PRINCIPLES OF FLUIDS AND INTERFACES IN ULTRAFAST INVERTEBRATES

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PRINCIPLES OF FLUIDS AND INTERFACES IN ULTRAFAST INVERTEBRATES

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Nature’s grandeur surpasses our imagination
For my dear father, Joseph
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3.1 Dynamics of the slingshot spider web. a The spider stores elastic energy by pulling on the tension line, stretching the radial lines and deforming the web to form a conical structure. The spider remains in this position, waiting for prey. It is worth noting that field observations show no specific preference for the spider web’s orientation concerning gravity. b Upon detecting a stimulus, the slingshot spider releases the web, moving explosively, covering almost nine times its body length in under 30 ms. The web is horizontally oriented, with the tension line at the bottom of the frame. The primary motion upon release is in the positive y direction, facing upwards in this case. c Quantification of multiple trajectories of a single slingshot spider during repeated launches (triggered by finger snapping). The red line indicates the average trajectory of multiple displacement curves. Trajectories are adjusted to start at $(x = 0, y = 0)$ at $t = 0$. d Movement in the $x$ direction is negligible before the first oscillation.

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3.4 **Simulation 1: Two-dimensional slingshot spider dynamics.** 

a By solving the equations of motion, we determine the $x$-$y$ displacement of the spider. The simulation output aligns with the rise time, maximum peak, and maximum output $y_{\text{max}}$, as well as the minimal oscillations in the $x$ direction. However, the model does not anticipate any subsequent oscillations in the $y$-direction beyond the first fluctuation.

b The temporal evolution of the forces shows that the system begins with forces in the radial lines in the $x$-$y$ directions. As the system gains speed, web drag resists the motion - spider drag is negligible. The restoring force in the tension line, which has been zero up to this point, comes into play as the tension line stretches ($t \sim 15\, ms$).

c,d The simulation also forecasts the apparent 2D displacement of the spider, starting from ($x_0, y_0$) at $t = 0$. The simulation displays a qualitatively similar trajectory in the $x$-$y$ plane, with the spider initially launching in the $y$-direction before experiencing low amplitude oscillations in the $x$-direction as it gradually approaches equilibrium.

3.5 **Simulation 2 with increased $x$-motion contributions.** 

a To account for the dynamics of the subsequent vibrations in the $y$-direction, we perform a second simulation with a larger initial displacement in the $x$-direction ($4 \times$ that used in simulation 1). This demonstrates the additional complexity introduced by enhanced orthogonal motion. The model more closely aligns with field data regarding temporal parameters and the subsequent low amplitude fluctuations after the initial overshoot. The spider’s motion is 3D and may include twisting and rotation due to mass and geometry asymmetries. These extraneous factors become increasingly significant at low amplitudes and frequencies.

b The evolution of forces in the $x$-$y$ plane displays similar dynamics to those observed earlier in Figure 3.4 b. Interestingly, the tension force in the $x$-direction becomes more prominent here, as the influence in the $x$-direction is magnified due to the initial conditions.
3.6 **Examining web dynamics based on model parameters.** We investigate the influence of various forces on the slingshot dynamics derived from Simulation 2. The output displacements are normalized by the spider body length (BL) and parameters ($K_{r,ss}$, $K_{r,ss}$, and $C_{w,ss}$) from Simulation 2 (Figure 3.5 a) as a reference. a Increasing the stiffness of the radial line $K_r$ results in both a faster initial displacement increase and higher overshoots (approximately 4 BL above equilibrium), along with subsequent larger amplitude vibrations around the equilibrium point. Reducing the radial lines stiffness by an order of magnitude gradually causes the system to approach the equilibrium point without any observable overshoot. b Altering the tension line stiffness $K_t$ only impacts the dynamics beyond the equilibrium line. Without any tension force, the system achieves a higher overshoot and more subsequent vibrations. As the tension line stiffness increases, the vibration peaks become sharper above the equilibrium with larger and slower undershoots. c The model demonstrates high sensitivity to web drag $C_w$. Halving the damping coefficient causes the system to vibrate significantly over two body lengths around the equilibrium line. Doubling the damping coefficient results in a small overshoot as the system quickly approaches equilibrium without noticeable oscillations, similar to a critically damped oscillator.

3.7 **Overview of web dynamics based on model parameters.** We quantify the changes in various simulations by focusing on the percentage overshoot, peak time ($t_p$), and settling time ($t_s$). We highlight the reference values in red. a. The overshoot increases monotonically from 0 (no peak) to 80% with the increase in $K_{r,ss}$. At low $K_{r,ss}$, the system does not vibrate around the equilibrium point, causing $t_p$ and $t_s$ to exceed the maximum simulation time of 200 ms. This behavior resembles an overdamped dynamical system, as the damping forces overcome the spring forces. b. The overshoot decreases by almost 35% as $K_t$ increases from 0.01 to $100 \times K_t$. Similarly, the peak time $t_p$ slightly decreases from 24 ms to 15 ms as $K_t$ increases. Interestingly, the settling time ($t_s$) decreases to a minimum of 40 ms around the reference value of $K_t$ before sharply increasing. This is mainly due to the larger undershoot caused by a higher $K_t$. c. The simulation is highly sensitive to the damping coefficient. The overshoot decreases from around 60% to almost no overshoot as damping increases. The settling time shows a minimum around the reference point, as low drag causes the system to oscillate violently around the equilibrium point. In contrast, high drag causes it to approach equilibrium slowly. Both effects increase in the settling time.

4.1 **Semiaquatic Springtail *Isotomorus retardatus.*** (a) Notice the manubrium-furcules and collophore highlighted in green and red, respectively. Image composites are from recordings of springtails taking off (b) and landing (c). (b) Details of the collophore’s water adhesion and the droplet collected after detaching from the water surface are shown above their respective frames. (c) Notice that during a successful landing, springtails attach to the water surface using the collophore.
4.2 **Springtails adhesive landing on the air-water interface** (a) Before impact, springtails bend their bodies to extend their collophore further as they come into contact with the water surface. The collophore primarily interacts with the water surface during this impact. (b) The body orientation of the springtail is crucial for a successful landing. A controlled landing occurs when the collophore quickly adheres to the water’s surface. Post-impact capillary waves are observed as the organism stabilizes. However, if the springtail lands in other configurations (such as on its side or back), it experiences uncontrolled rebounding. (c) The progression of hydrodynamic forces over time shows that collophore adhesion helps slow the springtail’s upward movement after reaching its maximum depth. (d) We create a simplified mathematical model to analyze the influence of collophore adhesion on springtail landing dynamics. The hydrodynamic forces involved include weight, drag, surface tension, and collophore adhesion. Both experimental and theoretical outcomes of the normalized displacement $\bar{z} = (z(t) - z_{t \to \infty})/D_s$ demonstrate the significance of collophore adhesion in rapidly halting the springtail’s landing dynamics. The springtail would be propelled off the water’s surface without the collophore force.
SUMMARY

Life thrives within a complex and diverse fluidic landscape, including air, water, and their interfaces. As almost all organisms are constantly surrounded by fluids, they must continuously grapple with the dynamics of fluids to carry out essential biological functions. This ongoing interplay leads to specialized structural and behavioral adaptations that shape living systems’ designs [1].

In nature, some organisms can carry out extreme impulsive movements, with accelerations up to a million times greater than gravity, enabling them to achieve their biological functions, such as jumping, striking, excretion, and predator avoidance, in as brief as one millionth of a second. Dubbed ultrafast organisms, these extreme systems must contend with fluids, whether it is air, water, or their interface both in their surroundings or within their internal conduits, to carry functions such as predator avoidance, hunting, and excretion [2, 1].

This dissertation delves into the interactions between millimeter-sized biological movements of small organisms and fluids. We specifically study three systems interacting with fluids for different functionalities: sharpshooter insects (excretion), slingshot spiders (hunting), and semi-aquatic springtails (landing/predator avoidance).

The hydrodynamics of these interactions may stem from an external structure constructed by the organism (spider silk), the organism’s entire body (springtail, slingshot spider), or a specific appendage undergoing cyclical and impulsive movement (sharpshooter). Our studies emphasize the impact of fluids on these invertebrates’ behavior and design.

Combining experimental observations, mathematical modeling, and computational simulations, the work presented here aims to uncover the biophysical principles, hydrodynamics, and constraints governing ultrafast systems interacting with fluids. Exploring the interactions between organisms and fluids, particularly at small scales, offers a unique perspective and reveals a unifying and integrated framework that unravels the connections between hydrodynamics, organismal adaptations, and animal behavior.

From an engineering standpoint, investigating these biological phenomena allows us to learn from nature’s extraordinary engineers – the organisms that have mastered fluid dynamics at small scales. Drawing inspiration from these remarkable living systems, we can stimulate the development of innovative bioinspired solutions for a wide range of engineering challenges.
Guide for Thesis

The chapters in this dissertation are standalone and may be read independently. Chapters 2, 3, and 4 contain an introduction, methods, results, discussion, and conclusion.

Chapter 1 lays the groundwork for understanding the fluid dynamics challenges encountered by small-scale organisms, focusing on issues such as surface tension and viscous forces. This chapter also elucidates how these organisms exert control over their movement in response to external forces exerted by fluids. The strategies they employ include structural adaptation, elasticity, and energy dissipation. To establish a comprehensive framework for our discussion, we employ dimensionless numbers and scaling arguments. Additionally, we provide a brief overview of the control framework that we use to analyze how these organisms regulate their impulsive movements.

Chapter 2 focuses on sharpshooter insects and explores the fluidic, energetic, and biomechanical principles that enable these tiny xylems sap-feeding insects to survive on a nutrient-sparse diet. The chapter investigates how sharpshooters leverage superpropulsion during droplet ejection by achieving temporal coordination between the stylus and the droplet. The text and figures in this chapter are adopted from Challita et al., 2023 [3].

Chapter 3 investigates the intricate web dynamics of slingshot spiders. Using a 2D damped oscillator model of the web, this chapter uncovers three critical insights into the dynamics of slingshot motion. The tension line serves a dual purpose: allowing the spider to store elastic energy in the web for rapid launching and enabling the spider to stop quickly while dampening inertial oscillations. The predominant energy dissipation mechanism is viscous drag by the silk lines. The web exhibits underdamped oscillatory dynamics through a finely-tuned balance among radial line forces, tension line force, and viscous drag dissipation. The text and figures in this chapter are adopted from Challita et al., 2021 [4].

Chapter 4 examines the adhesive landing mechanisms of springtails on water surfaces. Through a combination of experimental observations and mathematical modeling, this chapter reveals how collophore adhesion helps slow the springtail’s upward movement after reaching its maximum depth. The text and figures in this chapter are adopted from Ortega-Jiménez et al., 2022 [5].
Scholarly achievements

During my Ph.D., I have published six works [3, 4, 6, 7, 5], including three as the first author and three as a co-author. In addition, several papers are in progress and approaching publication, which I hope to submit after my Ph.D. defense. As the lead author, I have two papers in the pipeline that explore the mechanical determinants of how organisms manipulate fluids to form droplets and jets, as discussed in Chapter 1, and another examining the dynamics of liquid lassos generated by neotropical cone-head termite soldiers based on my field trips to Costa Rica, Panama, and the Peruvian Amazon. Furthermore, I co-authored three projects involving frugal science with undergraduates and high school students. My research has been presented at various interdisciplinary conferences, such as the American Physical Society (APS), the Society of Integrative and Comparative Biology (SICB), and the Society of Rheology (SoR). Detailed information about my publications and contributed talks can be found in Appendix B.
1.1 Fluids shape living organisms

Life is immersed in fluids. Surrounded by air, water, or their interfaces, living organisms have evolved a myriad of structural and behavioral adaptations to successfully navigate the physical forces imposed by fluids. This is evident in the internal transportation of fluids within organisms’ bodies during respiration, digestion, feeding, and excretion. Externally, it can be observed when they interact with moving fluids, either by actively moving through swimming, jumping, or flying, or while being sedentary and influenced by external forces like wind gusts and aquatic currents. [1].

The interplay between biology and fluid mechanics has long captivated biologists, physicists, and engineers as they strive to decipher the principles governing the diverse strategies and morphologies organisms have developed in their fluidic environments to fulfill their biological functions. Understanding these strategies holds the potential for creating bioinspired designs that can address engineering challenges in areas such as microfluidic systems, microrobotics, and soft robotics. [8].

1.1.1 Fluid challenges at small scales

Tiny organisms, in particular, face fluid mechanical challenges predominantly shaped by surface tension and viscous forces, each presenting unique constraints at interfaces and within bulk fluids.

At fluid interfaces, surface tension emerges from the imbalance of intermolecular attractions at the liquid-air interface, causing small volumes of fluids to form droplets, climb up narrow spaces, and cling to hydrophilic surfaces with capillary adhesion [9]. We consider several dimensionless numbers used to scale surface tension with respect to gravity and inertia. These numbers include (among others) the Bond number ($Bo$) and Weber number ($We$):

$$Bo = \frac{\text{gravitational forces}}{\text{surface tension forces}} = \frac{\rho g L^2}{\gamma}, \quad We = \frac{\text{inertial forces}}{\text{surface tension forces}} = \frac{\rho v^2 L}{\gamma},$$

where: $\rho$ represents fluid density, $v$ stands for fluid velocity, $L$ is the characteristic length scale, $g$ is the gravitational acceleration, and $\gamma$ is the surface tension.

For small organisms (i.e. $Bo < 1$), surface tension presents a formidable challenge. The
cohesive forces between liquid molecules at an interface are relatively strong compared to the size and mass of micro- and millimeter-scale organisms such as insects, arachnids, and hexapods. This causes fluid to stick surfaces of tiny organisms, making it hard to remove and, in some cases, poses a lethal threat, as it can create an elastic barrier that can trap small organisms and drown them.

