



# Unifying fluidic excretion across life from cicadas to elephants

Elio J. Challita<sup>a</sup> and M. Saad Bhamla<sup>a,1</sup>

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Can insects weighing mere grams challenge our current understanding of fluid dynamics in urination, jetting fluids like their larger mammalian counterparts? Current fluid urination models, predominantly formulated for mammals, suggest that jetting is confined to animals over 3 kg, owing to viscous and surface tension constraints at microscales. Our findings defy this paradigm by demonstrating that cicadas—weighing just 2 g—possess the capability for jetting fluids through remarkably small orifices. Using dimensional analysis, we introduce a unifying fluid dynamics scaling framework that accommodates a broad range of taxa, from surface-tension-dominated insects to inertia and gravity-reliant mammals. This study not only refines our understanding of fluid excretion across various species but also highlights its potential relevance in diverse fields such as ecology, evolutionary biology, and biofluid dynamics.

excretion | biofluid dynamics | organismal biomechanics | physics of living systems | cicada

Feeding and excretion are hallmarks of life. Although research on fluid-sucking insects such as moths, mosquitoes, and sharpshooters often focuses on feeding dynamics (1), waste elimination—despite playing a vital role in an organism's ecological and metabolic regulation (2)—is frequently overlooked and less explored. This overlooked aspect of biology, particularly in smaller organisms, compels us to reexamine and challenge the existing paradigms in animal waste excretion.

Our study specifically challenges the mammal-centric fluid excretion model that suggests jetting is exclusive to animals weighing over 3 kg due to increased surface tension and viscous forces at microscales. We have found that cicadas (Cicadidae), weighing about (2 g) can form fluidic jets using some of the smallest known orifice diameters—averaging 350  $\mu\text{m}$ . This contrasts with Wistar rats, weighing approximately 100 times more (200 to 450 g), yet they release waste in droplets or weak jets (3).

Moreover, we offer a perspective on the energy dynamics of cicada excretion. Contrary to tiny xylem-sap feeding insects like sharpshooters (Cicadellidae), which use “droplet superpropulsion” for waste expulsion (4), cicadas use fluidic jets despite feeding on nutrient-deficient xylem sap. This sap, about 95% water, requires significant energy for extraction due to its negative tension ( $\leq -1 \text{ MPa}$ ). The cicadas’ jetting behavior reveals that their larger body size not only eases the energy cost of jet formation but also enables them to expel larger fluid volumes, highlighting a previously unexplored aspect of their biology.

These findings underscore cicada’s unique strategy in fluidic jetting, reflecting their physiological and ecological adaptations. Inspired by these findings, our paper introduces a unifying framework for understanding fluidic excretion across various species, opening doors to ecological, morphoevolutionary, and biomechanical research avenues.

## Quantitative Analysis of Cicada Fluid Jetting in Natural Settings

We report on the jetting behavior of cicadas *Fidicinoides* sp. and *Guyalna* sp. feeding on non-native Indian almond trees (*Terminalia catappa*) in the Peruvian Amazon and *Chremistica umbrosa* in Singapore (*SI Appendix*). We quantified their jetting behavior in detail as shown in Fig. 1 b, which includes the following ( $n$  = individual,  $N$  = excretion events): *Fidicinoides* sp.:  $n = 3$ ,  $N = 7$ ; *Guyalna* sp.:  $n = 1$ ,  $N = 3$ ; *C. umbrosa*:  $n = 6$ ,  $N = 9$ . The cicadas generated fine, continuous jets with a diameter  $d \sim 160$  to 500  $\mu\text{m}$  with durations of  $\tau \sim 80$  to 560 ms (*Movie S1*). The average speed of the jet for cicadas is around ( $u \sim 0.6$  to 3.16 m/s) and the total volume per excretion event ranges from ( $\sim 6$  to 574  $\mu\text{L}$ ). Cicadas employ large cibarial muscles and a specialized digestive system to process significant volumes of xylem fluid—up to 300× their body weight per day (5). Dimensional analysis indicates that inertial forces primarily drive cicada jetting behavior with a Weber number  $We = \rho du^2/\gamma \sim 2$  to 90, a Reynolds number  $Re = \rho du/\mu \sim 100$  to 1,900, and a Bond number  $Bo = \rho gd^2/\gamma \sim 0.003$  to 0.08 (Fig. 1 C).

