Utilization of granular solidification during terrestrial locomotion of hatchling sea turtles

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Biological terrestrial locomotion occurs on substrate materials with a range of rheological behaviour, which can affect limb-ground interaction, locomotor mode and performance. Surfaces like sand, a granular medium, can display solid or fluid-like behaviour in response to stress. Based on our previous experiments and models of a robot moving on granular media, we hypothesize that solidification properties of granular media allow organisms to achieve performance on sand comparable to that on hard ground. We test this hypothesis by performing a field study examining locomotor performance (average speed) of an animal that can both swim aquatically and move on land, the hatchling Loggerhead sea turtle (Caretta caretta). Hatchlings were challenged to traverse a trackway with two surface treatments: hard ground (sandpaper) and loosely packed sand. On hard ground, the claw use enables no-slip locomotion. Comparable performance on sand was achieved by creation of a solid region behind the flipper that prevents slipping. Yielding forces measured in laboratory drag experiments were sufficient to support the inertial forces at each step, consistent with our solidification hypothesis.

Keywords: Loggerhead sea turtle; biomechanics; locomotion; granular media; drag; limb

1. INTRODUCTION
Locomotion (Dickinson et al. 2000; Alexander 2003) on sand, a granular medium (Jaeger et al. 1996), is challenging because sand surfaces can flow during limb interaction and slipping can result, causing both instability and decreased locomotor performance (Lejeune et al. 1998). An important parameter that governs interaction of limbs with sand is the yield stress, defined as the force per unit area at which non-reversible material deformation occurs (Nedderman 1992). For a given geometry, for forces below $F_{\text{yield}}$ the material behaves like an elastic solid, while above $F_{\text{yield}}$ the material flows like a fluid dominated by friction between grains. This transition can have major effects on locomotor performance: our systematic studies of...
was used to mimic hard ground. Two high-speed cameras (Sony Handycams, 240 fps under infrared light) recorded dorsal (figure 1a) and lateral images. Natural and removable markers (located on the carapace and the mid-point of the flipper) aided tracking of movement. Three runs per animal, with up to five animals, were recorded in a 2 h span. A run was considered successful if the animal took more than three steps, such that cycle average velocity returned to within 35 per cent of the velocity of the preceding step. Hatchlings were released at their collection location.

We performed laboratory measurements on a model flipper to estimate thrust forces. The model flipper consisted of a thin (1.45 mm) aluminum plate 3 cm long (comparable to flipper length) that was inserted into the Jekyll Island sand to the given penetration depth ($d = 0.25–1.25$ cm) and dragged at 0.05 cm s$^{-2}$ over a distance of 5 cm; as in other experiments (Maladen et al. 2009), drag force was independent of speed up to 20 cm s$^{-1}$. Calibrated strain gauges mounted to the model flipper provided force measurements during drag. Displacement was controlled by a stepper motor and lead-screw. Force data were sampled at 1 kHz. Yield force of the media was determined from the $y$-intercept of a linear fit to the drag force after motion of the plate began (figure 2b).

3. RESULTS

Despite the different contact mechanics associated with sand and sandpaper, forward velocity of the body (close to centre of mass) $v_x$ versus time was
similar on both substrates. At each step, \( v_x \) increased from zero to a maximum then dropped rapidly to zero again (figure 1b). Average speed on sand was reduced by 28 per cent (better than SandBot performance loss) relative to hard ground, but maximal speeds were the same in both treatments. Turtles employed a diagonal gait (Wyneken 1997) with average stance duty factors of 0.66 ± 0.05. During each stride, the body was lifted off the ground by an average of 2.2 ± 0.9 mm, and then touched down at the end of the cycle (figure 1b). Average \( v_y \) increased linearly with stride frequency \( f \) (in hertz) as \( (v_y) = sf \) (figure 1c) with similar stride length, \( s = 4.0 ± 1.9 \) cm on sand and \( s = 4.7 ± 2.9 \) cm on hard ground; \( s \) was significantly different from 0 for all treatments \( (p < 0.0001) \) and the slope of the regressions were not statistically different \( (p > 0.05) \). Average inertial force \( (ma) \) on sand increased with frequency (figure 2c). Limb kinematic measurements revealed that the angular extent of the shoulder excursion did not depend on the treatment (sand: 111 ± 17°; sandpaper: 114 ± 6°; \( p > 0.05 \)) in accord with the derived stride length.

