for land locomoting animals and has not yet been quantified with torques for climbing Hexapoda (Table 1). The calculation of the torques builds upon the preceding measurements of the ground reaction forces (Section 2.1), and includes additional geometric information of the locomoting animals.

It has been introduced in depth in Section 1.4.3 how either a shift of the center of gravity relative to the supporting polygon (geometric strategy, Figure 11) and/or a pulling by the leg which opposes the critical tipping axis (adhesive strategy) during a three-feet stance helps to counterbalance unintended tipping on slopes. Inspired by the observations on *Cataglyphis* which lowered their center of gravity whereas *Formica* did not show this behavior[257] and the lack of normal pulling

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[256] Labonte, D./Williams, J. A./Federle, W.: Surface contact and design of fibrillar 'friction pads' in stick insects (Carausius morosus): mechanisms for large friction coefficients and negligible adhesion, in: Journal of the Royal Society Interface 2014.

[257] Weihmann/Blickhan: Comparing inclined locomotion in a ground-living and a climbing ant species: sagittal plane kinematics. (see n. 225, p. 40).

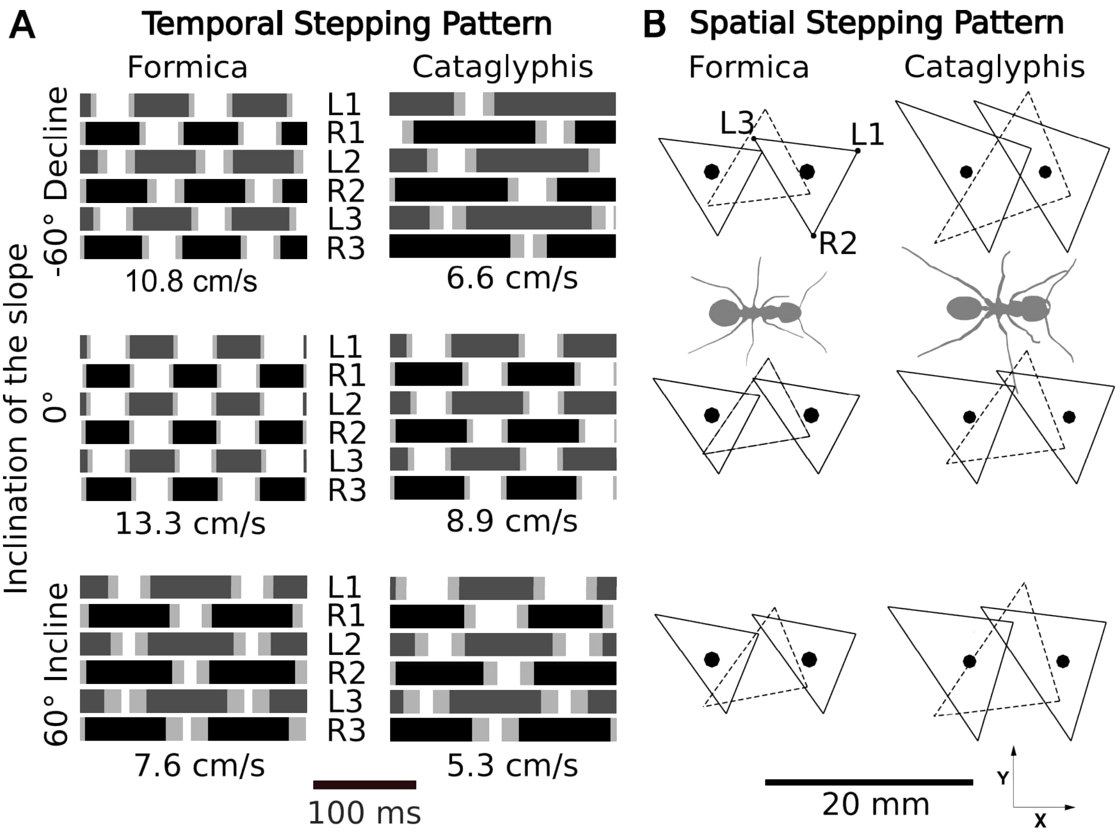

Figure 9: (A) Mean temporal stepping pattern (12 measurements per slope per species, unpublished data) with mean speed in cm$\cdot s^{-1}$ and (B) mean spatial stepping pattern (15 measurements per leg per slope per species) of *Formica* and *Cataglyphis* on -60 deg decline, level locomotion and 60 deg incline (L1: left front leg, R2: right middle leg, L3: left hind leg). In the temporal stepping patterns, the white gaps and the light gray shaded bands visualize the swing durations and the standard deviations of the contact durations of the legs, respectively.

forces on the 60 deg incline (Section 2.1), the question of how ants prevent tipping over has been worked out in Section 1.4.3 and 2.2. It was first quantified whether *Cataglyphis* keeps its center of gravity inside the supporting triangle during the three feet stance (geometric strategy) and whether it was sufficient for *Formica* to not lower down its center of gravity to keep its center of gravity inside the supporting polygon. In a second step, the torques of the center of gravity and the leg which opposes the critical tipping axis were calculated with respect to the critical tipping axis to quantify the quasi-static torque equation and to evaluate a potential righting impact of the legs (adhesion strategy). From this analysis several conclusions were drawn.