Author affiliations: <sup>a</sup>Chemical & Biomolecular Engineering, Georgia Institute of Technology, Georgia 30332, Atlanta

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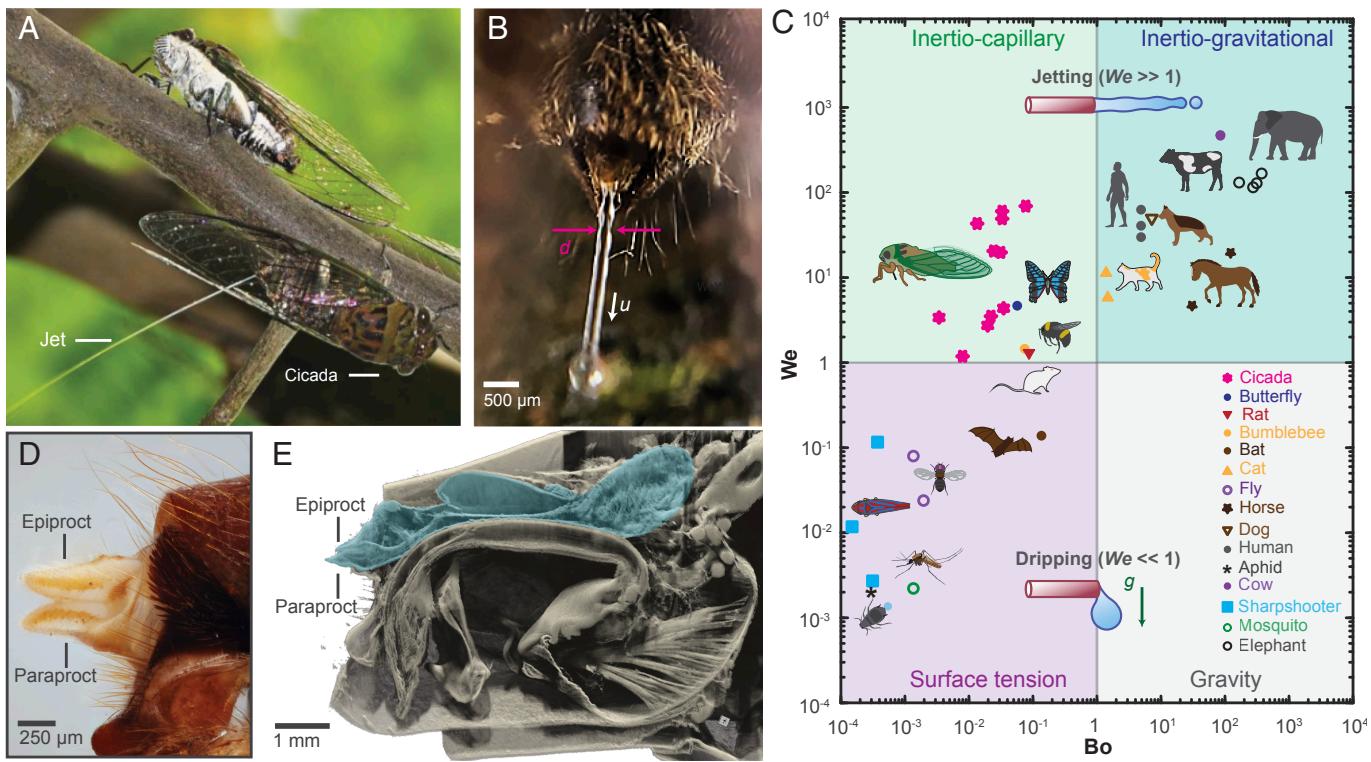
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<sup>1</sup>To whom correspondence may be addressed. Email: saadb@chbe.gatech.edu.

