How a beetle catches fog

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ABSTRACT

In the face of humanity’s increasing problems of water insecurity, useful lessons in moisture management may be learned from organisms living in extreme climates. The Namib desert beetle uses its own body to extract water, in the form of fog, from the wind, and its dorsal features have inspired designs based on controlled wettability. Here, we revisit the beetle’s physical adaptations from the fluid dynamics perspective of aerosol impaction. Coupled experiments and simulations show that subtle modulations in shape and texture create large gains in water harvesting performance by encouraging droplets to ‘slip’ toward targets at the millimetric scale, and by disrupting boundary and lubrication layers effects at the microscopic scale. Our results offer a lesson in biological fog collection, and design principles for controlling particle separation in a variety of contexts.

With compounding effects of climate change and growing populations, humanity will need new technologies to satisfy its fundamental need for clean water. Where and when surface and ground sources are insufficient, the atmosphere itself can offer a supply not only as humidity, but as suspended liquid droplets in the form of clouds and fog. The potential for supporting human needs is hardly negligible: water in the atmosphere amounts to ~3% of all fresh water, ~13 quadrillion liters or ~10,000 times our yearly global consumption1. In some regions, such as the Namib desert in Southwestern Africa, windborne fog is the primary source of life-sustaining water, and entire ecosystems have developed around mechanisms which separate it from the air2,3. When fog-laden air blows through vegetation, its slender elements present obstacles for the droplets to dodge as they are dragged along fluid streamlines. Their greater inertia causes droplets to lag behind sharp turns, and their occasional collisions lead to accumulation, enough to support both plants and animals which drink from wetted surfaces. Among the tenebrionid beetles that depend on fog harvesting in the Namib Desert, two species have adopted the unusual strategy of direct fog basking, using their own bodies instead of relying on vegetation4,5. Climbing to the top of a dune on cold foggy mornings, groggy and defenseless, a beetle will lean its back into the wind, and as a solitary filtration element, wait for the microscopic droplets to accumulate and roll mouthward.

From the perspective of the beetle, there are two problems, and therefore two complementary directions for adaptation: how to get more droplets to collide, and how to direct those accumulated to its mouth. Much has been written about possible adaptations in wettability to drive transport and solve the second problem6,7. Here we focus on the first, significantly less explored issue, and hypothesize the dominant role of fundamental fluid mechanics over that of wettability. We reinterpret local morphology and surface roughness as primary design parameters for manipulating flow streamlines and droplet trajectories to promote.

Fundamentals of the same flow physics guide the design of fog meshes8,9, which have proven a practical source of fresh water in rural communities, from the Andes to Macaronesia10,11. Similar to vegetation, they employ sparse fibers to intercept droplets. Deposition efficiency $\eta_D$ (intercepted droplets over those initially heading toward collecting element) is controlled by the Stokes number $St$ (droplet inertia over viscous drag), as empirically determined by13

$$\eta_D \sim \frac{St}{(\frac{9}{2} + St)} \quad \text{with} \quad St = \frac{2 \rho_w}{9 \mu_a} \left(\frac{ur^2}{R}\right) \quad (1)$$

where $R$ is the target radius, $r$ and $\rho_w$ the droplet radius and density, $\mu_a$ the dynamic viscosity of air, and $u$ the wind speed. This expression explains why slender elements are used: all else being equal, $St$ increases linearly with decreasing target radius, and $\eta_D$ increases monotonically with $St$. It also shows why small droplets ($St \ll 1$) are hard to catch, and suggests that a beetle should struggle to catch any appreciable fog with its bulky body. Indeed, for a $\sim 1\text{cm}$ beetle in fine fog and light wind, $St$ becomes $\lesssim 0.01$ and $\eta_D$ negligible. So, how does a beetle catch fog?