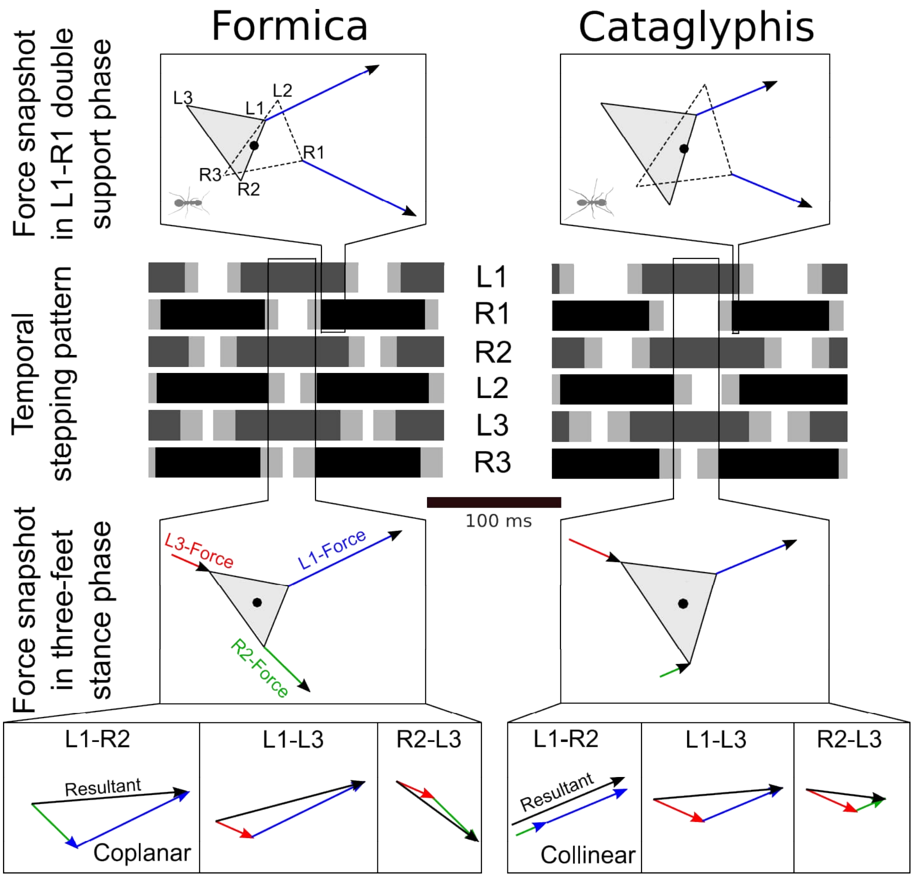

Figure 10: Snapshots of the ground reaction force vectors attached to the spatial stepping patterns of *Formica* and *Cataglyphis* on a 60 deg inclined slope illustrate shear-loading forces (i) within a set of leg (L1,R1) and (ii) between the left front L1, right middle R2 and left hind leg L1 (compiled from Figure 7 and 9). First, one notable difference occur in the prolonged double support phase of the front legs L1 and R2 in *Formica* compared to *Cataglyphis*, where the force vectors (blue arrows) point longer away from each other in the lateral plane (lateral front leg pulling). Second, during the three-feet stance, the left front leg L1 and right middle leg R2 work against each other in the lateral direction for *Formica* (coplanar vectors), whereas they point in the same direction for *Cataglyphis*.