In moving fluids, two principal forces come into play: inertial forces, caused by the fluid’s mass and acceleration, and viscous forces, arising from the fluid’s innate resistance to flow. The dimensionless Reynolds number \( (\text{Re}) \) offers a means to gauge the relative significance of these forces: \( \text{Re} = \frac{\text{inertial forces}}{\text{viscous forces}} = \frac{\rho v L}{\mu} \), where: \( \mu \) is the fluid’s dynamic viscosity. As the length scale decreases (small \( L \)), the Reynolds number is reduced, leading to the predominance of viscous forces over inertial forces.

For small organisms, the primary challenge arises from viscous forces, either when pumping fluids through small conduits or moving through these fluids through flying (air) or swimming (aqueous). Highly viscous fluids (low \( \text{Re} \)) significantly influence fluid behavior at small scales and profoundly affect tiny organisms in two ways: (1) time reversibility and symmetry make locomotion difficult in high-viscosity environments, and (2) energy costs arise from pumping fluid through small conduits and nozzles.

1.1.2 Navigating fluids at small scales

To face these challenges, tiny organisms have developed a myriad of strategies to achieve control over their movements, thereby fulfilling their biological imperative. Within this context, we define control as the various mechanisms and strategies these organisms use to navigate, overcome, or exploit the challenges posed by fluid dynamics. The strategies must be regarded holistically and are interdependent but these themes are individually highlighted as they are recurrent throughout this dissertation and highlighted as follows:

*Structural adaptations and innovative mechanisms*

The interplay between structure and function in small organisms leads to innovative adaptations that allow them to navigate fluidic environments.

Small organisms have evolved remarkable structural adaptations and mechanisms to overcome the forces of surface tension - or even turn surface tension to their advantage. For instance, water
Striders possess long, slender legs that generate hemispherical vortices on water surfaces [10]. Similarly, by secreting a lipid-laden droplet on the surface of the water, Mesovelia insects have developed a unique locomotive strategy, capitalizing on the interfacial Marangoni effect, which utilizes surface tension gradients to propel themselves across the water surface [11].

Alongside handling surface tension, some organisms have utilized capillary action to transport fluids. In arid environments, desert beetles collect water droplets from fog using a combination of hydrophilic and hydrophobic surfaces on their bodies, turning surface tension to their advantage [12]. Similarly, shorebirds utilize capillary ratchets for feeding [13], while Araucia plants have external leaf conduits to control fluid transport [14].

To prevent fluids from sticking, certain insects and plants have evolved hydrophobic structures. This is evident in various insects’ exoskeletons and plant leaves, such as the lotus. Additionally, collective behavioral adaptations like the formation of ‘ant rafts’ help certain species survive floods [15].

In highly viscous environments (low Re), swimming organisms have evolved a range of gaits that help break time symmetry and enable non-reciprocal locomotion, as elucidated by Purcell’s seminal work [16]. This could be seen in the diverse swimming patterns of microorganisms using flagella, whip-like structures, and cilia for propulsion that can be rhythmically waved to create propulsion in viscous fluids.

Lastly, an essential strategy lies in the strategic distribution of forces and adjustments in body posture. By geometrically altering their posture, organisms can effectively manage forces and harness their environment. This is seen in larger mammals like falling cats and squirrels, which can self-right mid-air and shift their body forces to achieve a controlled landing. Similarly, wingless hexapods, nematodes, and stick insect nymphs demonstrate controlled air-to-land transitions, highlighting the range of adaptive strategies organisms employ in response to fluidic environments.

_Elasticity and tuning to enhance their impulsive movements_

Elasticity is integral to controlling kinematic output, significantly enhancing impulsive movements in various organisms, from minute insects to large vertebrates.

In vertebrates, tendons epitomize the utilization of elasticity in the mechanics of movement. These structures, embedded within muscles and connective tissue, serve as elastic connectors, fa-
cilitating a range of locomotion activities such as hopping, running, and walking, akin to the dynamics of a spring. The benefits conferred by these elastic mechanisms are manifold, including metabolic energy conservation, muscle power amplification, and the mitigation of power demands during strenuous movements. A classic example is jumping treefrogs, which have evolved to passively adapt their locomotion mechanisms to compliant substrates, thereby reducing energy loss [17, 18].

Elastic components are also found in invertebrates. Planthoppers and leafhoppers, for instance, employ the use of resilin springs - elements composed of a rubber-like protein called resilin - as part of their locomotion strategy, enabling them to leap off diverse substrates [19].

Interestingly, elasticity can also be sourced externally, rather than from internal morphological components, as evidenced in aquatic invertebrates. Here, regulating movement through the elasticity of fluidic interfaces, specifically surface tension, becomes a critical survival strategy. This is demonstrated by semi-aquatic springtails and water striders that leverage the inherent elasticity of water’s surface tension to perform their impressive feats of water-surface jumping [20, 5, 10]

*Damping and dissipation through the external environment*

Damping and dissipation constitute significant factors that all organisms must grapple with when maneuvering through fluidic environments. For instance, viscous dissipation in bulk fluids through air and liquid drag can considerably impact an organism’s control over its movements. This is evident when jumping from the water, as seen in penguins or orcas [21], or when reducing drag during a dive into the water, exemplified by the kingfisher’s beak [22].

While this is shared among all organisms, this process becomes increasingly crucial for ultrafast and impulsive tiny organisms, where rapid launch and reset mechanisms are necessary for survival, whether for predator avoidance or precision hunting. Water-dwelling insects such as water striders offer a case in point. When landing on the water’s surface, they effectively dissipate kinetic energy by generating capillary waves, thereby achieving dynamic stabilization [23].

However, dissipation through fluidic drag is a delicate balancing act: If the dissipation is too high, the organism becomes overdamped, hindering its ultrafast movements - the very objective it’s trying to achieve. Conversely, if dissipation is too low, the organism becomes underdamped, resulting in chaotic, uncontrolled movements.
A condition often sought is the critically damped state, which balances energy dissipation and movement control, which is generally ideal for most organisms. However, achieving this state is not the only consideration. Organisms must also consider other factors, such as minimizing the risk of fracture, as well as their ability to adapt to changes in their environment. These considerations make up a complex parameter space that organisms must navigate to survive. Therefore, an intriguing question arises: What is the design parameter space for these variables in different organisms, and how does it evolve in response to changing environments?
In this study, we investigate the hydrodynamics of three different biological systems, emphasizing the interplay between morphological structures (highlighted in purple) and fluids. Sharpshooter insects tackle a dual fluidic challenge: 1) managing xylem-fluid during feeding and excretion, and 2) overcoming capillary forces to catapult droplet excreta from their anal stylus. Slingshot spiders exploit air drag and a special structure called a “tension line” to regulate the dynamics of their web and body during ultrafast launches. Springtails utilize their hydrophilic collophore to adhere to water surfaces during landings.

The invertebrate world is rife with innovative strategies that warrant further exploration. Capitalizing on our curiosity-driven scientific approach, this dissertation delves into the interplay of fluid mechanics within three biological systems Figure 1.1, shedding light on novel control strategies employed by these organisms to accomplish their biological functions. However, this dissertation does not provide a comprehensive overview; rather, it aims to shed light on the diverse range of control strategies utilized by small organisms as they navigate fluid forces at their physical scales. We underscore various mechanisms, from temporal tuning to specialized structural adaptations, that facilitate the achievement of their biological functions:

1) We study the strategy used by sharpshooter insects to overcome the high energetic costs of pumping their fluid excrements during urination. By catapulting individual droplets, these insects utilize the elasticity of droplets modulated by surface tension to effectively overcome capillary adhesion through superpropulsion.
(2) We look at the ability of slingshot spiders to launch themselves along with their cone-shaped silk webs through the air at high accelerations (≈ 130 m/s²). We demonstrate how viscous forces resulting from air drag, along with the tension line, play an important role in determining how the spider rapidly decelerates, allowing them to reset quickly in case they don’t capture prey.

(3) We demonstrate the mechanism by which springtails control their landing on the water’s surface, using capillary waves and capillary adhesion.

Control in extreme, impulsive systems

The organisms examined in this dissertation fall within a category of biological systems known as ultrafast or latch-mediated spring actuation (LaMSa) systems. LaMSa systems span almost all known biological taxa, from fungi to animals [24]. At their core, LaMSa systems are composed of a latch, a spring, and one or more motors, such as muscles. Through power amplification strategies, these systems frequently surpass the force-velocity limitations of muscles. They store energy in a biological equivalent of a spring, held in place by a latch-like structure, before being swiftly released.

One key principle of impulsive systems is their capacity to store energy in elastic structures (biological springs) [25, 26] over a long period using a motor, then quickly and controllably release energy (power) over a brief timescale with a latch – a concept analogous to an archer using a bow and arrow.

Controlled impulsive movements are often vital for various reasons, particularly when repetitive impulsive movements can mean the difference between life and death. We aim to understand these systems holistically, exploring how organisms that exhibit impulsive behaviors employ these control strategies to navigate their surrounding fluids, either by exploiting the elastic properties of surface tension or dissipating their kinetic energy in bulk fluids after rapid movements.

Despite their high speeds and accelerations, many small impulsive systems moving within fluids are primarily constrained to low and intermediate Reynolds number regimes due to their small size (L). There are, however, exceptions. For instance, large ciliated protozoan cells such as Spirostomum ambiguum can temporarily escape low Reynolds number conditions by reaching speeds of
20 cm/s. This allows them to generate hydrodynamic waves that are crucial for rapid cell-to-cell communication when confronted with predators [27].

1.1.3 Approach

Our framework consists of three components: 1) identifying the governing forces through dimensional analysis, 2) developing reduced-order mathematical models, and 3) understanding the fundamental biological limits set by these forces, specifically focusing on energetics and the influence of scale on these aspects.

To address these questions, we will examine the mechanics of fluidic interfaces and moving fluids, identifying the relevant dimensionless numbers that dictate the behavior of these ultrafast invertebrates. Dimensionless numbers are essential in grasping the dominant forces at different scales, providing a comprehensive understanding of how fluid dynamics influence various biological functions, such as locomotion and fluidic pumping. Throughout this analysis, these numbers will be utilized to make sense of the prevailing forces and their effects on the behavior of biological systems in fluid environments.

To unravel the intricate relationships between fluid mechanics and invertebrates, as well as to comprehend the limits and constraints imposed by the physical world on these organisms, we will employ reduced-order mathematical models (e.g. oscillator theory, hydrodynamic models) and scaling arguments. This will lead to the development of a theoretical framework inspired by the control theory of mechanical systems [28].
CHAPTER 2
DROPLET SUPERPROPULSION IN ENERGETICALLY CONSTRAINED INSECTS

2.1 Introduction

Consumption of nutrients and subsequent waste elimination are hallmark functionalities of a living organism. Although fluid feeding in insects (moths, mosquitoes, leafhoppers) has received considerable attention since Darwin’s time [29], little is known about the science and biofluid dynamics phenomena associated with waste elimination, despite having important ecological, morphological and evolutionary implications [30]. Specifically, we focus on how excretion influences small-bodied animals’ behavior, morphology, and energetics since they face unique challenges due to their high metabolic rate [31] and physical limits set by the natural world [32]. Millimeter-sized xylem-feeding insects exemplified here with sharpshooter insects (Cicadellidea) face dual fluid dynamic challenges of surface tension due to their small size and energy constraints due to their xylem sap diet. Plant’s xylem sap is very poor in nutritional compounds (95% water [33]) and energetically costly to pump out since it is under negative tension [34] (≤ −1 MPa). To survive on this frugal diet, sharpshooter insects use large cibarial muscles and an efficient digestive system (filter chamber) to extract and filter large volumes of the xylem fluid (up to 300× body weight/day [35, 36] compared to ~ 1/40× body weight/day for humans). Subsequently, sharpshooters must constantly and efficiently excrete their fluidic waste (~ 99% water, ‘leafhopper rain’), contributing to their role as plant disease vectors [37]. Here, we ask: what are the fluidic, energetic, and biomechanical principles that enable tiny xylem sap-feeding insects to survive on a nutrient-sparse diet?

2.1.1 Sharpshooter insects

To investigate the proposition that sharpshooters leverage superpropulsion during the droplet ejection process by achieving temporal coordination between the stylus and the droplet, we implement the two-spring oscillator theory, physical models, and computational fluid dynamics (CFD) to elucidate the underlying principles and constraints of superpropulsion. Furthermore, we examine the energy-related advantages of employing superpropulsion in droplet ejection for the survival of these
Figure 2.1: **Imaging and rendering of glassy-winged sharpshooter** a. Fluorescence with DAPI filter of the sharpshooter anal stylus highlighting the resilin blob at the bottom of the stylus b Confoocal image of the anal stylus c Close microCT render of the anal tube and anal stylus d Cross-sectional microCT of a glassy-winged sharpshooter *Homalodisca vitripennis* showing various parts of its digestive system

insects that rely on an energetically scarce xylem-sap diet.