The beetle cannot change the low $St$ that limits its baseline efficiency without changing its size, for which there are likely evolutionary constraints. It can, however, subtly modify its...
Experimental Setup

A fog impaction wind tunnel is used for controlled fog collection experiments. A fog chamber is equipped with an adjustable cover to regulate fog stream resistance and houses nebulizers. A DC fan located at downstream pulls air from the fog chamber and outside. Fog stream passes around target, that is connected to a high-precision load cell, which measures initial misting of the surface. The slope of linear fit of fogging period indicates the mass of water collected on the surface per second. Droplet pathlines around a cylindrical target, illuminated by a laser sheet. (c) Simulation of flow with fog particles incident on cylinder with $Re = 2000$, $r = 1\mu m$ droplet radius, and free stream velocity $u = 2 m/s$. (d) Time-averaged normal slip velocity field $w_\perp$ (black line represents contour of $w_\perp = 0$), (e) $w_\perp$ evaluated near surface, along dotted line in (d), is integrated (red region) to form metric $\bar{W}$, a proxy of efficiency $\eta_D$.

Experiments

Simulations

Figure 1. (a) Table-top wind tunnel used for controlled fog collection experiments. A fog chamber is equipped with an adjustable cover to regulate fog stream resistance and houses nebulizers. A DC fan located at downstream pulls air from the fog chamber and outside. Fog stream passes around target, that is connected to a high-precision load cell, which measures initial misting of the surface. The slope of linear fit of fogging period indicates the mass of water collected on the surface per second. Droplet pathlines around a cylindrical target, illuminated by a laser sheet. (b) Measured weight of a droplet radius, and free stream velocity $u = 2 m/s$. (d) Time-averaged normal slip velocity field $w_\perp$ (black line represents contour of $w_\perp = 0$), (e) $w_\perp$ evaluated near surface, along dotted line in (d), is integrated (red region) to form metric $\bar{W}$, a proxy of efficiency $\eta_D$.

\[
\eta_D = \frac{\text{measured collection rate}}{(\text{fog density}) \cdot (\text{flow rate}) \cdot (\text{target projected area})}.
\]

Complementary direct numerical simulations of the flow–collector system are coupled with the general Maxey–Riley model to capture inertial droplet dynamics (Methods). This approach accurately obtains droplet trajectories up to approximately one discretization grid point ($\Delta x = R/512$) from the target interface, beyond which numerical convergence degrades (a generic problem not specific to our approach). Figure 1c shows a distribution of fog droplets before and after advection past a 2D circular cylinder at beetle-relevant scales ($Re = 2000$, $St = 0.003$). Only a small portion of droplets, exclusively on the windward side, comes close to contact, having slipped across the sharply diverging streamlines near the stagnation point. Which of these droplets actually make contact, we expect to depend on their slip velocity ($\vec{w} = \vec{v} - \vec{u}$) in the proximity of the surface, where $\vec{v}$ is droplet velocity and $\vec{u}$ that of the surrounding fluid. Figure 1d shows $w_\perp$, the field of average slip velocity normal to the interface, and its value along the dotted blue line is plotted in Fig. 1e as function of the angle $\theta$ from the horizontal axis. As expected, $w_\perp$ is greater where collection takes place, near the stagnation point, suggesting its practical use in identifying regions of high impact probability and, as we will see, to estimate deposition efficiency.

Noting that $w_\perp$ depends on the flow curvature, we can already suspect that target morphology modulations could be used to locally inject sharp turns and induce droplet collisions. In Figure 2 we then consider four cylindrical targets with added sinusoidal perturbations of wavenumber $n = \frac{2\pi R}{\lambda} = 0, 4, 8$, and 12 about their circumference. Across a range of conditions...
We turn back to simulations for physical insight. Based on the intuition that large $w_\perp$ and surface extent over which $w_\perp > 0$ both contribute to increasing collisions, we propose the proxy metric $W = \int w_\perp d\theta$, for $w_\perp > 0$. Under the assumption that $W$ captures the macroscopic flow mechanism underlying actual deposition efficiency $\eta_D$, we build the mapping $\eta_D = \phi(W) = aW^b$ where $a$ and $b$ are calibrated once, using data exclusively from the smooth ($n = 0$) cylinder, and then fixed throughout ($a = 0.069, b = 0.41$). Figure 2a1 illustrates the close comparison between simulations and experiments for $n = 0$. Figure 2a2-4 illustrate how the numerically computed $\eta_D$ reliably predicts experimental deposition efficiencies across $Re, St$, and wavenumbers ($n = 4, 8, 12$). A mechanistic justification of the mapping is also seen in the agreement between predicted collision regions, where $w_\perp > 0$ (red profiles in Fig. 2b), and observed collection regions (Fig. 2c, and Fig. S1 for droplet pathlines).