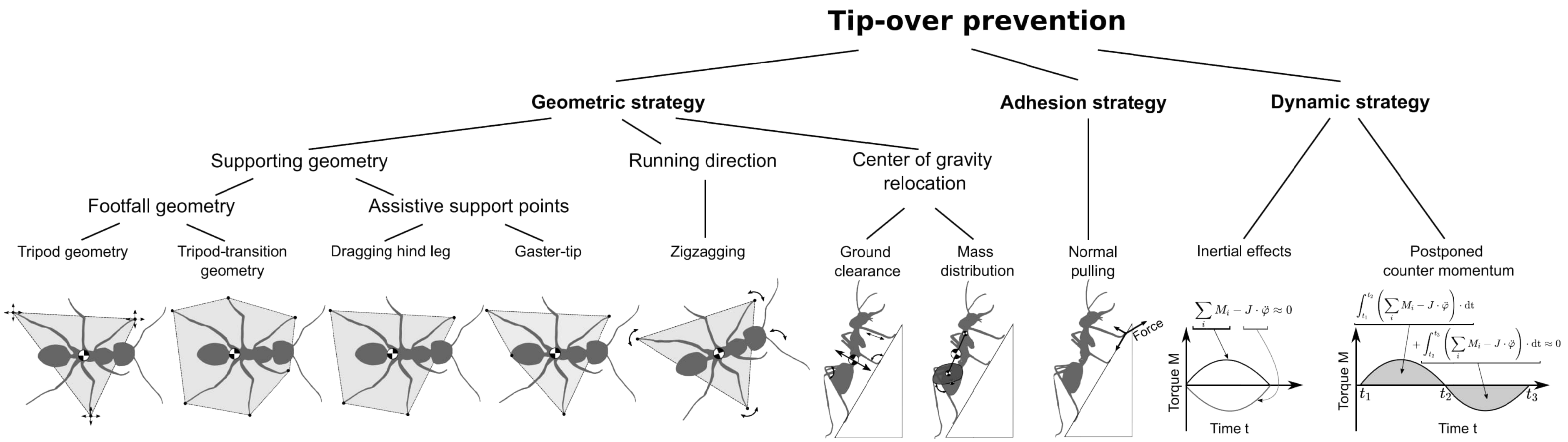

Figure 11: Tip-over prevention strategies, geometry, adhesion, and dynamics. Please note that the behaviors cannot be distinguished as clearly as the diagram may communicate. For instance, a change of the supporting geometry may likely be intertwined with a center of gravity shift and a change in the sum of the torques M_i, the moment of inertia J and the angular acceleration $\ddot{\varphi}$ with respect to the critical tipping axes.

It was found out that the *Cataglyphis* ants avoid toppling during the three-feet stance on steep inclined slopes by geometric changes which helped them to move their center of gravity into the vertical projection of their supporting polygon. In more detail, the observed geometric changes were not only caused by a significant lowering of the center of gravity but also by a significant increase of the supporting area. In contrast, Seidl/Wehner[258] concluded from their preceding measurements on climbing *Cataglyphis* ants that "after removing the effect of speed, slope had only marginal influence on kinematic parameters"[259]. However, even if slope had only marginal (direct) influence on their measured step length, or metrics such as the anterior and posterior extreme positions, the enclosed area of the tarsi (supporting area) may sum up the several small changes of the footfall positions and hence change the orientation of the critical tipping axis or the supporting area notably as measured in our study on *Cataglyphis* (Figure 3 in Section 2.2, an effect of speed was not removed, instead the total effect of slope on the supporting area was investigated).

Moreover, even if the anterior and exterior extreme positions did not change notably on slopes in *Cataglyphis*[260] and *Formica* (Figure 12 A), the intra-leg kinematics could still change as measured for *Formica* in the femur-tibia angle (Figure 12 B) or *Cataglyphis* in the tibia-surface angle (Figure 12 C). Additionally, it is very likely that alterations in the the coxa-femur joints and/or the femur-tibia joints caused lowering of the center of gravity on slopes in *Cataglyphis*[261] (Figure 5B in Section) , because another plausible cause such as variations in the petiolus-gaster joint can be ruled out in our measurements since we calculated the center of gravity as a quasi-fixed point between the petiolus and the neck according to McMeeking/Arzt/Wehner[262] and Reinhardt/Blickhan[263].

Thus, an ongoing investigation may quantify, for instance, how a raising gaster impacts their stability (Figure 11), and how the intra-leg kinematics (Figure 13) affect the supporting geometry and the center of gravity trajectory. This may then contribute to the investigations on graviception and the path-integrating mechanisms in *Cataglyphis* [264] which have been referenced in more detail in the research

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[258] Seidl/Wehner: Walking on inclines: how do desert ants monitor slope and step length (see n. 229, p. 41).

[259] Ibid.

[260] Ibid.

[261] Weihmann/Blickhan: Comparing inclined locomotion in a ground-living and a climbing ant species: sagittal plane kinematics. (see n. 225, p. 40).

[262] McMeeking, R. M./Arzt, E./Wehner, R.: Cataglyphis desert ants improve their mobility by raising the gaster, in: Journal of Theoretical Biology 2012.

[263] Reinhardt/Blickhan: Level locomotion in wood ants (see n. 215, p. 38).