### 2.2 Methodology

#### 2.2.1 Data collection and analysis

*High-speed imaging and field work at USDA*

Like other leafhoppers, sharpshooter insects exhibit notable agility on plant stems and foliage, adeptly camouflaging themselves as they secretly feed and eject their liquid droplet waste (hence the name “sharpshooter”). This made data-gathering efforts in the field challenging, as sharpshooters were quick to either turn around the plant stem or even fly away as we set up our high-speed cameras and lights. Consequently, we decided to collect our high-speed footage of waste expulsion from two sharpshooter species (Glassy-winged sharpshooters, *Homalodisca vitripennis*, and Blue-green sharpshooter, *Graphocephala atropunctata*) was mainly collected at the USDA-Agricultural Research Service (ARS) facility in Parlier, California. Additional data, primarily featuring the red-banded sharpshooter, *Graphocephala coccinea*, were obtained from my garden in Atlanta, Georgia,
where the insects were discovered feeding on a basil plant. To collect data, high-speed video recordings were made using a Chronos 1.4 high-speed camera attached to a Canon MPE 65 mm Macro lens and a portable Zaila high-intensity light. During recordings, the liquid droplet and stylus were kept in focus with the camera during liquid expulsion. The resulting trajectory and displacement for both systems are presumed to exist within a 2D plane.

**Kinematics: Tracking stylus and droplet**

The analysis of data is conducted using MATLAB and ImageJ (FIJI). We manually track the angular displacement of the stylus $\theta_s(t)$ with respect to the axis that runs along the insect’s body. A stationary origin point is chosen at the intersection of the stylus and body axes. It is important to note that in some cases, the basal area of the stylus is not entirely stationary during the movement. To compensate for the kinematics of this relative movement, we separately track the base of the stylus relative to a fixed point on the insect’s body and subtract it from the displacement of the stylus. Raw data are filtered using a moving average with windows of 3 and 5. The angular velocity $\dot{\theta} = \partial_t \theta$ and angular acceleration $\ddot{\theta} = \partial_t \dot{\theta}$ are computed and presented in Figure 2.6 of the main text. The maximum linear speed of the stylus is calculated as $V_s = L_s \dot{\theta}_{max}$.

Similarly, we manually track the centroid of the droplet post-take-off. Ejection is the moment when the droplet is entirely detached from the stylus following the droplet extension. At ejection time $t_e$, we measure the 2D location of the droplet $P(x_e, y_e)$ and subsequently at at one-time step before and after ejection ($t_e - dt$, $t_e + dt$). For each of these frames, we skip three frames ($3 \times dt$) and measure the centroid’s final location $P(x_f, y_f)$. The displacement is calculated by measuring the Euclidean distance $d = \sqrt{(x_f - x_e)^2 + (y_f - y_e)^2}$ of the droplet. The ejection velocity is acquired by averaging the three velocities as $V_d = \partial_t d$. Both the stylus and droplet kinematic values are validated with DeepLabCut [38], which exhibited similar trends and velocity ratios $V_d/V_s$. To extract the temporal dynamics of the stylus, we study the shape of the angular displacement curve. We approximate the displacement of the stylus as a step function and fit the data using the MATLAB curve fitting tool to the following kinematics models $\theta(t) = a \times \text{erf}(b \times t + c) + d$ where $a$, $b$, $c$, and $d$ are fitting factors. This model helps to overcome the difficulty of estimating the beginning and end of the movement. To estimate the effective frequency of the stylus movement, a sinusoidal function $\theta(t) = \theta_0 \sin(2\pi f_s t + \phi)$ can be fitted to the angular speed curve of the raw
Figure 2.2: **Kinematic analysis of stylus during droplet ejection** The angle $\theta$ between the stylus and the axis running along the body of the sharpshooter is tracked over time and smoothed with a moving average of size ranging between 3 and 5. A step function is fitted to the kinematic profile and used to extract the maximum velocity timestamp $t_v$ and frequency of the stylus $f$. The frequency $f$ is obtained by fitting a sinusoidal function to the angular velocity profile.
An alternative method for calculating the frequency $f_s$ is directly extracting it from the kinematics data by considering the peak-to-peak duration in the angular acceleration curve, which corresponds to half the movement period. However, this approach is more vulnerable to the higher level of noise that naturally arises from taking the second derivative of displacement and is primarily used in hairless kinematics, where the angular speed curve resembles a sinusoidal function. Regardless of the chosen method, the variations observed within the calculated frequencies $f_s$ do not alter the conclusions drawn in this work. The droplet frequency is approximated as the second mode of the Rayleigh frequency for freely oscillating droplets, given by $f_o = (1/2\pi)\sqrt{8\gamma/\rho R_o^5}$. The diameter $D_o (= 2R_o)$ is determined from high-speed footage by averaging the vertical and horizontal diameters of the droplets. We assume a surface tension of water at $25^\circ C$ by $\gamma = 72 \times 10^{-3} \ N/m$ and water density of $\rho = 996 \ kg/m^3$.

### 2.2.2 Mathematical approach: Two spring model

We investigate the spatiotemporal dynamics of the stylus and the droplet using a reduced-order mathematical model consisting of a connected dual mass-spring-damper system. The model is inspired by previous models that model elastic connected systems such as the wave model [39], linked spring systems [40, 41], and the bouncing model [42] (Figure 2.4). The upper mass-spring-damper signifies the water droplet, while the lower mass and spring correspond to the compression of resilin within the stylus. Given the high efficiency of resilin, we disregard energy dissipation in the lower spring [43].

**Droplet spring**

Surface tension mediates elastic deformation in water droplets. We consider the Weber number, $We = \rho R_o V_d^2 / \gamma$, which denotes the proportional impact of inertial forces arising from the forceful collision of the stylus relative to surface tension. In the case of a water droplet (Surface tension: $\gamma = 72 \ mN/m$, Density: $\rho_w = 996 \ kg/m^3$), the Weber number is $We \sim 10^{-1}$, highlighting the predominance of surface forces. Furthermore, due to the comparatively low acceleration of the actuating substrate ($14 - 28 \ g$, where $g$ is the gravitational constant), the droplet continues to exist within the linear droplet deformation domain and does not give rise to non-linear water
puddles [44]. Under such conditions, kicked water droplets \((Bo < 1)\) transform from a spherical cap into an oblate spheroid, exhibiting the characteristics of a near-Hookean spring with a stiffness of \(k_d = 32\pi\gamma/3 = 2.41 \text{ N/m} \) [45, 46].

**Resilin spring**

Resilin is an elastic protein renowned for its high efficiency (approximately 97% efficiency) in energy loading and release during insect locomotion [43]. The elastic modulus \((E_r)\) of natural resilin varies between \(0.1 – 3 \text{ MPa} \) [47]. In the spring-loading phase, the stylus undergoes bending and deformation, causing the resilin blob to adopt a complex configuration. To approximate the effective spring constant \(k_s\), we postulate that the diminutive resilin blob adheres to Hooke’s law of elasticity during compression and extension cycles. For simplicity, we also assume that the resilin blob takes on a spherical shape, with a contact area with the stylus \(S_r \sim 0.25 - 1 \times 10^{-8} \text{ m}^2\), as estimated through video analysis and high-resolution microscopic imaging. Based on these assumptions, the effective spring constant of the resilin is calculated using \(k_s = S_r E_r / d \sim 2.5 - 600 \text{ N/m}\), where \(d\) represents the maximum compression of the blob, assumed to range \(\sim 50 - 100 \times 10^{-6} \text{ m}\). Given that the ratio of \(k_d/k_s \sim 0.004 – 1\), we assume little to no coupling between the two springs. Furthermore, the effective mass of the stylus, which combines the droplet and the stylus \(m_{eff} = m_d + m_s > m_s\), indicates the absence of inertial coupling.

**Equations of motion**

The equations of motion in the upward \(z\)-direction may be written as follows:

\[
M \ddot{z} + C \dot{z} + K z = 0
\]

\[
\begin{bmatrix}
m_s & 0 \\
0 & m_d
\end{bmatrix}
\begin{bmatrix}
\ddot{z}_s \\
\ddot{z}_d
\end{bmatrix}
+ \begin{bmatrix}
c_d & -c_d \\
-c_d & c_d
\end{bmatrix}
\begin{bmatrix}
\dot{z}_s \\
\dot{z}_d
\end{bmatrix}
+ \begin{bmatrix}
k_s + k_d & -k_d \\
-k_d & k_d
\end{bmatrix}
\begin{bmatrix}
z_s \\
z_d
\end{bmatrix}
= 0
\] (2.1)

The simulations start with the compression of the lower spring by a displacement \(dz_s\) beneath the equilibrium point, emulating the deformation of resilin during the spring-loading phase. At \(t = 0\), the compressed lower spring is released. The spatiotemporal dynamics of both springs are
obtained by numerically solving the system’s equations of motion using the 4th-order Runge-Kutta method in MATLAB. Dissipation within sessile droplets is modeled as a simple linear damper. Damping within sessile droplets originate from several factors, including bulk viscous dissipation, interfacial boundary layer damping, and moving contact line [48, 49, 50]. The impact of dissipation is assessed by conducting simulations for varying damping ratio values \( \zeta = c/2\sqrt{k_d m_d} \), ranging from \( \zeta = 0 \) (no dissipation) to \( \zeta = 1 \) (critically damped) (Figure 2.3). We note that as damping increases, the influence of elasticity diminishes, with the elastic projectile progressively behaving like a rigid projectile \( (\lambda \to 1 \text{ as} \ zeta \to 1, \forall f_o/f) \). Moreover, increasing the damping coefficient \( \zeta \) causes a shift in \( \tau \), as the frequency of the upper spring now corresponds to the damped \( f_d = f_o\sqrt{(1 - \zeta^2)} \).

**Assumptions and limitations of model**

The two-spring oscillator model is chosen because it is 1) a classical example used to model a two-degree of freedom system and 2) for its straightforward representation of the droplet’s vibrations and resilin’s dynamics. This model is not intended to provide an exact replication of the system; instead, it aims to elucidate key features of two coupled oscillating systems, such as temporal matching and ejection velocity.

Complex bouncing droplet dynamics have previously been modeled using various spring-based models, including the ‘bouncing model,’ in which a droplet is approximated as a Kelvin-Voigt material [51]. In this case, a Molecular dynamics approach is employed to assess the contact mechanics between the actuator and the droplet. The contact force is modeled as a damped spring which is active only during the compression of the upper spring and null otherwise. Like the two-spring models; the bouncing model predicts superpropulsion within a distinct frequency range and \( \lambda \) versus \( f_o/f \) profiles (Figure 2.4).

Another simplification in this model is the omission of any potential contact line dynamics that may arise due to the sessile nature of the formed water droplet. Sharp et al. (2011) demonstrated that the resonant frequency response of sessile droplets depends on the contact angle such that

\[
 f_i = \frac{\pi}{2} \sqrt{\left( i^3 \gamma \cos^3 \theta_e - 3 \cos \theta_e + 2 \right) / \left( 24 m_d \theta_e^3 \right)}
\]

where \( i \) represents the \( i^{th} \) vibrational mode of the droplet, and \( \theta_e \) is the contact angle between and \( m_d \) is the mass of the quasi-spherical droplet [53]. This equation exhibits a similar functional form to the classical equation developed
Figure 2.3: Effect of damping on ejection kinematics in the two-spring model a. Speed ratio \( \lambda = V_d/V_s \) b. Compression time and maximum velocity \( \tau = (t_c - t_v)/T \) c. normalized ejection time \( t_e/T \)

Figure 2.4: Comparison between different droplet models for superpropulsion a. Bouncing model adapted from [52] that models the deformation of the droplet using a spring-damper connected between two half-masses (Kelvin-Voight model). The contact force between the lower and upper systems is modeled using a very stiff spring. b. Superpropulsion is predicted with different reduced-order models and CFD. The wave model is adapted from [39].
by Lord Rayleigh for the natural frequency of free oscillating droplets (which is used in this work for $n = 2$), $f_n = \frac{1}{2\pi} \sqrt{n(n-1)(n+2)\gamma/3\pi m_d}$, where $n = 2, 3, 4...$ corresponds to the mode number [53]. Adjusting the natural frequencies $f_o$ by considering the contact angle $\theta_e$ would shift the theoretical, computational, and experimental data, but the same trends would still be preserved.

2.2.3 Experiments: Droplet-on-plate

We investigate the ejection of droplets with a diameter of 1 mm situated on a vertically oscillating plate featuring a superhydrophobic surface with a contact angle $\theta_e \approx 180^\circ$. The plate is subject to a sinusoidal displacement given by $z = A \sin(2\pi f_st - \pi/2)$, where $A$ denotes the displacement amplitude, $f_s$ represents the vibration frequency, and $-\pi/2$ corresponds to the phase shift, simulating the lower spring’s compression at $t_0 = 0$. The simulations are carried out for a wide range of $f_o/f_s$ values by adjusting the input vibrational frequency $f_s$ while maintaining a constant $f_o$ (by holding the droplet diameter constant). The experimental data reflect the general form of the theoretical and computational curves across a broader $f_o/f_s$ range.

2.2.4 Numerical simulation: Computational Fluid Dynamics

Numerical simulations were conducted in collaboration with Dr. Prateek Sehgal. Employing time-dependent two-phase flow physics, we conduct finite element simulations of a 2D droplet on a moving plate using COMSOL Multiphysics 5.6. The Navier-Stokes equations are resolved within the liquid and air domains. Interfaces between liquid, air, and solid are modeled utilizing the level-set method. Before imposing motion on the plate, the droplet is allowed to reach equilibration on the stationary plate, achieving its equilibrium shape based on the specified contact angle. After equilibration, a sinusoidal displacement is prescribed to the plate through a moving mesh interface, modeling it as a moving boundary within a deforming domain. To avert excessive deformation of the mesh elements due to the moving boundary, automatic re-meshing is executed at designated timesteps.