On sand, at touchdown, pressure owing to the thin (approx. 2 mm wide) edge of the flipper exceeded the vertical yield stress and it penetrated into the sand. The limb (shoulder) rotated as the flipper penetrated until the flipper was perpendicular to the surface. The rotation served to lift (figure 1b) the body (see discussion of model below and in the electronic supplementary material, SI). During thrust, the portion of the flipper in the sand (approx. 3 cm long and 0.76 cm deep on average) at first remained perpendicular to the direction of motion (relative flipper surface-forward velocity angle during mid-stance was 99.4 ± 16.9°) and later was adducted, as both the wrist and shoulder rotated and the body moved forward and upward (electronic supplementary material, video S2). On sandpaper, a claw at the wrist engaged irregularities and propelled the animal forward; during thrust the shoulder rotated towards the body and the wrist did not bend keeping the limb fully extended. A tracked marker on the mid-point of the flipper (figure 1a,b) demonstrated that limb slip was minimal on both substrates (net displacement of >1 flipper-width in only 2.6% of steps on sandpaper and 5.6% on sand) during forward movement, consistent with equivalent stride lengths.

4. DISCUSSION

Our results imply that speeds on sand and hard ground are similar, because for both treatments limbs do not slip during locomotion, stride length is constant and \( (v_y) = sf \). On hard ground, no-slip is maintained by a claw engaging irregularities. On sand, entirely different mechanics account for no-slip: in successful runs, material behind the flipper did not move during the thrust phase, supporting the hypothesis that the turtle advances via solidification of the material behind it.

Forward movement of the body on sand without slipping of the flipper requires that net thrust forces \( F_{thrust} \) remain below the yield force of the granular medium, \( F_{thrust} < F_{yield} \). We assume that the mechanics of the large front flipper (maintaining surface normal vector parallel to \( v_y \)) produces the dominant contribution to \( F_{thrust} \). Observation of the smaller hind limbs indicate that at initiation of stance, the foot remains plantar and above the surface during the entire step, presumably contributing to lifting the body and less to thrust (force measurements in a different turtle species (Wyneken 1997) shows evidence that they are used for lifting although no force data exists for Loggerheads). Since the animal lifts at each stride using both hindlimbs and forelimbs (figure 2a), we assume that the plastron is not in contact during the thrust phase and thus body drag is not significant.

Therefore, \( F_{thrust} \) needs to generate only the inertial forces \( (mass \times acceleration; ma) \) required to accelerate the animal from rest to its maximum velocity (figures 1b and 2a). As plastron elevation removes drag during the stride, locomotion is governed by \( F_{thrust} = ma \). We estimate average inertial forces from linear fits of the body velocity during the acceleration phase of the movement (figures 1b and 2b). Since \( v_{peak} = 2.88 \) \( v_y \) \( (r^2 = 0.88) \), and \( v_y \) is proportional to \( f \), we expect average inertial forces \( (ma \propto v_{peak} f) \) during a step to increase as \( f^2 \) (see electronic supplementary material). The data are consistent with this prediction (figure 2c).

We estimated ground reaction forces from the drag of a model flipper. Drag force on a plate (figure 2b) increased sharply within the first millimetre of displacement. We identify the force at the end of this sharp increase as \( F_{yield} \) since it is generated in a short distance and no large-scale flow of material occurs. \( F_{yield} \) increases as the square of the penetration depth (figure 2b) and linearly with plate width (Wieghardt 1975). The existence of \( F_{yield} \) thus provides a possible mechanism for solidification and generation of thrust forces on sand without slipping, by using the solid properties of the media. If \( ma < F_{yield} \) (or \( ma / F_{yield} < 1 \)), material solidifies during the power stroke.

Choosing \( F_{yield} \) at the average measured flipper insertion depth, \( d = 0.76 ± 0.13 \) cm, reveals that the majority of the derived fore-aft acceleration data satisfy the criterion \( ma / F_{yield} < 1 \) (figure 2c) and thus indicates that the material can remain solid with the use of a single flipper. Only at the greatest accelerations does the model predict slip. We do not observe limb slip in these runs, and speculate that, at these large accelerations, the hind limb contributes by friction from its plantar surface (we estimate that if the hind flipper supports half the turtle’s weight on sand, with a measured surface friction coefficient of \( \mu = 0.6 \), the thrust/\( F_{yield} \) from friction, \( \mu mg / (2F_{yield}) \approx 0.6 \) would be sufficient to account for the largest observed inertial forces). Force platform data are needed to determine the individual contributions to thrust from forelimbs and hindlimbs. In addition, we hypothesize that \( F_{yield} \) can be increased if limb rotation during entry (which could enhance normal loading and material compaction) is considered; further physics experiments are needed to test this hypothesis.