With numerical tools in hand, we set to computationally guide the rational design of target shapes, so as to improve fog collection while testing our slip modulation hypothesis. We start by introducing an approximately flat profile perpendicular to the flow, in the form of an elliptical cylinder (Fig. 3b). This has the effect of both retaining sharp streamline curvatures (as in the circular cylinder) and increasing the area of positive $w_\perp$. Naively, one would expect this shape modification to favor droplet capture. Nonetheless, the quantitative inspection of $w_\perp$ reveals that while the region of $w_\perp > 0$ is indeed enlarged (Fig. 3b), the slip magnitude $|w_\perp|$ over this region is reduced, rendering $\eta_D$ comparable to the smooth circular cylinder, as confirmed experimentally across a range of $Re/\text{St}$ in Fig. 3a. To increase $w_\perp$ in magnitude as well as area, we introduce a protruding rounded-nose at the stagnation point, which reasonably fits experimental data for both smooth and wavy cylinders for fixed values of $a$ and $b$ and a range of target $St$. (b) Color-coded normal component of slip velocity fields of droplets in flow around a simulated smooth and wavy 2D cylindrical targets, evaluated for $Re=1000$, $St=0.0066$. Black contours represent $v_x - u_x = 0$, and the red line represents the region at which radial slip velocity $w_\perp$ is positive. (c) Water accumulated on the surface after 4 minutes of fogging period (to indicate range of collection), for the same $Re$, $St$. Collision region is in agreement with simulation results of regions where $v_x - u_x > 0$.
point of the elliptical collector, as shown in Fig. 3c,e. Past its own stagnation region, the nose streamlines the incoming flow, thus re-accelerating the droplets along its surface towards the flat regions of the collector, with the consequence of producing two more stagnation points. This design results in overall larger range and magnitude of favorable slip velocity, facilitating impaction and enhancing $\eta_D$ up to $\sim 1.7x$ (blue in Fig. 3a) compared to the elliptical cylinder.

Our metric thus reliably correlates with collection efficiency by accounting for droplet inertia in the target proximity, as determined by the upstream flow field. This allows us to accurately identify regions of high-probability impact. It also underscores a design principle based on “slip traps”, whereby streamlined surfaces are interrupted by high curvature features, causing fluid to alternate between undisturbed accelerations and sudden turns. This manifests in multiple stagnation points where objects’ and fluid elements’ trajectories are separated, the necessary condition for collision.

Experiments with smooth cylinders reveal that a second level of design, no longer at the macroscale, might be relevant. From high speed imaging near the stagnation point, we see that many droplets which make apparent collision with the target continue to roll or slide along the surface before eventually reentraining with the flow (SI-movie1, Fig. S2). This behavior may be attributed to a complex competition between droplet surface tension, lubrication and boundary layer effects. We then hypothesize that surface manipulation at a compatible, microscopic scale may interfere with these dynamics, countering sliding, and improving collection. We test this hypothesis by varying roughness in experiments. We employ sandpaper of different grit sizes to obtain circular cylinders of surface roughness varying from 1$\mu$m to 250$\mu$m (by average equivalent particle diameter – Fig. 3g,h and Fig. S3), and test them in the wind tunnel. Data are collapsed in Fig. 3f, where efficiency is scaled with the Stokes number $St$, and roughness with the laminar boundary layer thickness $\delta$, estimated through the Blasius equation $\delta = \frac{D\sqrt{\nu}}{Re}$, where $D$ is the cylinder diameter$^1$. As can be seen, upon increasing surface roughness, and for all cases, deposition efficiency first rapidly increases to then plateau, more than doubling collection. Finally, because of separation of scales, the effects of macroscopic and microscopic design may be approximately additive, presenting the opportunity to combine them and further increase collection. Indeed, as can be appreciated in Fig. 3j, combined effects of macroscopic shape design (2.1x) and subsequent roughening (1.5x) leads to a cumulative efficiency increase of up to $\sim 3.6x$.