[264] For instance, Seidl/Wehner: Walking on inclines: how do desert ants monitor slope and step length (see n. 229, p. 41); Ronacher, B.: Path integration in a three-dimensional world: the case of desert ants, in: Journal of Comparative Physiology A 2020

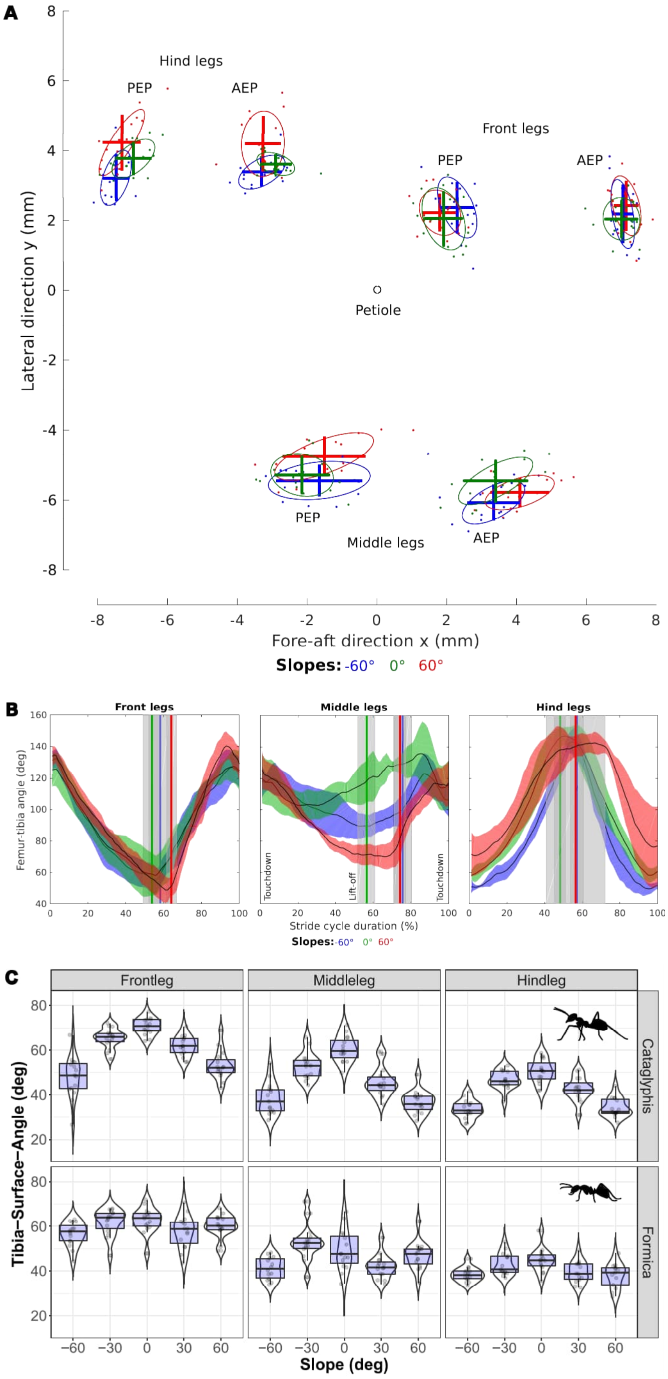

Figure 12: Footfall geometry (A) and femur-tibia angle (B) of *Formica* on a -60 deg declined slope (blue), 0 deg level locomotion (green) and a 60 deg inclined (red) slope. The (arithmetic) mean anterior extreme positions (AEP) and posterior extreme positions (PEP) of the front, middle and hind legs did not change notably (15 measurements per leg per slope, bars indicate the standard deviations), whereas the (arithmetic) mean femur-tibia angle of the middle legs changed on slopes during the lift-off and swing duration (5 measurements per leg per slope, shaded area shows the standard deviation). The mean tibia-surface angles during the ground contacts (C) changed for *Cataglyphis* on different slopes, but not for *Formica*. The data for the subfigures (A) and (B) were presented on the *Motions Systems Perspectives Conference* on the 21st of July, 2016 in Jena, whereas the data for subplot (C) were presented on the 19th of November, 2019 at the Institute of Zoology and Evolutionary Research in Jena.

article in Section 2.1.