Our model reveals that a major challenge for rapid locomotion on sand is the balance between high speed, which requires large inertial forces, and the
potential for failure through fluidization, which can occur when inertial forces (which increase sensitively like $f^2$) exceed $F_{\text{yield}}$. In the SandBot experiments, failures through fluidization could be induced by the reduction of $F_{\text{yield}}$ through changes in material compaction (Li et al. 2009). Since $F_{\text{yield}}$ depends on many factors, including particle properties and hill angle, it may be ecologically important to examine performance (and possible locomotor failures) as a function of substrate properties like beach topography (inclines) or sand type (e.g. through renourishment (Steinitz et al. 1998)).

In conclusion, high-performance locomotion on yielding substrates such as sand can be achieved using the solid-like response governed by the yield stress. Further biological studies and physical models of turtles (and other organisms) are required to determine if and how organisms control limb movements to remain below the yield stress on granular media. More broadly, to discover principles of passive and active nervous and mechanical system control (Nishikawa et al. 2007), as well as to understand energetic costs (Lejeune et al. 1998) in locomotion on and within realistic terrain, will require advances in theory and experimental characterization of complex media. Otherwise we must continue to rely on empirical force laws specific to particular geometries, kinematics and granular media.

Fieldwork permitted under State of Georgia Scientific Collecting Permits 29-WBH-08-122 and 29-WCH-07-96.

We thank Robert Dudley for helpful discussion and Danny Guigou, Katelyn Gordon, Wendy Applegate, and the Georgia Sea Turtle Center for field help. Work supported by the Burroughs Wellcome Fund Career Award at the Scientific Interface. Work related to physics was supported by NSF CMMI-0825480 and the ARL MAST CTA under cooperative agreement number W911NF-08-2-0004.

Alexander, R. M. 2003 Principles of animal locomotion. Princeton, NJ: Princeton University Press.

Dickinson, M. H., Farley, C. T., Full, R. J., Koehl, M. A. R., Kram, R. & Lehman, S. 2000 How animals move: an integrative view. Science 288, 100. (doi:10.1126/science.288.5463.100)

Hirth, H. F. 1980 Some aspects of the nesting-behavior and reproductive-biology of sea turtles. Am. Zool. 20, 507–523.

Jaeger, H. M., Nagel, S. R. & Behringer, R. P. 1996 Granular solids, liquids, and gases. Rev. Mod. Phys. 68, 1259–1273. (doi:10.1103/RevModPhys.68.1259)

Lejeune, T. M., Willems, P. A. & Heglund, N. C. 1998 Mechanics and energetics of human locomotion on sand. J. Exp. Biol. 201, 2071–2080.

Li, C., Umbanhowar, P. B., Komsuoglu, H., Koditschek, D. E. & Goldman, D. I. 2009 Sensitive dependence of the motion of a legged robot on granular media. Proc. Natl Acad. Sci. 106, 3029–3034. (doi:10.1073/pnas.0809095106)

Maladen, R. D., Ding, Y., Li, C. & Goldman, D. I. 2009 Undulatory swimming in sand: subsurface locomotion of the sandfish lizard. Science 325, 314. (doi:10.1126/science.1172490)

Nedderman, R. M. 1992 Statics and kinematics of granular materials. Cambridge, UK: Cambridge University Press.

Nishikawa, K. et al. 2007 Neuromechanics: an integrative approach for understanding motor control. Integr. Comp. Biol. 47, 16–54. (doi:10.1093/icb/icm024)

Steinitz, M. J., Salmon, M. & Wyneken, J. 1998 Beach renourishment and loggerhead turtle reproduction: a seven year study at Jupiter Island, Florida. J. Coast. Res. 14, 1000–1013.

Tritton, D. J. 1989 Physical fluid dynamics. Oxford, UK: Oxford University Press.

Wieghardt, K. 1975 Experiments in granular flow. Ann. Rev. Fluid Mech. 7, 89–114. (doi:10.1146/annurev.fl.07.010175.000513)

Wyneken, J. 1997 Sea turtle locomotion: mechanics, behavior, and energetics. In Biology of sea turtles (ed. P. L. Lutz), pp. 168–198. Boca Raton, FL: CRC.