For the domain’s outer boundaries, we impose the outlet boundary condition, setting the static pressure to zero. For the wetted wall, that is, the plate’s surface, a static contact angle is defined along with a Navier-slip equal to the mesh element’s maximum size. We employ a free triangular mesh featuring a maximum element size of 0.015 mm and a minimum of 0.0001 mm. The reinitializa-
tion parameter for the level-set method is set at 0.5 m/s, while the parameter governing interface thickness equals the maximum mesh element size. We perform simulations for droplets exhibiting various contact angles, ranging from 100° to 180°. In 2D simulations, we maintain the droplet area equivalent to a droplet diameter of 1 mm, forming an impeccable circle and using the identical area to equilibrate droplets under gravity at varying contact angles. Considering the absence of coupling between the upper and lower springs, we imposed sinusoidal motion on the plate using the expression \( z = A \sin(2\pi f_s t - \pi/2) \), where \( f \) denotes the plate’s frequency with a constant peak acceleration of 140 m/s\(^2\). The vibration frequencies ranged from 50 Hz to 300 Hz. Furthermore, we conducted simulations for droplet sizes of 1.2 mm and 1.4 mm, as well as an acceleration of 80 m/s\(^2\), which displayed a good match with the drop-on-plate experimental results. However, we observed no significant disparities between the superpropulsion curves for 1 mm droplets.

2.2.5 Hairless sharpshooters

One salient feature of the anal stylus is the spread of large mechanosensitive sensilla with tiny coeloconic sensilla (hair) along its surface. These hair structures help sharpshooters select host plants and detect the moisture content in plants by acting as hygrosensors [54]. To understand their role in excretion, we perform ablation experiments. Glassy-winged sharpshooter insects \((n = 5)\) were captured and sedated under CO2. The hairs at the tip of the stylus were carefully snipped using scissors while avoiding damage to the stylus or the overall insect. The ‘hairless sharpshooters’ were released in an isolated and confined area. After trimming the sensilla, insects were maintained on host plants for a 48-h acclimatization period before being used in recordings. We observe that ‘hairless’ sharpshooters eject smaller droplets having diameters of \(D_o^- = 523 \pm 48 \mu m\) at higher speeds for both their stylus and droplet with \(V_s^- = 0.89 \pm 0.2 \ m/s\) \((n = 5, \ N = 10)\) and \(V_d^- = 0.45 \pm 0.07 \ m/s\) respectively. The calculated speed ratio is \(\lambda^- < 1\) indicating that droplet ejection in hairless sharpshooters does not fall in the superpropulsion regime.

To study the effect of removing hairs, we began by positing the null hypothesis \((H_0)\) that there would be no discernible changes in the speed of droplets and stylus in control and hairless sharpshooters, as well as no alteration in droplet size. This hypothesis assumes that removing the hair-like sensilla from the stylus of sharpshooters would not significantly affect these parameters.
To test our null hypothesis, we employed the two-tailed Mann-Whitney U test, a non-parametric statistical test that does not assume a normal data distribution. This test is useful for comparing differences between two independent groups when the dependent variable is ordinal or continuous, as with our parameters of interest (droplet size, stylus speed, and droplet speed). Our test population comprised two groups: the control group of unmodified sharpshooters and the test group of hairless sharpshooters. Both groups were subjected to identical conditions, except for the deliberate alteration in the test group (i.e., removal of the hair-like sensilla from the stylus). Our results revealed that hairless sharpshooters indeed expelled smaller droplets with diameters of $D_0^- = 507 \pm 50; \mu m$ ($p < 0.02$). The stylus speed in these insects was observed to be higher, $V_s^- = 0.83 \pm 0.16 \, m/s$ ($p < 0.02$), implying a significant effect of sensilla removal on these two parameters. These p-values indicate that the probability of observing these results, given that the null hypothesis is true, is less than 2%, leading us to reject the null hypothesis for these parameters. Interestingly, the test revealed no significant change in the speed of the ejected droplets between the control and hairless sharpshooters, suggesting that droplet ejection speed may not be influenced by the presence or absence of the hair-like sensilla.

Thus, our findings imply a potential role of the hair-like sensilla in modulating droplet size and stylus speed in sharpshooters. However, their involvement in regulating the speed of droplet ejection remains ambiguous, warranting further investigation.

2.3 Results

2.3.1 Kinematics of droplet ejection

We use high-speed imaging to investigate the droplet ejection dynamics of glassy-winged sharpshooters (GWSS, Homalodisca vitripennis, $n = 5$ individuals, $N = 22$ droplet ejections). By tracking the angle $\theta$ between the anal stylus and the insect’s body axis, we identify three successive phases: droplet formation, spring loading, and droplet ejection (Figure 2.6 d). The anal stylus initially rotates from a neutral position to start the extrusion of the fluidic waste. Throughout the pumping process, a water droplet ($\gamma = 72 \, mN/m$, $\rho = 996 \, kg/m^3$) progressively forms perpendicularly to the stylus, attaining a diameter of $D_o = 725 \pm 188 \, \mu m$ (Mean of mean $\pm$ SD) within a formation time ($\tau_d$) of approximately 80 $m.s$, while the stylus maintains a nearly constant angle
Figure 2.5: **Elasticity of the stylus is mediated by resilin a.** We manually bend the stylus using a pulled capillary tube. The stylus returns to its initial position b. The elasticity of the stylus may be disrupted by dissolving soft tissues such as resilin with KOH. The anal stylus loses its elasticity and does not return to its initial position.
As the pumped droplet nears its ultimate sessile state, the stylus further rotates by around \( \sim 15^\circ \) (Figure 2.6 e), compressing and storing elastic energy in the soft resilin structure, which is encased by stiffer sclerotized layers. During the droplet ejection phase, the stylus rotates rapidly, attaining a peak angular speed \( \dot{\theta} \) of \( 3.31 \pm 1.31 \times 10^4 \degree / s \) and a peak linear speed \( (V_s) \) of \( 0.23 \pm 0.07 \text{ m/s} \). Interestingly, the launched water droplets achieve approximately 40\% faster speeds \( (V_d = 0.32 \pm 0.1 \text{ m/s}) \) than the stylus. Computing the speed ratio \( \lambda = V_d/V_s \) shows that \( \lambda > 1 \), indicating a superpropulsive regime (Figure 2.6 g). **Is this a case of superpropulsion?**

### 2.3.2 Ballistics of elastic projectiles

The physics of elastic projectiles had been previously explored in the context of throwing or hitting sports balls [55, 56], kicking water droplets from superhydrophobic surfaces [39, 44], and propulsion of soft materials [40, 41]. One critical feature in elastic propulsion is the importance of sequential timing and synchronization between an actuator and projectile to enhance propulsion by optimizing energy transfer [2, 39, 40]. Superpropulsion is a principle previously described in synthetically engineered systems, where a water droplet may be ejected at a higher speed (up to 1.6 times) than the maximum speed of a superhydrophobic vibrating plate (i.e. \( \lambda > 1 \)) [39]. Such counterintuitive propulsion is achieved only in elastic projectiles (such as a water droplet) by carefully tuning the underlying actuator’s vibrational frequency to the projectile’s natural frequency. The superpropulsion principle may be exploited to enhance the throwing of rigid projectiles through the elastic tuning offered by compliant substrates [40, 41]. By adding a soft layer with specific geometrical properties to a rigid projectile, the reaction force between the thrower and the projectile might be delayed to increase the initial take-off speed [40]. Here, we discover and present the superpropulsion phenomenon for the first time in a biological system, i.e., sharpshooter insects. Based on the kinematic and physical properties of the ejected droplets in sharpshooters, the Weber number \( We = \rho D_o V_d^2/\gamma \sim 10^{-1} \) and Bond number \( Bo = \rho g D_o^2/\gamma \sim 10^{-1} \) (where \( D_o < 1 \text{ mm} \) is the diameter of the droplet and \( g \) is the gravitational constant) indicate that surface tension forces dominate the ejection dynamics over bulk forces. As a result, the droplets visibly deform into oblate spheroids reaching maximum compression at \( t_c \) before extending, supporting elastic energy storage for superpropulsive principles (Figure 2.6 d, f).
Figure 2.6: Sharpshooter insects display ultrafast droplet waste ejection. a. A blue-green sharpshooter (BGSS) Graphocephala atropunctata feeds on xylem fluid from a basil plant stem. The insect extracts fluid from the xylem tubes using its stylet and expels water-based waste as droplets through its anal stylus (anal ligulae). b. A close-up microscopic view of the anal stylus of a glassy-winged sharpshooter (GWSS) Homalodisca vitripennis shows a transparent resilin blob near the pivot point at its base and tiny hair-like extensions (sensilla) along its surface. c. A confocal image of the stylus (GWSS) demonstrates that the stylus is a complex combination of chitin (sclerotized) and resilin (flexible). A canal runs along the stylus, channeling the expelled fluid during excretions. d. Droplet ejection takes approximately \( \sim 100 \text{ ms} \) and can be divided into three distinct stages: 1- Droplet formation, where a droplet waste is created on the anal stylus, 2- Spring loading, during which the insect compresses the resilin located on the anal stylus, and 3- Droplet release, in which the stylus rapidly rotates to eject the droplet in the dorsal and posterior plane. Before takeoff, the elastic droplet experiences compression and extension. e. Kinematic analysis of the anal stylus \((n = 1 \text{ GWSS individual, } N = 3 \text{ droplet ejections})\) and the insect’s body axis emphasizes the various excretion stages. f. Owing to the elasticity provided by the droplet’s surface tension, the maximum compression time \(t_c\) and ejection time \(t_e\) occur after the stylus attains its top speed. g. The maximum droplet speed at ejection \(V_d\) surpasses the top speed of the stylus \(V_s\) \((n = 5, \text{ GWSS, } N = 22 \text{ droplet ejections, mean of means } \pm \text{ STD})\). The speed ratio \(\lambda = V_d/V_s\) is greater than one. Po: Posterior, Do: Dorsal, An: Anterior, Ve: Ventral.
2.3.3 Supepropulsion of droplet excrement in sharpshooter insects

We employ a simplified mathematical model to simulate the droplet ejection mechanism, comprised of a one-dimensional, two-spring oscillator. In this model, the upper mass-spring-damper system \((m_d, k_d, c_d)\) represents the droplet, while the lower mass-spring system \((m_s, k_s)\) symbolizes the stylus and resilin (Figure 2.7 b). Both the droplet \((We \sim 10^{-1}, 14 - 28 \text{ g acceleration})\) and resilin are depicted as elastic Hookean springs \([45, 46, 43, 44]\). To account for dissipation in sessile droplets due to viscous effects, interfacial boundary layer damping, and moving contact line \([48, 49, 50]\), a linear damper with a damping ratio \((\zeta)\) varying between 0 (low dissipation) and 0.75 (high dissipation) is utilized. We determine the frequencies \(f_o\) and \(f\), where \(f_o = (1/\pi)\sqrt{\frac{k_d}{m_d}}\) corresponds to the second harmonic of the undamped natural frequency of the upper spring, and \(f = (1/2\pi)\sqrt{\frac{k_s}{m_s}}\) corresponds to the frequency of the lower spring. The theoretical speed ratio \(\lambda_{th} = \frac{V_{d,th}}{V_{s,th}}\) is extracted for various values of the frequency ratio \(f_o/f\) and \(\zeta\), where \(V_{d,th}\) is equal to the maximum speed of the upper mass, and \(V_{s,th}\) is equal to the maximum speed of the lower mass. The superpropulsion regime is characterized by \(\lambda_{th} > 1\), while the subpropulsion regime is represented by \(\lambda_{th} < 1\) (and \(\lambda_{th} = 1\) corresponds to a rigid-projectile-like behavior). The two-spring model predicts a range of characteristic curves depicted in (Figure 2.7 c, d) and highlighted by the shaded area. The model predicts that superpropulsion (i.e., \(\lambda_{th} > 1\)) occurs at \(f_o/f \geq 1.16 - 1.5\) with a peak ranging from \(\lambda_{th} = 1.25 - 1.76\) at frequencies \(f_o/f \sim 3.23 - 3.44\), respectively. Intriguingly, the two-spring model also forecasts the subpropulsion \((\lambda_{th} < 1)\) regime for \(f_o/f < 1.16\), implying that at these frequency ratios, the elasticity of the projectile compromises its kinematic performance during take-off. We compare the theoretical prediction with field data from three different species of sharpshooter insects: Glassy-winged sharpshooter *Homalodisca vitripennis* (GWSS, \(n = 5, N = 22\)), blue-green sharpshooter *Graphocephala atropunctata* (BGSS, \(n = 3, N = 9\)) and red-banded sharpshooters *Graphocephala coccina* (RBSS, \(n = 1, N = 3\)).

We calculate the frequency of droplet vibrations \((f_o)\) as the second mode of the Rayleigh frequency \(f_o = (1/2\pi)\sqrt{\frac{8\gamma}{\rho R_o^3}}\) [57] using high-speed footage, and the frequency of stylus \((f)\) using the kinematics analysis of the stylus. Our results demonstrate that the velocity ratio \(\lambda\) is \(> 1\) for all species and aggregates within a small range of \(f_o/f \sim 3 - 4\) (Figure 2.7 e), conclusively establishing that sharpshooters exploit the superpropulsion phenomenon for excretion. We supplement our
Figure 2.7: **Limits and principles of superpropulsion combining experiments, theory and modeling.**

**a.** An ideal rigid projectile sitting on a vibrating plate will take-off when the plate reaches maximum velocity $V_{\text{max}}$ at $t_v$ with an ejection speed $V_e = V_{\text{max}}$ (i.e. $\lambda = 1$). Alternatively, an elastic water-droplet ($Bo < 1$) experiences deformation mediated by surface tension during ejection, reaching maximum compression at $t_c$ before ejection.