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**Fig. 1.** Cicadas urinate in fluidic jets. (A) Cicadas (*C. umbrosa*) feed and excrete on a Leopard Tree (*Caesalpinia ferrea*) at Labrador Nature Reserve, Singapore. Image reproduced with permission from Tzi Ming Leong (6). (B) A close-up reveals the fluidic jet, characterized by diameter  $d$  and speed  $u$ , exiting a cicada's anus. (C) Across taxa and physical scales, organisms employ various fluidic waste release strategies, quantifiable on a  $We$ - $Bo$  framework, with Bond number  $Bo = \rho gd^2/\gamma$  and Weber ( $We = \rho du^2/\gamma$ ) numbers. Our data show that some cicadas have the smallest orifice diameter to form fluidic jets (pink stars), despite being in a surface tension-dominant regime ( $Bo < 1$  and  $We > 1$ ). In comparison, slightly larger bats and mice excrete in droplets on the same  $x$ -axis ( $Bo$  no.), further underscoring the unusual high-speed jet ejection in tiny cicadas. The data plotted here may be accessed through the accompanying dataset. (D) A detailed view of a cicada's anus shows the separation of the epiproct and paraproct during fluidic ejection (*Guyalna* sp.). (E) A MicroCT scan highlights a cicada's hindgut, revealing a sizable reservoir for fluidic waste (*Fidicinoides* sp.).

## Energetics and Functionality of Cicada Jets

Why do cicadas, operating in the same surface-tension-dominated regime as other xylem-sap feeders ( $Bo < 1$ ), employ jetting instead of droplet excretion for waste elimination? This is particularly striking given the energetically demanding nature of their diet—xylem sap, which is nutritionally dilute and under negative pressure. We suggest that jetting enables cicadas to efficiently address both these dietary challenges simultaneously.

Cicadas, some of the largest insects in the Hemiptera order, face different physical limitations than their smaller counterparts like sharpshooters (7). This size difference significantly impacts their feeding and excretion mechanics. For instance, the largest cicada species, the empress cicada (*Megapomponia imperatoria*), is larger than some hummingbirds (8). Such size provides cicadas with lower energetic costs for generating fluidic jets compared to smaller insects, which require higher pressures for fluid flow. Specifically, cicadas require substantially less pressure for excretion due to their larger orifice sizes ( $d \sim 160$  to  $500 \mu\text{m}$ ) compared to sharpshooters ( $d < 100 \mu\text{m}$ ), as the required pressure within their hindgut scales inversely with the square of the orifice diameter and directly with the length of the hindgut  $P \propto l/d^2$ . Our analysis aligns with Novotny and Wilson's findings on the allometric scaling of suction feeding pressure in xylem-sap feeding insects (7). Thus, larger xylem-feeding insects like cicadas exert less energy in both feeding and excreting, rendering jetting both energetically efficient and mechanically feasible (9).

Moreover, fluid mechanics principles indicate that cicadas' use of fluidic jets facilitates expelling larger volumes rapidly ( $Q \propto u$ ), enhancing nutrient extraction efficiency from xylem-sap.

This adaptation not only proves energetically efficient but also suits their need to process large volumes of nutritionally poor food. The ability to process larger volumes may also supplement nitrogen, a critical growth element, but one that is scarce in plant xylem (<0.01%N) (10). Furthermore, the capacity to ingest and eject large volumes potentially offers cicadas a polyphagous lifestyle, enabling access to a wide range of host plants (7).

Beyond their primary feeding and excretion mechanics, these jet secretions may further serve multifunctional roles. For example, adult cicadas have been reported to spray incoming intruders with their anal jets when disturbed (11), and nymphal cicadas may exploit the copious amount of their watery excretion to agglutinate soil to build underground hallways and chambers, remove mud from integuments (12), and on some rare occasions observed to build aboveground turrets (13).

## Unifying $Bo$ - $We$ Framework for Urination

To bridge knowledge gaps, we conceptualize urination within a framework defined by two key dimensionless numbers in fluid dynamics: the Bond number ( $Bo$ ) and the Weber number ( $We$ ) (Fig. 1C and *SI Appendix*). Here,  $Bo$  acts as a physical scale proxy with respect to capillary length, expressed as  $(d/l_c)^2$ , where  $l_c$  is the capillary length ( $\sim 2.4 \text{ mm}$  for water). The Weber number  $We$  describes the fluid's morphology upon exiting the nozzle, varying from a dripping at low  $We$  to a jetting at high  $We$  (14). In our work, we simplify jetting as a phenomenon that occurs when inertial forces overcome surface tension forces ( $We > 1$ ), leading to a continuous fluid stream.