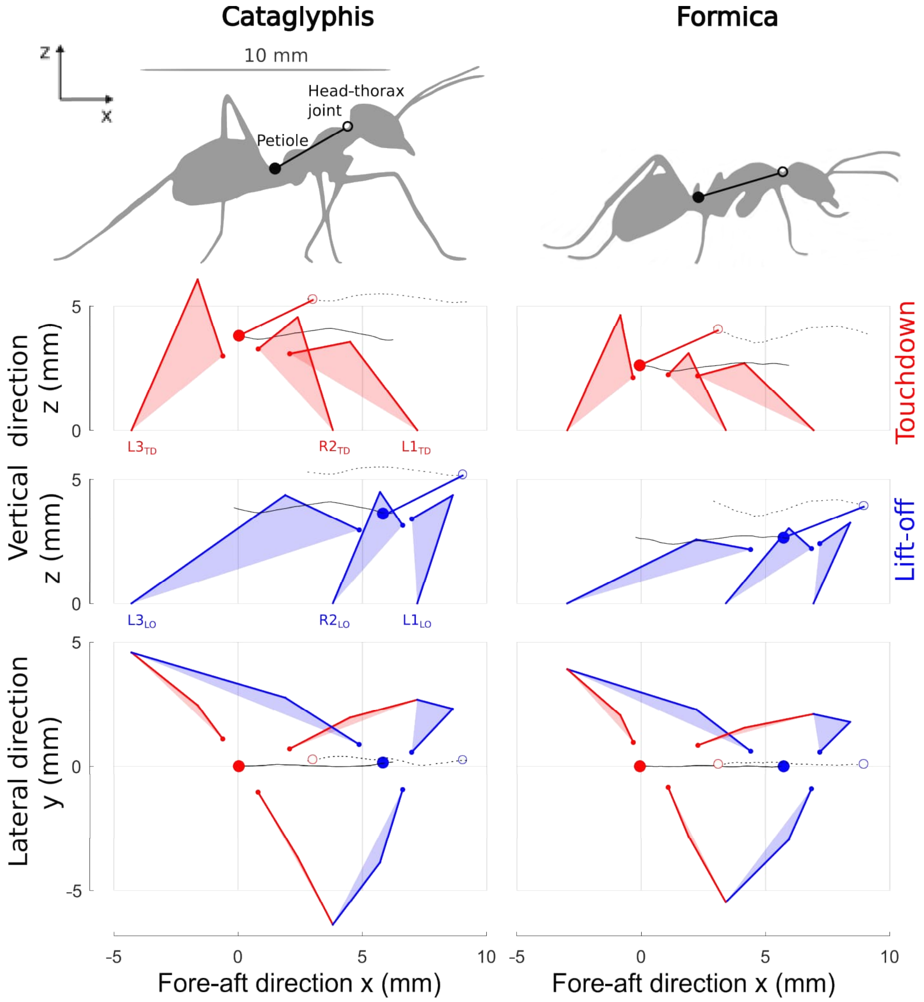

Figure 13: Mean leg geometries during the touchdown (red) and lift-off (blue) of the tarsi for *Cataglyphis* and *Formica* on level locomotion from side and top view (5 measurements per leg per species, unpublished data).

Zigzagging as a geometric sub-strategy helps to quickly re-orient the critical tipping axis

Ants seldom ran along a straight path over several gait cycles. Whereas changes in the direction of progressions could, for instance, be assigned to "random walks"[265] for searching, escaping, or geographic mapping behavior, it could also function to

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[265] Kareiva, P./Shigesada, N: Analyzing insect movement as a correlated random walk, in: Oecologia 1983.

balance the ants while they are in motion. This is because some relatively small left-right turns (zigzagging) can have a relatively high effect on the vertical projection of the supporting polygon, and thus the equation of the tipping moments. For instance, if the ants “roll over” the slanted axis formed by the right front and left middle leg while they are progressing (Figure 2A of the research article in Section 2.2), the next footfall geometry will likely happen to be slightly rotated with respect to the current supporting polygon (one can image something like a tetrahedron tilting up or down a slope). Subsequently, the zigzagging supporting polygon can function to fetch a falling center of gravity iteratively. Since *Cataglpyhis* operates on the edge of not falling backwards on upslopes (see center of gravity location in the zenithal view in Figure 2A of the research article in Section 2.2), small twists of the supporting polygon should affect their balance notably. Thus, zigzagging should help in particular the type of Hexapoda which aim to climb but which do not have sufficient adhesive capabilities to counterbalance unintended tipping (Figure 11). To verify this theoretically, an ongoing sensitivity analysis could, for instance, compare the effect of changes in the running direction, body height adjustments and supporting area size on the vertically projected minimum stability margin on slopes.

3.2.2 Adhesion

Formica prevents tipping-over on slopes by pulling on the substrate; gaster contact with the ground was not necessary to stabilize the posture

It was further found out that the *Formica* ants neither changed their supporting area, nor the effective lever arm of their counterbalancing leg, nor their center of gravity height, which subsequently led to a negative stability margin on steep slopes (Figure 3 of the research article in Section 2.2). A negative stability margin would have resulted in toppling over, if their leg righting torques would not have counterbalanced this behavior. Thus, their pulling on the substrate (Figure 4A of the research article in Section 2.2) helped them to stabilize their three-feet contact posture on steep slopes (Figure 4B of the research article in Section 2.2). From this results can be concluded that neither the gaster tip, which was observed to touch the ground occasionally in walking wood ants[266], nor the dragging hind legs[267] were necessary to stabilize on average the *Formica* ants in our measurements. However, increasing the supporting area and thus shifting the critical tipping axis by such an additional gaster contact point may still benefit the ants in cases, where they

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[266] Reinhardt/Weihmann/Blickhan: Dynamics and kinematics of ant locomotion: do wood ants climb on level surfaces? (see n. 230, p. 41).