**b.** Theoretical and computational modeling predicts two separate regimes: superpropulsion ($\lambda > 1$) and subpropulsion ($\lambda < 1$). Superpropulsion occurs at $f_0/f \sim 1.16 - 1.5$ and peak kinematics around $(f_0/f)^* \sim 3.23 - 3.44$ for different damping ratio $\zeta$ in the upper system. The solid line corresponds to the curve at $\zeta = 0.25$ and $(f_0/f)^* = 3.23$ corresponds to peak kinematics with no dissipation ($\zeta = 0$). These predictions are validated by data of three sharpshooter species (GWSS, $n = 5$, $N = 22$, BGSS, $n = 3$, $N = 9$, RBSS, $n = 1$, $N = 2$) and vibrating droplet-on-plate experimental data which lie the predicted region for superpropulsion.

**c.** Droplet dynamics reveal that peak normalized energy transfer $\bar{W}_{\text{t}_0\rightarrow\text{t}_e}$ occurs when the droplet reaches maximum compression $t_{c,\text{max}}$ matches the times the plate reaches maximum velocity $t_v$ where $\tau = (t_c - t_v)/T = 0$ at $(f_0/f)^* \sim 3.23$. For sharpshooters, the maximum compression of the droplets occurs around the maximum velocity of the stylus.

**d.** Findings with CFD simulations and droplet-on-plate experiments that are in good agreement with both the theory and organismal data (Figure 2.7 **b-d**).

We hypothesize that sharpshooters synchronize the maximum speed of their stylus with the deformation dynamics of their droplet-excreta. To test this, we compare the time at maximum droplet
compression \( t_c \) and the time at maximum stylus velocity \( t_v \). We define the dimensionless term \( \tau = (t_c - t_v)/T \), where \( T \) is the period of the engine oscillations. The two-spring model, CFD, and plate experiments show that the superpropulsion peak \( \lambda_{max} \) occurs when the maximum compression of the projectile coincides with the maximum velocity of the engine at \( \tau = 0 \) (Figure 2.7 d). Interestingly, in the case of sharpshooters, the max compression time of the droplet also occurs around or before the maximum velocity of the stylus. These results suggest that the sharpshooters exploit the temporal tuning between the stylus and droplets for excretion (see Figure 2.8 and next section).

To gain a deeper understanding of the superpropulsion phenomenon, we examine the frequency ratio \( f_o/f \) with respect to the energy transfer between the stylus and the droplet [40]. The work \( W \) accomplished by the lower spring on the upper system, from \( t = 0 \) until the upper mass achieves its peak velocity at ejection \( t = t_e \), is computed as \( W_{t_0 \to t_e} = f_o \int_0^{t_e} F_d(t)V_s(t)dt \). Here, \( F_d = k_d(z_d - z_s) \) represents the force on the upper mass, and \( \dot{z}_s \) denotes the velocity of the underlying stylus. We demonstrate that the normalized maximum energy transfer \( \bar{W}_{max} \) takes place at \((f_o/f)^* \sim 3.23\), where \( \lambda \) is at its maximum value (\( \lambda = 1.76 \)) and \( \tau = 0 \) (Figure 2.7 d). Consequently, the optimal energy transfer between the engine and the projectile arises from maximizing the product of force and velocity (power) throughout the ejection cycle. This process is influenced by the temporal delay induced by the projectile’s elasticity [40].

**Hairless anal stylus disrupts the temporal tuning**

Is it possible to disrupt the synchronization between the droplet and the stylus to create sub-propulsive sharpshooters? We conduct ablation experiments in which we mechanically trim the tips of hair-like structures (sensilla) at the top of the anal stylus in glassy-winged sharpshooters (\( n = 5, N = 10 \)) (Figure 2.8 a ). The two-tailed Mann-Whitney U test reveals that “hairless” sharpshooters expel smaller droplets with diameters of \( D_o^- = 507 \pm 50 \mu m \) (\( p < 0.02 \)) at higher stylus speeds, \( V_s^- = 0.83 \pm 0.16 \text{ m/s} \) (\( p < 0.02 \)) (Figure 2.8 b ), with no significant change in ejected droplet speed. Remarkably, the speed ratio \( \lambda^- \) is < 1, indicating that droplet ejection in hairless sharpshooters does not fall within the superpropulsion regime (Figure 2.8 b ). We examine the temporal tuning represented by the frequency ratio \( f_o/f \) concerning the peak kinematic performance predicted by the two-spring model. Hairless sharpshooters pump smaller droplets, resulting in higher
values of $f_o \propto D^{-3/2}$. Furthermore, we observe an increase in the frequency of the hairless stylus $f$. However, the resulting $f_o/f$ values are not conserved and are lower than their control counterparts ($p < 0.02$, two-tailed Whitney-Mann U test) (Figure 2.8 b). Control sharpshooter species exhibit a tightly tuned system—a hallmark of power-amplified ultrafast systems [2]—as they reside within the $(f_o/f)^* \sim 3.23$ regime, corresponding to peak kinematic performance (Figure 2.8 d and Figure 2.8 e, d). In contrast, stylus frequencies in the hairless case are dispersed well above this window, clearly emphasizing a disruption in the temporal matching between the stylus and the droplets.

Droplets undergo more deformation and rotation in hairless sharpshooters

What causes this temporal mismatch? This discrepancy is further substantiated by examining droplet behavior during ejection, which includes more pronounced droplet deformation and rotational effects. In hairless sharpshooters, video analysis demonstrates that droplet stretching and take-off happen after the stylus ceases motion (Figure 2.8 e). In contrast, in control sharpshooters, droplet ejection occurs while the stylus is still in motion. First, we detect significant droplet deformation in hairless sharpshooters. Deformation is measured as the droplet height $h(t)$ normalized to the initial height $h_o \approx D_o$. At ejection, $h/h_o|_{e}$ is roughly 1.6, which is 30% greater than droplets ejected in control sharpshooters. Additionally, the ejected droplets experience a significant rotation rate around their axis, with an angular velocity $\Omega^- \sim 2.4 \times 10^3 \text{ rad/s}$ compared to $\Omega^+ \sim 170 \text{ rad/s}$ (Figure 2.9). Second, in hairless sharpshooters, the ejected droplet experiences more significant rotation. To evaluate the relative influence of rotation, we consider both the translational energy $E_t$ and rotational energy $E_r$ transferred to the droplet from the rotating stylus. In hairless sharpshooters, the energy ratio of ejected droplets $(E_r/E_t)^- = (r_g \Omega/V_d)^2$ is around 0.2 (where $r_g = R_o/\sqrt{10}$ represents the radius of gyration of the spherical droplet). However, in control sharpshooters, energy is almost entirely translated to translational energy, with $(E_r/E_t)^+ \sim 10^{-2}$. This significant increase in energy lost to droplet rotation suggests that the rotational aspect of the stylus (previously overlooked) plays a crucial role in determining droplet dynamics during ejection. For example, the increase in the frequency of the stylus $f_s$ may lead to a substantial rise in the effect of inertial forces, such as the Euler and centrifugal force ($\propto f_s^2$), in the rotating frame of reference of the stylus. In extreme cases, these inertial forces may result in droplet movement (slip) parallel to
the stylus, countered only by capillary adhesion. Consequently, the moving stylus may generate a net tangential force that causes the droplet to rotate, akin to how an off-centered strike on a billiard ball would induce a sidespin. Another possible outcome of trimming is the artificial decrease in the effective size of the actuating appendage, composed of both the stylus and the hairs. Considering the substantial size of the hairs (at least 40% the length of the stylus), cutting the hair structures reduces the stylus length, potentially intensifying these inertial and geometrical effects.

**The anal stylus is parahydrophobic**

Next, we examine the influence of the stylus’s surface properties on droplet ejection dynamics. Efficiently detaching a droplet from a rotating substrate necessitates balancing two opposing requirements: low surface energy for effortless detachment and sufficient adhesion to prevent premature droplet rolling. The stylus exhibits parahydrophobic characteristics, with a high apparent contact angle $\theta_a$ and robust surface adhesion, a pattern seen in other natural and synthetic substrates [58, 59]. This parahydrophobicity is demonstrated by the constant contact area $S$ during droplet growth and observations that droplets do not roll off due to gravity or stylus orientation (Figure 2.6 d). During the emission of vibrational mating calls (while excreting), droplets can experience significant displacements of up to $\sim 10 \mu m$ and speeds $(V_d - V_s)$ of $\sim 2/; cm/s$ without detaching from the stylus (Figure 2.8) [60]. We hypothesize that droplet ejection occurs when the stylus's kinetic energy $E_k \propto \frac{1}{2} \rho V^2 (2\pi f A)^2$ (where $A$ is the amplitude of the arclength set by the stylus tip and $V$ is the droplet volume) surpasses the surface adhesion $E_s \propto S \gamma (1 + \cos \theta_a)$.

Calculating the ratio $E_k/E_s$ provides a critical frequency ratio $(f_o/f)_c$ necessary for detaching a droplet, $(f_o/f)_c \sim 4A \sqrt{\pi/(3S(1 + \cos \theta_a))} \leq 5.2 - 13.12$ for $\theta_a = 100^\circ - 150^\circ$, respectively. The significance of surface adhesion in superpropulsion is further supported by numerical CFD simulations on droplets with varying contact angles (Figure 2.8 f). These findings imply that superhydrophobicity and adhesion are vital for stable droplet ejection in unstable environments. Moreover, these properties allow for a larger droplet volume given a specific contact area $S$, resulting in the storage of more elastic energy through surface deformations $dh \sim R^{3/2} \gamma$ [45] and reduced critical velocities and accelerations [52, 42, 61]. A more precise analysis of droplet detachment would involve understanding the contact line’s dynamics and the droplets’ shape during the vibration cycle [59] (Figure 2.10).
2.3.4 Energetics of excretion

Next, we investigate whether superpropulsion could provide energetic benefits for these insects, which rely on a nutrient-limited food source. The net energy gain per unit volume (Energy Density) per feeding-excretion cycle for the organism can be approximated as follows:

\[ \eta \geq (\eta_x - \eta_f) - \eta_{ex} \]  

(2.2)

where \( \eta_x \) represents the energy content of nutrients in xylem sap, \( \eta_f \) denotes the energy per unit volume used by the cibarial pump during feeding, and \( \eta_{ex} \) is estimated from the energy required during excretion. It is crucial for the insects’ functioning and survival to maintain a net positive energy gain (\( \eta \)) from feeding on xylem fluid [62, 33]. Andersen et al. [33] assessed the net energy of xylem sap and cibarial pumping at negative pressures for sharpshooters, i.e., \( \eta_{in} = (\eta_x - \eta_f) \), as \( 2 \times 10^5 - 8.2 \times 10^6 \) J/m\(^3\), considering factors such as xylem tension, time of day, metabolic cost, cibarial pump efficiency, and nutrient concentration in xylem fluid. This range sets the upper limit for \( \eta_{ex} \), as any higher energy expenditure on excretion would result in an energy deficit for the organism.

Hydrodynamics of excretion in glassy-winged sharpshooter

To estimate \( \eta_{ex} \), we model fluid excretion through the anal tube as a pressure-driven flow of liquid water (Density \( \rho = 996 \) kg/m\(^3\), Surface tension \( \gamma = 72 \) mN/m, and Viscosity \( \mu = 1 \) mPa.s) through a straight, circular cylinder with a diameter \( d \) and length \( l \) estimated from microCT (Figure 2.12 b).

Histological analyses of the leafhopper digestive tract suggest an absence of significant corrugations [63, 64], leading us to assume a smooth inner cylinder surface. Micro-CT scans and high-speed video data provide cylinder dimension estimates, yielding an \( l/d \) ratio of approximately 0.12 (Figure 2.1). We presume this ratio is conserved across individual glassy-winged sharpshooters due to isometric body variations in leafhoppers [65].

We estimate the anal tube’s effective diameter by fitting the stylus’s bottom cross-sectional area to a circle with diameter \( d \) and perimeter \( P \). The canal exhibits an irregular, more elliptical shape.
than a perfect circle. The eccentricity $\epsilon = \sqrt{1 - a^2/b^2}$ is determined along the length of the stylus and rectum, with an average hydraulic diameter of $d = 4A/P$, where $A$ is the cross-sectional area obtained from microCT.

The volumetric flow rate $Q$ is determined by dividing the droplet’s final volume by its formation duration, resulting in $Q = V/\Delta t = 0.3 \pm 0.22 \, \mu L$. The exiting flow speed $u = Q/A = 0.39 \pm 0.08 \, m/s$, where $A$ represents the average circular cross-sectional area of the stylus and rectum, calculated as $A = \pi d^2/4$. The excretion speed is comparable to the velocity range reported for xylem sap suction (0.02 – 5 \, m/s) [33, 66]. We consider the flow to be laminar ($Re = \rho ud/\mu \sim 10 - 60$) and at steady-state, as the droplet growth rate ($\sim h(t)^3$) remains relatively constant (Figure 2.11). Due to the low Re, inertial effects from the anal stylus’s curvature during droplet formation are disregarded.