$^1$This relation, while referring to the flat plate, at leading order and near the windward edge, is valid for circular cylinders as well$^{19}$.  

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**Figure 3. Shape.** (a) Deposition efficiency of elliptical, cylindrical and designed collectors. (b,c) Normal slip velocity field, $w_\perp$, around elliptical and designed collectors. (d,e) Water collected on the targets after 4 minutes of fogging. Collection in both cases occur at the positive slip velocity regions. **Roughness.** (f) Deposition efficiency of roughened cylinders. $St$ and $Re$ numbers were altered by varying cylinder diameter. Data collapses, when deposition efficiency is scaled by $St$ and roughness by laminar boundary layer thickness, $\delta$. (g) Minimum and (h) maximum roughness on the cylindrical targets, obtained by optical profilometry. Average equivalent particle diameter was used as the measure of roughness. **Shape and roughness.** (i) Cumulative effects of macroscopic morphology (designed) and microscopic texture enhances the efficiency to up to 3.6x (designed+r-roughness) compared to the equivalent smooth cylinder. (j) Designed target is covered with $\sim 100$ micron rough coating (roughness profile shown on right).
we determine that these design principles have been incorporated in the physical adaptations of actual fog basking beetles. First, we can measure their performance against our synthetic analogs in the same experimental setup, and for the same flow conditions. The left side of Fig. 4a summarizes the effects of surface modulation on the performance of targets of equal nominal diameter (and St = 0.0066), and the right side shows the performance of the two known fog basking species, Onymacris bicolor and Onymacris unguicularis. Unadulterated specimens (Fig. 4a) show efficiencies ∼3 times that of a smooth cylinder of equal St, and comparable to the rationally designed (shape + roughness) target of Fig. 3.

From microCT scans and SEM images we can visualize the beetles’ shape and microscopic texture (Fig. 4b,c, Figs. S5,S6). Black Onymacris unguicularis exhibits subtle ridges parallel to the flow when in basking pose (∼200µm) and scattered bumps of two distinct scales, ∼50µm (Fig. 4b,v) and ∼10µm (Fig. 4b,vi). White-bodied Onymacris bicolor has shallows bumps of ∼400µm (Fig. 4c,iv-v) and small protrusions of ∼1µm (Fig. 4c,vi). To isolate the role of shape −O(100)µm− and roughness −O(1−10)µm−, while testing the consistency of our hypotheses, we prepare the beetle specimens in two ways. In one case, the beetle is sputter-coated with a nanoscopic gold film which preserves the finest features while creating a uniform surface chemistry of high wettability. In the other, nail polish is carefully applied until observable features disappear, and then gold is coated to match the surface chemistry of the previous case (Fig. 4b-c,iii). In support of our thesis that pure fluid mechanics, rather than wettability patterns, dominates droplet harvesting, the gold film alone causes no significant change in ηD (Fig. 4a). Smoothing, however, causes ηD to drop by factor of ∼2 for unguicularis and ∼1.5 for bicolor (Fig. 4a). This result is consistent with our experiments with artificial analogs, and illustrates the functional role of the beetle’s surface features for fog harvesting.

Our study then reframes, in purely fluid dynamic terms, the morphology of fog-basking beetles as adaptations for droplet separation. In this context, we uncover a two-scale strategy – to form ‘slip traps’ out of flow curvature at the macroscopic
scale, and to disturb droplet sliding at the microscopic scale. Toward application in improved fog harvesting, we demonstrate their additive effect on performance, and rational design principles. Further, we offer computational, predictive metrics to evaluate target shapes’ propensity for droplet collection. Broader implications of the relationship between surface morphology and inertial impaction extend to other biological systems and engineering contexts, where particulate collection can be desirable, or unintended consequence.

**Methods**

**Apparatus**

**Aerosol Generation.** Droplets of average diameter $\sim 2\mu m$ were generated using ultrasonic nebulizers (OT-SMG02, DC24V, 500 mA) submerged in DI water upstream in a chamber (Fig. 1a). The water level in the fog chamber was kept constant to sustain homogeneous droplet size distribution and production rate, using a closed-loop control system between a pressure sensor and solenoid valve which refills water to a pressure set point.