[267] Reinhardt/Blickhan: Level locomotion in wood ants (see n. 215, p. 38).

suddenly may not counter the torques of the center of gravity with their normal pulling, or adhering, legs.

Adhesive pulling with the front legs could increase normal load on the hind legs to prevent slipping

The differences in the leg pulling behavior of the front legs among the ground living desert ant *Cataglyphis* and the mound dwelling wood ant *Formica* became also evident in the angle between the leg impulse of the hind legs and the substrate (Figure 6 of the research article in Section 2.2): The wood ants burdened their hind legs more in the normal direction which eventually led to bendings and increased side contacts of their tarsal hairs and thus to higher (potential maximal) friction forces. Such improvements of the friction forces through an increased side contact of tarsal structures induced by higher normal loads have been described in weaver ants *Oecophylla smaragdina*[268]. The higher potential maximal friction forces could subsequently prevent *Forimca* from slipping, too, and allow their hind legs to push stronger on inclines. However, to verify this, experiments in the style of Endlein/Federle[269] which simultaneously record the bending of the tarsal hairs are necessary, while the animals are in motion.

3.2.3 Dynamics

Cataglyphis and Formica balance dynamically

Both ants must balance dynamically. This can be concluded from the tracings of the summed torques in Figure 4B of the research article in Section 2.2. Since the sum of the quasi-static torques does not equal zero (tipping into the support polygon), it can be concluded that either the neglected inertial effects balance the torque equation, or the obvious accumulated negative angular momentum (integral of the sum of the torques) during the three-feet stance has to be counterbalanced later during the successive tripod-transition phase (see dynamic mechanisms in Figure 11). Thus, the torque analysis in Section 2.2 provides a template for later studies to indirectly conclude the necessity of dynamic balance in legged animal locomotion.

Stabilizing functions of the three-feet transition phases

In hexapedal running gaits, the “risky” triangular support bases alternate with no (aerial phase), or only relatively short lasting alternative supporting shapes in

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[268] Endlein/Federle: On Heels and Toes: How Ants Climb with Adhesive Pads and Tarsal Friction Hair Arrays. (see n. 219, p. 38).

[269] Ibid.

the tripod transition phases. Thus, the likely larger supporting shapes during the tripod transitions function to change the critical tipping axis and re-stabilize the animals for the next tarsal lift-offs. Thereby, the prolonged duration on slopes, where the ants are supported by more than three feet (Figure 9), help them to "recover" from the aforementioned accumulated negative angular momentum during the three feet stance (see Paragraph "*Cataglyphis* and *Formica* balance dynamically" and Figure 4B of the research article in Section 2.2). Such a "falling into a new and (potentially) larger supporting shape" and "absorption of energy by more than three legs" can clearly be seen in the tracings of *Formica's* center of gravity[270] and mechanical energy[271] in the beginning of the tripod transition phases. Although this description may sound like the ants prolong purposefully the triopd transition phases on upslopes, it is probably still a consequence of the animals limited metabolic energy flow (power) and muscle architecture, because the inclined walking not only requires additional work against gravity compared to level locomotion. Thus, they walk slowlier on slopes with prolonged tripod transition phases (Figure 3 and Table 4 in the research article in Section 2.1) as a consequence of the intrinsic metabolic system of the animals, which in turn also benefits mechanically intelligent their tip-over prevention mechanisms.

Outlook: How does Cataglyphis climb in underground nests?

Since the desert ants showed difficulties in surmounting the steep slope and did not pull notably on the substrate on steep inclines (Section 2.1) and generated subsequently no notable leg righting torques (2.2), it would be interesting to know how they climb or move in their underground nests (personal note by R. Blickhan in 2021). Thus, future investigations in the field should reveal more insights on the characteristics of their fossorial habitat (e.g., inclination, substrate properties) in conjunction with their subterraneous climbing capabilities to describe how they employ their legs on their natural substrate compared to the standardized graph paper surface in the lab. Such experiments would eventually help to add further meaningful biological relevance to the interpretation of the findings and contribute to the "emerging interdisciplinary hotspot of 'mechanical ecology"'[272].

3.3 Stabilization and destabilization in locomoting and self-righting animals

Tip-over prevention behaviors may not always suffice to prevent the animals from toppling and ending up in an upside-down orientation. In such cases, they must

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[270] Figure 4 in: Reinhardt/Blickhan: Level locomotion in wood ants (see n. 215, p. 38)

[271] Figure 7 in: ibid.