We approximate the average pressure (since $1 \, Pa = 1 \, J/m^3$) using the energy balance equation to pump water at a steady state with a flow speed $u$ across the hindgut and form a droplet on the stylus. The total energetic cost has two contributions: 1) viscous forces (low Re) within the cylinder donated as $P_{flow}$ due to fully developed flow estimated using the Hagen-Poiseuille equation $\Delta P = 128\mu lQ/\pi d^4$ with $Q = u\pi d^2/4$, and 2) surface tension $P_{ST} = 4\gamma/d$ as the fluid exits the nozzle ($Bo < 1$) [67]. Therefore, the energetics per unit volume of excretion may be expressed as follows:

$$\eta_{ex} = \frac{32\mu lu}{d^2} + \frac{4\gamma}{d}, \quad (2.3)$$

From Equation 2.3, we observe that the energetic cost of pumping fluid depends on the flow’s speed and the tube’s size. Note that the inertial term $\rho u^2/2$ used in [3] may be dropped since it is much lower ($< 0.3\%$) than the viscous and surface tension terms (Table A.2). The average energy per unit volume to form a droplet for a sharpshooter insect (GWSS) $\eta_{ex} = 1.3 \times 10^4 \, J/m^3$ ($N = 22$) is lower than $\eta_{ha}$, ensuring a net positive energy gain to support other biological functions (Figure 2.12 c). However, transitioning to a ‘jetting’ regime instead of droplet formation necessitates increasing the speed of the exiting flow, which is energetically expensive ($\eta_{ex} \propto u$, Figure 2.12 c). Specifically, for GWSS, we estimate that ejecting a droplet requires $4 - 8 \times$ less energy than forming a jet at $We \geq 1$, i.e., when inertial forces overcome surface tension forces [68, 69] (Figure 2.12 c).

Upon forming a droplet on the stylus, kinetic energy is imparted by the stylus to eject the droplet

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(either sub- or super-propulsively) to overcome surface adhesion. The average kinetic energy per unit fluid volume $\bar{E}_k \sim \frac{1}{2} \rho V_d^2$ is approximately $10^2 \ J/m^3$, which is two orders of magnitude smaller and negligible compared to $\eta_{ex}$. Moreover, we find that the energy required to eject droplets in superpropulsion mode is lower compared to subpropulsion when $f_o/f < (f_o/f)_c$, suggesting energetic penalties associated with subpropulsion as $\bar{E}_k \propto f^2$. These findings highlight the ultra-low energy cost of the superpropulsion mechanism in sharpshooters.

2.3.5 Scaling

Lastly, we examine the fluid excretion mechanism of sharpshooters in comparison with other organisms that excrete fluid through an opening (Figure 2.12 d). The approaches organisms use for such ejections are varied and primarily influenced by the organism’s behavior and the dominant forces at its length scale. These forces are typically characterized by the Reynolds number ($Re$), the Bond number ($Bo$), and the Weber number ($We$) (Figure 2.12 d). Animals with an orifice size $d > 100 \ \mu m$ (mammals, archerfish, and large insects) rely on inertial forces for consistent fluid ejection by forming jets or large sheets of liquids during urination [67] or hunting [70]. Smaller organisms, on the other hand, living in a world dominated by surface tension ($Bo \ll 1$ and $We < 1$) develop ingenious mechanisms to overcome capillary adhesion.

Sharpshooters (studied here) utilize their specialized resilin-powered and tuned anal stylus to transfer kinetic energy to the droplets. A similar droplet catapulting strategy is also observed in phloem fluid-feeding aphids (Hemiptera: Aphididae) that kick their sugar-rich excrement (with either their legs or caudas). Aphids also manipulate surface tension forces by coating their excrement with powdery wax, transforming them into non-sticky liquid marbles [71]. However, not all xylem-feeders employ droplet ejection to eliminate their fluidic waste. Cicadas (Hemiptera: Cicadidae) form powerful jets to remove their excreta because they are approximately $2 \ - \ 7 \times$ larger than an adult sharpshooter (Figure 2.12 d) [72] and do not face the same energetic constraints as sharpshooters. Outside the animal kingdom, small fungal species such as ballistospores and fungal cannons with characteristic length $1 \ \mu m < d < 100 \ \mu m$ resort to explosive jets or droplet coalescence to disperse their spores [73]. Both these fluid ejection mechanisms are destructive and non-repeatable, unlike the one used by the sharpshooters.

Overall, these diverse fluid ejection techniques emphasize the importance of physical and ener-
getic constraints in determining the mechanism employed by a given organism.

**Fluid mechanics of Dripping vs Jetting**

The form of water flowing out of a circular orifice (nozzle) with a diameter \( d \) at speed \( u \) relies on the interplay of surface tension and inertial forces, characterized by the Weber number \( We = \frac{\rho u^2 d}{\gamma} \).

When \( We < 1 \), the exiting fluid gradually forms a large pendant droplet with a diameter \( D > d \). ‘Dripping’ occurs as the growing droplet’s weight surpasses the nozzle’s surface adhesion. In this situation, the pendant droplet detaches and falls, leaving a residual fluid portion on the nozzle’s outer surface (e.g., a dripping faucet). When \( We > 1 \), the exiting fluid transitions to a jet, where inertial forces overcome surface tension forces. With increasing fluid speed and \( We > 8 \), a continuous liquid jet forms at a critical Weber number \( We > 8 \) [69]. For simplicity, we assume the transition to a jetting regime occurs at a critical Weber number \( We = 1 \) [68].

Why don’t sharpshooters take advantage of gravity-induced dripping? There are several reasons that we hypothesize would make catapulting droplets more desirable than gravity-based dripping. First, ‘dripping’ generates droplets at low production rates (given the same pumping speeds), which is not ideal for sharpshooters, as they need to pump out large volumes of fluids to obtain sufficient nutrients. Second, due to their high feeding rate, sharpshooters tend to remain in one location for extended periods, making dripping a less-than-ideal strategy for maintaining hygiene and avoiding fouling. Third, dripping leaves fluid residue at the nozzle level, rendering it an ineffective method for expelling large fluid volumes and increasing the likelihood of fouling [69]. Fourth, flinging droplets over long distances have been hypothesized to evade predators, such as the tiny parasitic wasp *Cosmocomoidea*, which may be attracted to chemical cues in accumulating their excreta. Fifth, field observations indicate that sharpshooter insects primarily feed with their heads facing the ground. If droplets were to drip from their excreta, it could obstruct the abdominal spiracles, resulting in the reduced inhaled air and potentially causing asphyxiation. However, sharpshooter insects have been observed feeding in rainy conditions, even when completely covered in rainwater (personal observation).
2.4 Discussion

In summary, our research uncovers that droplet ejection through superpropulsion is an energy conservation strategy per feeding-excretion cycle for these small, xylem-sap consuming insects. An energy-efficient excretion method is crucial because the increased miniaturization of these xylem-feeding insects (e.g., juveniles or smaller species) results in higher energetic losses during fluid pumping due to viscous and surface tension forces $\eta \propto d^{-2}$, suggesting a fundamental limit on the minimum body size of xylem-sap feeders [65]. Additionally, flinging droplets to vast distances could decrease the likelihood of detection by predators such as the parasitic wasp *Cosmocomoidea*, which may be attracted to chemical cues in accumulating sharpshooter excreta [74].

The necessity to create a significant distance between insects and their waste is primarily observed in shelter-dwelling or site-faithful insects, which typically face pressure to maintain hygiene at their location to prevent pathogen growth and reduce chemical cues for potential predators. Ballistic ejection of excrement is not rare among insects. Many insect species, often referred to as ‘frass-shooters,’ ‘butt-flickers,’ and ‘turd-hurlers,’ have developed unique strategies to launch away both liquid and solid excrements [30]. For example, frass-shooting skipper larvae use biological latches on their anal plates combined with a hydrostatic blood pressure buildup to propel solid pellets up to 38 times their body length at speeds exceeding 1.5 m/s. Some noctuid species violently shake their abdomen while releasing their frass pellets, and some geometrid larvae utilize their thoracic legs to kick away their frass pellets [30]. Insects, in particular, display a broad range of innovative waste disposal strategies influenced by their environment, diet, and overall lifestyle. Thus, our comprehensive analysis of excretion dynamics in sharpshooter insects emphasizes the importance of investigating waste elimination to gain a holistic understanding of organismal behavior.

Lastly, our examination of the droplet catapulting mechanism in sharpshooters offers the first observation and quantification of superpropulsion in a living organism. Fundamentally, superpropulsion presents an opportunity to propel an elastic projectile faster than the maximum speed of its actuator through temporal tuning and can be considered a single-shot resonance system [39]. In physical systems dominated by surface tension forces, superpropulsion provides a clever mechanism that uses this impeding force as a spring, albeit with strict temporal tuning for optimal advantage. This superpropulsion mechanism, however, may not be exclusive to surface tension-dominated sys-
tems. It could be employed by other small power-amplified and impulsive biological systems that rely on elastic structures to overcome the power limitations of striated muscles [2]. Our research takes these insights from nature and offers a fundamental framework for implementing an energy-efficient superpropulsion mechanism for manipulating elastic objects in synthetic systems, ranging from pick-and-place nano- and micro-fluidic devices to smart wearable electronics and soft, elastic robotic engines [75, 39, 40, 41].
Figure 2.8: **Temporal tuning in superpropulsion and role of surface adhesion from droplet stability and ejection.**

a. We trim the mechanosensitive hair structures (sensilla) located at the top of the anal stylus to disrupt temporal tuning between the droplet and the stylus. b. The maximum speed of the stylus ($V_s$) and droplet ($V_d$) in hairless sharpshooters is higher than in control sharpshooters ($p < 0.01$, $p < 0.02$, respectively). In addition, the calculated frequency ratio $f_o/f$ is lower than the expected frequency ratio in control sharpshooters, whereas the speed ratio $\lambda < 1$ indicates a disruption in superpropulsion. c. High-speed imaging shows that ejected droplets undergo significant deformation, and take-off occurs after the stylus stops moving. d. The mean stylus frequencies $f$ in control sharpshooters lie within a tight window of $(f_o/f)^{-1} \sim 0.27 - 0.35$ (inverse of $f_o/f$) which falls around peak kinematics and energy transfer at droplet take-off. This matching is disrupted in hairless sharpshooters where associated $f$ are scattered away from that window. e. The anal stylus exhibits strong capillary adhesion where excreted droplets remain adhered despite lateral and vertical displacements $V_d - V_s \sim 2$ cm/s observed during mating calls. f. Computational fluid dynamics (CFD) simulations reveal a theoretical limit for droplet ejection of a sessile droplet having a contact angle $\theta$. Sessile droplets with a relatively high contact angle ($\theta^\circ > 130$) do not take off from the surface of the vibrating plate. Superpropulsion is conserved where $\lambda = V_d/V_s > 1$ even if ejection does not occur. Due to adhesion, the maximum speed of the droplet is not equivalent to its ejection speed.
Figure 2.9: **Droplet size and dynamics in hairless GWSS** a. Hairless sharpshooters form droplets having smaller diameters than control sharpshooters. Two-tailed Mann-Whitney test, \( **p = 0.016 < 0.02. \ n = 5 \) Control; \( n = 5 \) Hairless, Mean of means \( \pm \) Standard deviation) b. During droplet ejection, droplets experience larger deformation with \( h/h_o \) reaching up to 1.6 – 1.8

Figure 2.10: **Dynamics of droplet ejection on a vertically vibrating substrate having different contact angles:** a. Detachment of droplets from the surface of a vibrating substrate requires that the contact line \( L \) goes to zero while the relative speed between the droplet and the substrate is \( \geq 0 \). b. Tracking \( L \) over the period of oscillations. At a contact angle of 120°, the contact line \( L \) shrinks to a minimum during droplet extension but does not reach zero (separation).
Figure 2.11: **Droplet growth on parahydrophobic and patterned stylus** Droplets are formed on the anal stylus on a constant contact area $S$. The apparent contact angle $\theta_a (\approx \theta_e)$ increases as the size of the droplet increase. 

b. Highlighting the hydrophilic area of contact $S$ between the droplet and the stylus (Hairless sharpshooters). 

c. The energy of adhesion decreases as the droplet grows. 

d. The droplet growth approximated by $h^3(t)$ is constant, indicating a constant flow rate.
Figure 2.12: **Energetics of superpropulsion and physical scaling:** a. MicroCT scan of a GWSS revealing the morphology of their hindgut. Digested fluidic waste is excreted through the rectum into the narrow anal stylus before being ejected. b. The hydrodynamics of excretion in sharpshooters is modeled as a pressure-driven flow across a cylindrical tube. Fluid exiting a nozzle forms a pendant droplet at low speeds ($Bo >> 1$ and $We < 1$) or jet when inertial forces are dominant ($We > 1$). c. The pressure (Energy per unit fluid volume) exerted by sharpshooter insects increases proportionally to the speed of the exiting fluid and the orifice diameter. At their small scale, forming jets to expel their fluid waste is $4 \times$ more energetically taxing than forming individual droplets and flicking them d. Small organisms living in a surface tension-dominated world face the challenge of overcoming capillary adhesion. Ballistospores and sharpshooters exploit surface-tension properties (coalescence and superpropulsion) to eject droplets at high speeds. Error bars represent average value ± one standard deviation.
CHAPTER 3
SLINGSHOT SPIDERS BUILD TENSED, UNDERDAMPED WEBs FOR ULTRAFAST LAUNCHES AND SPEEDY HALTS

3.1 Introduction

Many orb-weaving spiders are known for their sit-and-wait technique, which effectively captures prey by utilizing sticky silk and quickly dissipating the prey’s kinetic energy [76, 77, 78, 79]. Slingshot spiders, a specific group of orb-weavers, are recognized for stretching and releasing their webs like slingshots to catch prey [80, 81, 82, 83, 84, 85, 86, 87, 88]. These spiders have developed an orb web with a central tension line, which permits them to transform their web into a 3D cone-shaped structure. This design stores elastic energy in the radial lines, facilitating rapid accelerations (> 1300 m/s²) to seize flying prey or potentially evade predators [84]. Although the way slingshot spiders use their webs like a spring to propel themselves has been described, it is still unclear how they utilize their unique web and tension line to quickly decelerate and halt after either capturing or missing prey, as well as how they reset their web for potential reuse. To explore these unresolved questions, we create a mathematical model to examine the dynamics of the slingshot spider web in this paper.