To measure droplets size distribution cellulose acetate (CA) electrospun nanofibers ($0.87 \pm 0.14\mu m$ in diameter) were used. The fibers were located at the outlet of the fog chamber with the same conditions as the experiments. The collision of microdrops on the fibers were imaged by a high-speed camera (Phantom VEO 410, lens InfiniProbe TS-160). Directly after impaction, the diameters were measured in ImageJ, eliminating chance of evaporation or absorption of the droplets. The average diameter of the droplets was measured as $\sim 2\mu m$.

**Aerosol Delivery.** The generated droplets were delivered to the target in the middle of the test section, through a funnel and a straight tube with minimal thickness ($\sim 0.7mm$) to reduce downstream disturbances. Uniform flow and fog column (without defects arising from introducing fog to the flow) was achieved by matching the flow speed between fog outlet and surrounding air; A DC fan at the end of the wind tunnel drew air for both sources while the resistance of the pathways were tuned.

Area contraction ratio from the opening of the tunnel to test section was set at 4 : 1 (linear ratio 2 : 1). The velocity of the tunnel, across the test section, for all experiments were kept at $2m/s$.

**Accumulation Measurements.** The collectors were hung at the center of the test section from a sensitive load cell (FUTEK LSB200, precision 0.01 g) by a stainless-steel rod. To eliminate the axial force caused by drag, a Teflon rod with one point contact was assembled at the leeward side of the connecting rod. The temperature of the laboratory was recorded throughout the experiments and to cancel the effects of temperature fluctuations on droplet size or loadcell output signal, only data recorded between 20.5° C and 21.5° C was presented.

To assure robust statistics, the experiments were executed in cycles of fogging and drying the surface (4 and 20 min respectively) for at least 20 cycles. This frequency (24 minutes, $6.9 \times 10^{-4}Hz$) while being much longer than the vibrational noise generated by the flow and environment, is much shorter than the frequency of the drift of the loadcell, aiding to achieve a desirable level of noise reduction from the raw signal. Here the high frequency flow fluctuation noise is eliminated by oversampling the load cell data (sampling frequency $= 40Hz$) and applying moving average window (averaging every 5s, 200 data points). The data representing the fogging period are then fitted with a linear function, whose slope indicates the deposition rate of the collector. Subsequently, the deposition efficiency of each cycle can be calculated by dividing deposition rate by the mass of water droplets that initially were headed toward the projected area of the target per second.

**Simulation**

Here we briefly describe the governing equations and numerical technique used in our simulations. We consider a 2D solid body (i.e. target) immersed in an unbounded domain of incompressible viscous fluid. We denote the computational domain as $\Omega = \Omega_t \cup \Omega_s$, where $\Omega_t$ and $\Omega_s$ represent the fluid and solid domains, respectively, and define the interface between the fluid and the solid body as $\partial \Omega_s$. The flow is then described by the incompressible Navier–Stokes equation

$$\nabla \cdot u = 0, \quad \frac{\partial u}{\partial t} + (u \cdot \nabla)u = -\frac{1}{\rho} \nabla p + \nu \nabla^2 u \quad x \in \Omega \setminus \Omega_s$$

where $\rho$, $p$, $u$ and $v$ are the fluid density, pressure, velocity and kinematic viscosity, respectively. We impose the no-slip boundary condition $u = u_s$ at $\partial \Omega_s$, where $u_s = 0$ is the body velocity. The system of equations is solved in velocity–vorticity form using the remesched vortex particle method combined with Brinkmann penalization. This method has been extensively validated across a range of fluid–structure interaction problems, from macroscale flow past bluff bodies and biological swimming, to microscale viscous streaming responses from arbitrary shapes. This numerical approach offers the advantages of simple computational representation of solid bodies with arbitrary shapes, a feature necessary for our study of morphological effects in fog harvesting, and inherent Eulerian–Lagrangian representation, which allows for direct fog particle representation within our simulation framework.