[272] Bauer, U./Poppinga, S./Müller, U. K.: Mechanical Ecology—Taking Biomechanics to the Field, in: Integrative and Comparative Biology 2020.

self-right to survive.[273] To describe self-righting behaviors mechanically, a potential energy landscape model was introduced for cockroaches in the article "Cockroaches use diverse strategies to self-right on the ground"[274] (Section 2.3). Thereby, the shapes of the animals are related to potential energy landscapes (Section 2.3) to describe self-righting (intentional *destabilizing*) paths from an energetic perspective. Certainly, energy concepts can also be used to shed new light on (intentional) *stabilizing* strategies during locomotion at inclines, which I aim to describe in the following section by linking the articles in Section 2.3 with the one in Section 2.2.

Intrinsic versus external potential energy landscapes

First, I want to emphasize again the explanatory value of morphological descriptions for the identification of mechanism and functions in animal locomotion. For instance, with the aid of geometric measures one can create a potential energy landscape model of an animal (Figure 7 of the research article in Section 2.3), which is not the same as the topographic map with relief features of the surrounding environment, to explain diverse motion behaviors. However, both the intrinsic potential energy landscape model of the animal and the one of the (external) surrounding environment together explain for example, how effective a change in the supporting pattern and the center of gravity would be to prevent unintended tipping, or how an energy barrier could be hurdled with the least energetic cost.

Ambivalence of stability in locomoting and self-righting animals

To be more specific, the lowering of the center of gravity and the increased supporting polygon of the desert ants (Section 2.1 and 2.2) eventually lead to a deepened potential valley which secures the animal against toppling. At the downside, the deepened potential valley increases the cost for the animals to lift up their center of gravity to roll over the tipping axis intentionally and fall into the subsequent support polygon for their locomotion. This may explain why many animals with relatively large supporting areas and low body heights, thus with possibly high static stability factors or tilting angles, move with, for instance, peristaltic or undulatory motions (e.g., millipedes, worms, snakes, see also Figure 3) and do not invest in high bouncing amplitudes in the vertical direction to move their center of gravity over their intrinsic potential energy barrier. In contrast, bipedal locomotors with a relatively high center of gravity and small supporting areas, for instance, invest in vertical oscillations to tip-over intentionally and "fall" with ease

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[273] Li, C. et al.: Cockroaches use diverse strategies to self-right on the ground, in: Journal of Experimental Biology 2019.

[274] Ibid.

into the subsequent support polygon for their locomotion. A raising of their energy barriers by changing their supporting geometry and lowering their center of gravity may not be energetically costlier and less functional for their locomotion.

If an animal tilts, for instance on a steep incline, its center of gravity may reach a potential ridge. From there, the center of gravity may travel down to a different potential valley, which associates most likely to the upside-down orientation of the animal. In this dangerous upside-down stage, the animal has to quickly switch its strategy by changing its shape to roll back more easily over a preferably lower potential energy ridge, and by accumulating sufficient kinetic energy to initiate the intended tipping. In contrast, a car as an ideograph for a moving block with a locked shape (Figure 14) cannot self-right.

Time-dependent potential energy landscape layers

For geometry-changing motion systems such as legged animals, the whole potential energy landscape of the animal changes over time while the animal is in motion. This is another reason why it is so complex to describe and emulate animal motions. For a brick-shaped stiff car in contrast, the potential energy landscape is more confined and does not change while the car moves. Furthermore, a stiff brick or primitive car cannot adjust its posture and therewith its own intrinsic morphological potential energy landscape layer to the external potential energy landscape layer of the surrounding environment to find the best path within the intermeshed landscape of the two energy layers (body-obstacle interaction). With this in mind, it is valuable to describe, classify, and preserve the diversity of animal morphologies together with their various motion behaviors while being confronted with different obstacles, to build up a systematic collection of legged locomotion mechanisms and their associated energy landscape models.