The slingshot spider holds the center of its web using four rear legs while gradually pulling and twisting the tension line, simultaneously coiling the silk with the claws on its anterior legs and pedipalps (non-locomotor front appendages). This process stores elastic energy in the radial lines of the web (Figure 3.1 a). When the spider detects external stimuli (e.g., a finger snap), it releases the tension line, propelling both the web and the spider backward (Figure 3.1 b). Multiple trajectories (n 5) are shown in Figure 3.1 c, with the full displacement taking place in about 30 ms. The primary movement occurs predominantly in the y-direction (10 – 15 mm or 10 – 15 × body lengths), with smaller displacements (±1.1 mm, less than one body length) in the x-direction. The spiders can reach vertical speeds of up to 4.2 m/s ($V_{\text{max}}$ 4.16±0.07 m/s) and accelerations beyond 1300 m/s² ($a_{\text{max}}$ 1163 ± 144 m/s²) [80]. Interestingly, the resulting vibrational response of the web also subsides within milliseconds, indicating that the web design enables energy storage, speed,
and energy dissipation. These characteristics could enhance prey capture, decrease the likelihood of harm to the spider or web, and/or enable a swift reset and reloading of the web.

Driven by the slingshot spider’s rapid motion attenuation and its non-planar configuration, we aim to create a theoretical model of the slingshot spider web’s dynamics. We approach the slingshot motion as the dynamic response of a step input, commonly used in process control design [89]. We focus on spatiotemporal parameters such as rise time, overshoot, and settling time. By modeling the forces in the radial and tension lines, we can investigate how they facilitate both rapid movement and a swift return to equilibrium. The mathematical model presented here provides insights into the balance of elastic forces in slingshot spider webs. It offers a deeper understanding of their design that would be challenging to achieve experimentally.

3.2 Methodology

3.2.1 Data Collection

In this chapter, Dr. Symone Alexander conducted high-speed video recordings and collected field specimens.

Field Videography

Field research was carried out in Puerto Maldonado, Peru, at the Tambopata Research Center (13.134°, 069.609°). The research permit no. 654-2018-GOREMAD-GRRNYGMADRFFS was granted by the Gerencia Regional Forestal y de Fauna Silvestre. The slingshot spiders were identified by inspecting dead branches and leafy plants for their distinctive conical webs and then snapping fingers near the web to verify the presence of slingshot motion. A Chronos 1.4 high-speed camera (Krontech) was employed to record high-speed videos (up to 38,500 fps) with a portable Zaila high-intensity light with battery packs for field use. Field videos were captured at a rate of 1057 fps.

Field Specimen and silk collection

The spider specimen was identified as an undescribed species belonging to the genus Epeirotypus sp. (Araneae: Theridiosomatidae). Videography was conducted using spiders that had constructed
Figure 3.1: **Dynamics of the slingshot spider web.**

- **a** The spider stores elastic energy by pulling on the tension line, stretching the radial lines and deforming the web to form a conical structure. The spider remains in this position, waiting for prey. It is worth noting that field observations show no specific preference for the spider web’s orientation concerning gravity.

- **b** Upon detecting a stimulus, the slingshot spider releases the web, moving explosively, covering almost nine times its body length in under 30 ms. The web is horizontally oriented, with the tension line at the bottom of the frame. The primary motion upon release is in the positive $y$ direction, facing upwards in this case.

- **c** Quantification of multiple trajectories of a single slingshot spider during repeated launches (triggered by finger snapping). The red line indicates the average trajectory of multiple displacement curves. Trajectories are adjusted to start at $(x = 0, y = 0)$ at $t = 0$.

- **d** Movement in the $x$ direction is negligible before the first oscillation.
webs in their natural environment. After observation and video recording, spider specimens were collected and preserved in 200-proof ethanol for species identification and additional analysis. Silk samples were obtained using a notched microscope slide.

High speed video analysis

We used MATLAB to analyze the high-speed video footage collected in the field. The code was developed to identify the spider in each frame using an intensity threshold and to record the position of its centroid. Precise tracking was confirmed through a binary output video that displayed the spider in white and the background in black. The code converted the units of the centroid measurements from pixels to meters and computed elapsed time based on the frame rate and the number of frames. This information was then used to calculate displacement, velocity, and acceleration.

3.2.2 Mathematical approach: 2D spring web

We develop a mathematical representation of the slingshot spider’s motion using a 2D mass-spring model in the $x$-$y$ plane (Figure 3.2). This model comprises three springs: two symmetric springs extending in the radial/horizontal $x$ direction ($F_{r1,2}$) and one in the vertical $y$ direction representing the tension line ($F_t$). We represent the spider as a point mass ($m_s$) situated at the intersection of the three springs (Figure 3.2). In the subsequent sub-sections, we provide a detailed description of the model’s components along with pertinent assumptions and constraints. We denote $\phi_{r1}$ and $\phi_{r2}$ as the angles formed between the radial lines and the $x$-axis, and $\phi_t$ as the angle between the tension line and the $y$-axis (Figure 3.2 b). Our model prescribes two equilibrium points (Figure 3.2 b). The first equilibrium point occurs before the spider launches ($t < 0, \phi_{r1,2} = \phi_{r0}$, (Figure 3.2 c) when the spider has deformed the web into a cone, awaiting prey within striking distance. At this point, the radial spring forces are balanced by the force in the tension line, and the system is in a static equilibrium. The second equilibrium point is defined when all the web lines (radial and tension line) are at their equilibrium lengths ($L_r=L_{r,eq}$, $L_t=L_{t,eq}$, $\phi_{r1,2} = \phi_t = 0$, Figure 3.2 c). This point occurs when the spider’s motion has stopped, and all web forces are equal to zero (Figure 3.2 e). We acknowledge that in the actual slingshot spider web, these equilibrium points may shift due to the web’s asymmetric architecture. Nonetheless, this assumption holds for our model’s purposes as we presume the springs are linear and the force variations are more crucial to
Figure 3.2: **Diagram of the mathematical model.**

a. We represent the conical web structure as two symmetrical horizontal radial springs and a vertical tension line situated in a 2D plane. The slingshot spider is assumed to be a point mass with a characteristic length $D_s$ of approximately 1.3 mm, located at the intersection of radial lines and the tension line. We define $L_{r,eq}$ and $L_{t,eq}$ as the equilibrium lengths of the radial and tension lines, respectively. The spider starts at $(x_0, y_0)$ at $t = 0$. Each force has projected components in the $x$ and $y$ directions. Our model disregards the effects of gravity on the slingshot dynamics, and the positive $y$ direction is set facing upward.

b. We examine the case of pure 1D motion, where at $t < 0$, the radial line forces are balanced by the tension line force. At $t = 0$, the spider releases the tension, resulting in a net force in the positive $y$-direction (upward in this case) caused by the radial lines and opposed by air drag. When the spider crosses the equilibrium point, the tension line begins to stretch, creating a restoring downward force. The spider continues to oscillate while gradually approaching equilibrium.
the dynamics than the absolute base forces. In this sense, our treatment resembles a vertical mass-spring system, where gravity’s effect is disregarded since the equilibrium point is defined when the spring’s initial extension balances the weight.

**Elastic silk springs**

We make two assumptions to represent the silk web lines, both the radial and tension lines, as elastic springs. First, we approximate the silk lines as linear Hookean springs \( F = K \cdot \Delta L \) and ignore any internal viscous damping. We acknowledge that this assumption considerably simplifies the actual behavior of silk fibers, which exhibit complex and nonlinear viscoelastic properties [90, 91, 92, 93, 94]. The spring constant \( K \) is defined by \( K = EA/L_{eq} \), where \( E \sim 1 - 10 \) GPa is the silk’s Young’s modulus [93], \( A \) is the silk’s cross-sectional area measured using SEM images, and \( L_{eq} \) is the equilibrium length.

Second, in contrast to traditional springs that can exert push or pull forces, our modeled silk springs react solely to extension and exert a pulling force, i.e., they cannot push [95]. Mathematically, we incorporate this behavior using the Heaviside function \( \Theta(\Delta L) \), which is defined as \( \Theta(\Delta L) = 1 \) when the silk spring is extended \( (\Delta L > 0) \) and \( \Theta(\Delta L) = 0 \) for compression when \( \Delta L < 0 \).

**Energy dissipation to the environment through aerial drag**

The system’s energy dissipates through viscous drag, affecting the rapidly moving spider and the web. We do not consider friction that could potentially occur between the spider’s pedipalps. Additionally, viscous damping within the silk lines is disregarded as previously discussed.

Aerodynamic drag, which influences an object moving through a fluid (air), depends on geometry, dimensions, and flow conditions. The Reynolds number is typically calculated to identify the type of damping involved in the system. This number determines the influence of inertial forces relative to viscous forces. The Reynolds number is estimated as \( Re = \rho V_{max} D / \mu \), where \( \rho = 1.225 \) kg/m\(^3\) represents air density, \( V_{max} \) is the spider’s speed, \( D \) is the characteristic length, and \( \mu = 1.81 \times 10^{-5} \) kg/ms) is the air viscosity. The Reynolds number is determined for both the spider and the web.

For the spider, the characteristic length is estimated to be \( D_s \sim 1.75 \) mm (Figure 3.2 a),
resulting in a $Re_s \sim 280$. The spider’s drag is approximated by flow around a sphere at finite Reynolds numbers as $F_{d,s} = C_s V_s^2$, where $C_s = \frac{1}{2} C_d A_s \rho_{air}$, $C_d \sim 1.25$ is the drag coefficient at $Re \sim 280$, and $A_s = \frac{\pi}{4} D_s^2$ represents the characteristic cross-sectional area, with $V_s$ being the spider’s instantaneous speed [96].

Considering the silk fibers’ much smaller size than the spider, the Reynolds number for the silk is expected to be significantly lower. Assuming each silk line as a cylinder and the web moving at the same speed as the spider, a Reynolds number of $Re_w \sim 0.2$ is obtained. For these low Reynolds numbers, the drag on the silk lines can be estimated using slender body theory in Stoke flows [97] as $F_{dw} = \frac{4\pi L_w \mu V}{ln \left( \frac{L_w}{D_w} \right)}$, where $L_w$ and $D_w$ denote the web length and diameter, respectively (see Table A.3). Assuming that the spider and the web share the same velocity, we can sum up the drag contributions from all the radial and capture lines by measuring them and summing the drag forces due to the principle of linearity in low Reynolds flow. Table A.3 provides a summary of the values used in the model.

**Equations of Motion of the 2D web**

Considering all the forces (inertia, web elasticity, and drag) along $x$ and $y$ directions, we write the 2D equations of motion that describe the trajectory of the slingshot spider as a function of time as follows:

\[
\begin{align*}
\textbf{x-axis} : \quad m_s \ddot{x} &= -F_{r1x} + F_{r2x} - F_{tx} - F_{dsx} - F_{dwx} \\
\textbf{y-axis} : \quad m_s \ddot{y} &= -F_{r1y} - F_{r2y} - F_{ty} - F_{dsy} - F_{dwy} 
\end{align*}
\]  

(3.1)
where:

\[ F_{r1,2x} = \Delta L_{r1,2} K_r \cos \phi_{r1,2}, \quad F_{r1,2y} = \Delta L_{r1,2} K_r \sin \phi_{r1,2} \]

\[ F_{tx} = \Delta L_t K_t \sin \phi_t, \quad F_{ty} = \Delta L_t K_t \cos \phi_t \]

\[ F_{dwx} = C_w \frac{x_s^2}{2}, \quad F_{dwy} = C_w \frac{y_s^2}{2} \]

\[ F_{dsx} = C_s (\dot{x}_s^2 + \dot{y}_s^2) \cos (\arctan \frac{\dot{y}_s}{\dot{x}_s}), \quad F_{dsy} = C_s (\dot{x}_s^2 + \dot{y}_s^2) \sin (\arctan \frac{\dot{y}_s}{\dot{x}_s}) \]

\[ \Delta L_{r1,2} = L_{r1,2} - L_{r,eq}, \quad L_{r1,2} = \sqrt{L_{r,eq1,2}^2 \pm x^2 - L_{r,eq1,2}} \]

\[ \sin \phi_{r1,2} = \frac{y}{L_{r1,2}}, \cos \phi_{r1,2} = \frac{L_{r,eq1,2} \pm x}{L_{r1,2}}, \quad \sin \phi_t = \frac{x}{L_t} \]

\[ K_{r1,2} = \frac{E_{rA_r}}{L_{r,eq1,2}}, \quad K_{t1,2} = \frac{E_{tA_t}}{L_{t,eq1,2}} \]

At \( t < 0 \), the spider is at static equilibrium at a position \((x_o, y_o)\) where the radial spring forces \( (F_{r1,2}) \) are opposed by the force \( (F_t) \) exerted by the tension line (Figure 3.2). At \( t = 0 \), the tension force is set to zero resulting in a net upward motion. This is akin to the spider launching itself when triggered by an external stimulus. The \( x-y \) trajectories are obtained by numerically solving the equations (1) and (2) using the 4th order Runge-Kutta approach in Matlab. The system starts from static equilibrium at \((x_o, y_o)\) at \( t = 0 \). The simulation is stopped after 200 ms has elapsed.

### 3.3 Results and Discussion

#### 3.3.1 Key parameters for response to impulsive input

We evaluate the fit’s effectiveness using four distinct spatiotemporal parameters: peak time \( (t_p) \), settling time \( (t_s) \), overshoot, which are depicted graphically in Figure 3.3.