The  $Bo$ - $We$  framework has rationalized scaling mechanisms for animal drinking (1) and walking on water (15). In our current study, we apply it to categorize urination into four quadrants, establishing a correlation between size and fluid ejection mechanism across eight orders of magnitude in  $Bo$  and  $We$ . Large mammals occupy the  $Bo > 1$ ,  $We > 1$  quadrant, where inertial forces ( $P \sim \rho u^2$ ) dominate, driven by bladder pressure and gravitational forces ( $P \sim \rho g l$ ). At extremely high values ( $Bo \gg 1$ ,  $We \gg 1$ ), fluids may exit as sheets, as in elephants and cows, where gravity drives inertial flows. Given the constant bladder pressure exerted by larger organisms, the effective fluid driving pressure remains constant, leading to scale-invariant flow speeds around  $0.1 < u < 1$  m/s and a constant urinary time for animals larger than 3 kg (3).

Insects and small mammals typically fall into the  $Bo < 1$ ,  $We < 1$  quadrant, where surface tension dominates. Here, surface tension leads to droplet formation and may cause capillary adhesion to surfaces, posing significant challenges for small organisms to get rid of their excreta. Overcoming these capillary forces requires additional mechanisms, like exploiting surface tension properties (e.g., droplet catapulting in sharpshooter insects, kicking in aphids, maternal licking in mice) or reducing its effect (e.g., hydrophobic coating in gall aphids) (3, 4). The predominant fluid forces are due to surface tension  $P \sim \gamma/d$  and viscosity  $P \sim \mu l/d^2$  (internal laminar flow) (4).

Invertebrates like cicadas, bumblebees, and butterflies, characterized by  $Bo < 1$ ,  $We > 1$ , demonstrate high-speed inertial jets for excretion, differing significantly from similarly sized mammals' strategies (e.g., bats, mice). Cicadas, notably the smallest known animals for jet excretion, exhibit higher volume and frequency due to their high-volume xylem-sap diet (7, 10). No organisms have been identified in the  $Bo > 1$ ,  $We < 1$  quadrant, which indicates exclusive reliance on gravitational forces for droplet-based excreta removal. This quadrant implies droplet buildup due to capillary pressure ( $P \sim \gamma/d$ ), with dripping occurring when drops exceed the capillary length scale  $l_c$  and capillary adhesion. In a small organism hypothetically using this mechanism, the lack of excreta control could lead to self, conspecific, or habitat fouling. It is important to note that fluid ejection from the jetting quadrants ( $We > 1$ ) may transition to this quadrant toward the end of fluid ejection (as driving pressure diminishes), with gravity managing the movement of fluid droplets (e.g., dribbling).

## Concluding Remarks

Cicadas, with their enigmatic nature, have long fascinated both artists and scientists, from Homer to Darwin. These insects

challenge numerous paradigms in biology: they possess some of the longest developmental periods of up to 17 y, rank among the largest insects with wingspans of up to 8 cm that rival small hummingbirds, and produce sounds as loud as chainsaws (100 dB), making them the loudest insects (8). Our study adds to this list by revealing cicada's ability to excrete powerful fluidic jets, contrasting the droplet formation observed in other Hemipteran-like sharpshooters. This jetting capability allows efficient processing of their nutritionally sparse xylem-sap diet and places them as the smallest known animals to form high-speed jets in a surface tension-dominated regime ( $Bo < 1$ ).

With their high population densities during emergence, the ecosystem impact of their fluid excretion is both substantial and largely unknown, presenting unexplored prospects for biomonitoring and bioinspired engineering. Future research directions involve addressing the challenges in studying cicadas in laboratory conditions. While this study relies on observations and analyses in natural settings, culturing cicadas in labs has proven difficult to date, leaving a gap in our comprehensive understanding of their feeding energetics and fluid expulsion mechanisms particularly during their developmental stages, which are typically subterranean.

The dimensional  $Bo$ - $We$  framework, covering eight orders of magnitude, provides insights into the dynamics of urination, ranging from dripping to jetting, across various species. It not only emphasizes cicadas as one of the smallest organisms capable of producing high-speed excretory jets but also suggests that in the future, it could open avenues to explore diverse fluid ejection behaviors in other organisms, extending beyond excretion to functions such as hunting, defense, and dispersal. This framework offers a forward-looking perspective to understand fluid excretions across scales, underscoring the remarkable adaptability and efficiency of biological systems.

**Data, Materials, and Software Availability.** All study data are included in the article and/or at an online data repository, <https://zenodo.org/doi/10.5281/zenodo.10645369> (16).

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