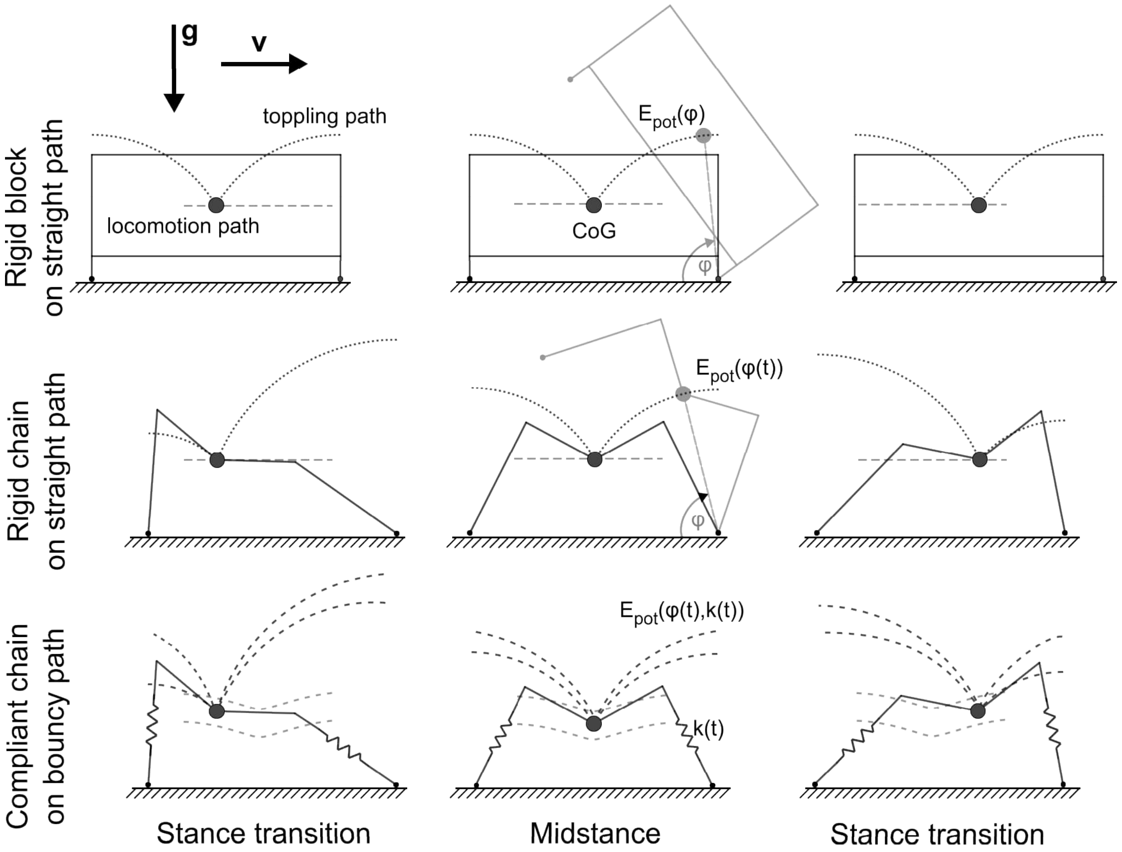

Figure 14: Potential energy landscapes of toppling locked motion systems (quasi-static scenarios, **g**: gravitational acceleration, **v**: velocity). For a rigid rolling or sliding block a fixed potential energy landscape E_{pot} can describe its postural stability. For a legged system which shifts its center of gravity (CoG) relative to its supporting points to progress, the potential energy landscape changes while the animal is in motion. The dashed E_{pot} paths illustrate how much the CoG had to be lifted up before the rigid block or the locked chains topple over (temporal tipping angle $\phi(t)$) at the illustrated motion snapshots (stance transition, midstance). To describe the toppling path for compliant chains with elasticities, more initial and boundary conditions such as velocity or temporal spring rate k(t) are necessary. However, such a complex mechanical system which approaches animal-alike locomotion more than a rigid block should facilitate more solutions for reacting to external disturbances.

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[275] DFG - GEPRIS - Verteilung der Bodenreaktionskräfte bei Ameisen, URL: `https://gepris.dfg.de/gepris/projekt/139222534?context=projekt&task=showDetail&id=139222534&`.

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Declaration of independent assignment

I hereby declare that I am familiar with the Faculty's applicable Doctoral Examination Regulations from the 17th of June 2018[276];

that I have composed and written the dissertation with the title "Towards understanding of climbing, tip-over prevention and self-righting behaviors in Hexapoda" on my own;

that I have not used any text passages from third parties or from my own theses or seminar papers without proper reference, and that I have cited in my dissertation any tools, personal communication, and sources used;

that only the following coauthors have assisted me in the selection and analysis of materials and/or supported me in preparing the articles for this cumulative dissertation: Reinhardt, L., Li, C., Lam, H. K., Full, R. J., Richter, A., Guo, S., Nowotny, M. and Blickhan, R.;

that only B. Boudinot proofread a penultimate draft of the manuscript;

that I have not received assistance from commercial consulting services for doctoral studies, and that no third party has received monetary or nonmonetary perquisites from me directly or indirectly for work performed in connection with the submitted dissertation;

that I have not submitted the dissertation as an examination document as part of a public or other academic examination;

that I have not submitted the same, a substantially similar, or a different work to another university as a dissertation.

Toni Wöhrl, date, place

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[276] Friedrich-Schiller-Universität Jena: Promotionsordnung der Fakultät für Sozial- und Verhaltenswissenschaften der Friedrich-Schiller-Universität Jena vom 17. Juli 2018 (Verkündungsblatt der Friedrich-Schiller-Universität Jena Nr. 5/2018 S. 209), 2018, URL: `https://www.hanfried.uni-jena.de/vhbmedia/promotion-+und+habilitationsordnungen/05_fakult%C3%A4t+f%C3%BCr+sozial-+und+verhaltenswissenschaften/promotionsordnung+fakult%C3%A4t+f%C3%BCr+sozial-+und+verhaltenswissenschaften.pdf`.