In order to include the fog droplets in our numerical simulation, we employ a one-way coupling method, where we capture only the fluid-to-particle effects and assume particle-to-fluid and particle-to-particle effects to be negligible, given their low volume fraction ($10^{-5} < \phi < 10^{-4}$, as suggested in Ref.29). We then describe the particle’s equation of motion...
through general Maxey–Riley (MR) equation\(^{17}\)

\[
d\vec{V}_i \over dt = m_p \vec{u}_i \bigg|_{Y(i)} - \frac{1}{2} m_f \over dt \left( \vec{V}_i(t) - \vec{u}_i[Y(t), t] - \frac{1}{10} a^2 \nabla^2 \vec{u}_i \bigg|_{Y(t)} - 6 \pi a \mu \left( \vec{V}_i(t) - \vec{u}_i[Y(t), t] - \frac{1}{6} a^2 \nabla^2 \vec{u}_i \right) \right)
\]

where \(m_p\) and \(m_f\) are the particle and fluid mass, \(\vec{V}_i\) and \(\vec{u}_i\) are the particle velocity and fluid velocity at particle position \(Y(t)\), \(a\) is the particle radius, \(\mu\) and \(\nu\) are the dynamic and kinematic viscosity of the fluid, and \(t\) is time.

Here, for simplicity, we assume a 2D problem where the effects of gravity and Basset history term (which does not make a significant contribution to integrated results\(^{30}\), such as the dispersion of particles here) are excluded in our model.

Therefore, on the right hand side of the equation, we retain only the pressure gradient term, added mass term, and the viscous Stokes drag term, including the Faxen terms (terms with second order derivatives) which we found to have insignificant effect in our simulation results. Nevertheless, we included them for completeness.

**Targets**

**Shape.** Cylindrical targets, were printed using a stereolithography 3D printer (Formlabs Form3, 25\(\mu\)m resolution). To conserve uniform surface energy and wetting properties of the collectors, only one type of resin (Formlabs GREY V4FLGPGR04) was used (static contact angle \(\theta_c \sim 66^\circ\), measured on a flat surface).

Millimetric scale surface modifications were created by defining the cross section using the following equation:

\[
r = R + k \cdot R \cos(n\theta)
\]

(5)

where \(n\) determines the number of waves (0 \(\leq n \leq 16\)), \(R\) is the radius of equivalent smooth cylinder (1000 \(\leq Re \leq 3000\)), \(k\) is a constant establishing the amplitude of the waves (wavy collectors \(k = 1/15\), designed collectors \(k = 2/5\)) and \(r\) is the radius of the surface at \(\theta\) angle (0 \(\leq \theta \leq 2\pi\)).

The equivalent ellipse geometries were generated by:

\[
\left( \frac{x}{p} \right)^2 + \left( \frac{y}{q} \right)^2 = R^2
\]

(6)

where \(p = 0.3 \times (1 + k)\) and \(q = 1 + k\) (\(k = 2/5\)).

**Roughness.** Commercially available Silicon Carbide sandpaper sheets with grit ranging from 60 to 15000 were used to generate rough surfaces (60 to 3000 from 3M, 5000 to 15000 from amazon). The SiC layer was carefully separated from the paper an then glued on the surface of the cylinders. The profile of the rough surfaces were then measured using IFM (Alicona Infinite Focus G5 Microscope, axial resolution 500nm). The roughness parameter was evaluated as averaged equivalent particle diameter.

**Beetles.** The dead beetles, *Onymacris unguicularis* and *Onymacris bicoloris*, were first dried and cleaned using acetone and DI water. To smooth the back morphology and evaluate the effect of surface features on collision efficiency, the beetle were coated with thin layers of nail polish until the features were disappeared. The morphology of their elytra (before and after coating) were characterized by Micro CT Scanner (Bruker Skyscan 1172, resolution 7\(\mu\)m), IFM (Alicona Infinite Focus G5 Microscope, axial resolution 500nm) and SEM (JEOL Scanning Electron Microscope, sputter coated with gold for 20 seconds). The beetles (in natural state, coated with nail polish and sputter coated with gold) were positioned perpendicular to the direction of the flow in the wind tunnel, regardless of their natural basking position, to only evaluate their deposition efficiency with respect to their back morphology and variation in surface chemistry.

**References**


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**Author contributions statement**

JF, AS, and HK designed and built experimental apparatus. AS performed experiments. FKC and MG designed computational methods. FKC ran simulations. AS, FKC, MG, and HK wrote the manuscript.
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