#### 3.3.2 Web dynamics in 1D motion

To comprehend the dynamics of the system, we initially examine the limiting 1D case, where the motion is exclusively in the y-direction \((\phi_t = 0, x = 0, \forall t)\) (Figure 3.2 c). This assumption might be valid during the initial stages of the motion, where the displacement is almost one-dimensional in the y-direction and relatively negligible in other dimensions (Figure 3.1 c-d). However, this assump-
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
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<tbody>
<tr>
<td>Time</td>
<td>lasts from least to most recent time point</td>
</tr>
<tr>
<td>Overshoot</td>
<td>$y_{\text{max}} / y_{\text{eq}}$ - maximum displacement to equilibrium point</td>
</tr>
<tr>
<td>Peak time, $t_p$</td>
<td>duration required to achieve the maximum displacement $y_{\text{max}}$</td>
</tr>
<tr>
<td>Settling time, $t_s$</td>
<td>time the displacement resides within an envelope above and below the equilibrium point $y_{\text{eq}}$</td>
</tr>
<tr>
<td>Equilibrium</td>
<td>$y_{\text{eq}}$ - final displacement when the system comes to rest</td>
</tr>
<tr>
<td>Amplitude to $y = 0$</td>
<td>$y_{\text{eq}}$ - final displacement when the system comes to rest</td>
</tr>
</tbody>
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Figure 3.3: **Key parameters for evaluating second-order damping response.** We use various spatial and temporal parameters to assess the compatibility between a mathematical model and field data. The equilibrium point is defined as the final displacement ($y_{\text{final}}$) when the system comes to rest. We define the peak time ($t_p$) as the duration required to achieve the maximum displacement ($y_{\text{max}}$). The overshoot is calculated as the ratio between the maximum displacement and the equilibrium point ($\frac{y_{\text{max}} - y_{\text{eq}}}{y_{\text{eq}}}$). We establish the settling time ($t_s$) as the time the displacement resides within an envelope above and below the equilibrium point ($y_{\text{eq}}$). We assume that the motion ceases and the system is prepared for reset once the spider crosses the equilibrium point for the first time. Finally, we determine the settling time as the duration needed for the spider to complete one oscillation with an amplitude within $\pm$ one body length surrounding the equilibrium point.
tion breaks down during the later stages of the displacement as the motion of the spider becomes more complex, and contributions from other dimensions become more pronounced. Nonetheless, this approach aids in shedding light on several key features of the slingshot motion and offers guidance for the iterative exercises of fitting the model to the data. During the time \( t < t_s \), the dynamics of the spider are mainly governed by the radial line forces \( F_r \) along with drag \( F_d \), while the tension line force \( F_t \) is zero (\( \Delta L_t < 0 \)). In the limiting 1D case, the rise time may be calculated as follows
\[
t_s = \frac{2\pi}{\omega_{d,n}},
\]
where \( \omega_{d,n} \) denotes the damped natural frequency. The tension line becomes active when \( \Delta L_t \geq 0 \) (i.e., the spider crosses the static equilibrium point). At this point, the restoring force \( F_t \) starts to impact the system’s dynamics. Specifically, the damped natural frequency is proportional to the combined effects of the radial lines and tension line (\( \omega_n \propto (K_r + K_t)^{\frac{1}{2}} \) when \( y > y_{eq} \)).

After reaching max amplitude, the mass oscillates back and around the equilibrium point with decreasing amplitudes as the kinetic and potential energies dissipate by aerodynamic drag. A notable geometrical result of the model is that when the mass approaches the equilibrium point (\( y \to 0, \phi \to 0 \)), the radial forces projected in the \( y \) direction decrease significantly.

### 3.3.3 Web dynamics in 2D motion

Next, we solve the equations of motion in 2D while changing the physical and geometric parameters to match the spider’s displacement better. To avoid larger deviations in geometry and initial conditions, we validate the simulation results with multiple firing events (\( n = 5 \)) of a single spider (Figure 3.1 b-d). By fitting the initial conditions of the model \((x_o, y_o)\) to the experimental data, we show the model’s output in Figure 3.4 a, denoted as Simulation 1. The model captures rise time, peak time, and maximum peak with less than 5% error, as quantified in Table 3.1. However, the model does not accurately capture the secondary oscillations (\( t > 30 \text{ ms} \)) and predicts a \( \sim 20 \text{ ms} \) longer setting time than experimental observations. In the \( x \)-direction, the model records both the amplitudes and the frequency of the oscillations with a phase shift, as can be seen qualitatively with the \( x - y \) map (Figure 3.4 d). The time evolution of the underlying forces is also calculated and highlighted along with the \( y \)-displacement. The radial forces projected in the \( y \)-direction start at a combined maximum value of about \( \sim 7.5 \times 10^{-4} \text{ N} \) or 75 dynes.

Interestingly, this falls within the force ranges previously measured in the radial silk lines of sling-
Figure 3.4: **Simulation 1: Two-dimensional slingshot spider dynamics.** a By solving the equations of motion, we determine the $x$-$y$ displacement of the spider. The simulation output aligns with the rise time, maximum peak, and maximum output $y_{\text{max}}$, as well as the minimal oscillations in the $x$ direction. However, the model does not anticipate any subsequent oscillations in the $y$-direction beyond the first fluctuation. b The temporal evolution of the forces shows that the system begins with forces in the radial lines in the $x$-$y$ directions. As the system gains speed, web drag resists the motion - spider drag is negligible. The restoring force in the tension line, which has been zero up to this point, comes into play as the tension line stretches ($t \sim 15\; \text{ms}$). c,d The simulation also forecasts the apparent 2D displacement of the spider, starting from $(x_0, y_0)$ at $t = 0$. The simulation displays a qualitatively similar trajectory in the $x$-$y$ plane, with the spider initially launching in the $y$-direction before experiencing low amplitude oscillations in the $x$-direction as it gradually approaches equilibrium.
shot spider webs with a custom-built device [81]. The net radial forces in the \( x \) direction are smaller and become more significant at \( t > 30 \) ms as the spider approaches equilibrium. The tension line force \( F_t \) is activated only when \( \Delta L_t > L_{t,eq} \), and is observed as a strong increase in the negative direction (deceleration of spider motion) by \( t = 14 \) ms (Figure 2.12 b). Drag forces in the \( y \) direction start at zero and rapidly increase in magnitude as the spider approaches \( V_{s,max} \) before decreasing as the mass reaches a standstill. We find that the radial orbital forces and the drag forces always act in opposite directions—the radial forces drive the motion, and the drag dampens it.

This model relies on two fundamental assumptions: that the slingshot spider’s trajectory is constrained to a 2D plane and that the spider acts as a point mass object. In reality, the slingshot motion is more complex and involves 3D movement, but we only record a 2D projection of the motion using a single high-speed camera in the field. Furthermore, the spider’s mass is unevenly distributed (asymmetric body), with most of its mass not facing the tension line. This uneven mass distribution causes the spider to behave like a 3D inverted pendulum that can rotate around the intersection point between the spider and the silk [98]. The model also disregards displacement biases due to web structure asymmetries, as the spider builds the web on small plant branches. To demonstrate the impact of displacement biases in an orthogonal direction (\( z \)-direction), we examine an exaggerated case where \( x_o \) is multiplied by 4. Figure 3.5 reveals a better agreement between the model and field data. The secondary oscillations in the experimental data are well-matched by the model, including the settling time (Table 3.1).

In summary, even with the significant dimensional simplifications made while developing this streamlined mathematical model, it still captures the essential spatiotemporal dynamics resulting from the intricate design of the slingshot spider web. The values employed in the model adhere to the biological limits concerning physical properties and geometric constraints (Tables 1, 2). We will now delve into the extensive parameter space offered by this model, examining the web dynamics as web stiffness \( (K_t) \), tension line stiffness \( (K_r) \), and drag force coefficient \( (C_w) \) are varied.

### 3.3.4 Slingshot Spider Dynamics in Relation to Web Parameters \( (K_t, K_r, C_w) \)

In this section, we examine the impact of three parameters - radial stiffness \( (K_r) \), tension line stiffness \( (K_t) \), and web drag \( (C_w) \) - on the slingshot motion dynamics. These parameters represent most of the web’s mechanical and geometrical properties and govern the system’s crucial dynam-
Figure 3.5: **Simulation 2 with increased $x$-motion contributions.** a To account for the dynamics of the subsequent vibrations in the $y$-direction, we perform a second simulation with a larger initial displacement in the $x$-direction ($4 \times$ that used in simulation 1). This demonstrates the additional complexity introduced by enhanced orthogonal motion. The model more closely aligns with field data regarding temporal parameters and the subsequent low amplitude fluctuations after the initial overshoot. The spider’s motion is 3D and may include twisting and rotation due to mass and geometry asymmetries. These extraneous factors become increasingly significant at low amplitudes and frequencies. b The evolution of forces in the $x - y$ plane displays similar dynamics to those observed earlier in Figure 3.4 b. Interestingly, the tension force in the $x$-direction becomes more prominent here, as the influence in the $x$-direction is magnified due to the initial conditions.
ics. Simulations are conducted by altering one parameter while maintaining the others constant. For easier physical interpretation, we normalize the output displacements by the spider body length (BL), using the results and parameters ($K_{t,ss}$, $K_{r,ss}$, and $C_{w,ss}$) from Simulation 2 as a reference. We present the resulting normalized displacement curves compared to the reference plot in Figure 3.6 and assess the sensitivity of the model outputs concerning the spatiotemporal parameters in Figure 3.7.

Figure 3.6a displays the normalized displacement curves when the radial line’s stiffness ($K_r$) is altered while keeping other variables constant. We observe that, with an order of magnitude decrease in $K_r$’s value, the web loses its oscillating ability and gradually approaches the equilibrium point. This behavior resembles an overdamped system where drag dissipation dominates. Increasing $K_{r,ss}$ results in a quicker rise in displacement and a more significant overshoot. These findings are quantified in Figure 3.7, demonstrating that as radial stiffness increases, the spider travels a more extended distance in less time and settles more quickly. It has been observed [87, 81] that slingshot spiders launch their webs in response to external vibratory or auditory cues (such as finger snapping). Thus, spiders might release their webs in response to the nearby frequency of an insect’s wingbeat.

Moreover, the spider must reset its web quickly to avoid missing potential prey. Our model indicates that slingshot $K_r$ appears to balance a finite overshoot at smaller peak and settle times, potentially allowing the spider to reach flying prey at a distance rapidly while minimizing oscillations to reset and repeat the motion if unsuccessful.

In the context of the slingshot spider’s motion biomechanics, altering parameters like the stiffness of the radial lines refers to changes in intrinsic molecular and geometric properties. Stiffness is defined as $K_r = \frac{N_r E_r A_r}{L_{r,eq}}$ and varies among spider species. *Epeirotypus* sp. has not been specifically measured, but the Young’s modulus generally ranges between 1-10 $\times 10^9$ Pa, depending on factors like strain, strain rate, temperature, and humidity. Radial stiffness can also be altered by adjusting other geometric parameters like the equilibrium length ($L_{r,eq}$) or the area ($A_r$). For instance, *Epeirotypus* sp. has been observed adjusting tension in radial and sticky lines using its legs during web construction, effectively changing $L_{r,eq}$ [85].

Next, we analyze the tension line’s role as depicted in Figure 3.6b. When the tension line is not initially stretched ($\Delta L_t < L_{t,eq}$), changing its stiffness doesn’t impact the rise time, which is
\[ t_s \approx 10 \text{ ms.} \] After this point, the tension line comes into play and exerts a pulling force on the spider. If there’s no tension line \((K_t = 0)\), the system surpasses the equilibrium point by almost two spider body lengths (BL) before slowly oscillating back to equilibrium. As tension stiffness increases, overshoot decreases, and undershoot increases. For example, at \(10 \times K_{t,ss}\), the maximum displacement reduces to less than one body length above equilibrium before bouncing nearly two body lengths below it. This occurs because the oscillation time scale is primarily determined by the tension line properties when slightly above equilibrium, specifically \( t = \frac{2\pi}{\omega_{nd}} \sim \sqrt{\frac{m_s}{K_t}} \). Figure 3.7 \(b\) presents these findings, showing a consistent decrease from 30\% to nearly 8\% across four orders of magnitude in \(K_t\). Meanwhile, the peak time is less affected, decreasing by roughly \(\sim 10 \text{ ms}\) over the same range in \(K_t\). Interestingly, we observe a minimum settling time of around 40 \text{ ms} near the reference value, attributable to the increase in undershoot as \(K_t\) rises.

Interestingly, our model suggests that the tension line is crucial during the slingshot motion beyond enabling the spider to store elastic energy and maintain static equilibrium in its web. Without the tension line, the spider would be subject to air drag near the equilibrium point, as radial forces become negligible. The tension line’s stiffness helps prevent excessive overshoot. It reduces settling time, enabling the spider to reach prey in its web more quickly or reset and repeat its hunting motion if it misses capturing prey. In addition, the tension line controls the spider’s vertical displacement at intermediate lengths. Lastly, we examine the effect of web drag on slingshot dynamics. The model is highly sensitive to the drag coefficient. With high damping coefficients \((2 \text{ to } 10 \times C_{w,ss})\), the system quickly becomes overdamped, approaching equilibrium without oscillations. With lower damping coefficients \((0.1 \text{ to } 0.5 \times C_{w,ss})\), the system becomes highly underdamped and vibrates several body lengths around the equilibrium point. Figure 3.7 \(c\) demonstrates the model’s sensitivity to damping, with overshoot reaching up to 60\% at 0.01 \(\times C_{w,ss}\) and minimal or non-existent overshoot at values greater than \(10 \times C_{w,ss}\). The settling time also highlights this sensitivity, showing a minimum near the reference value \(C_{w,ss}\), with overdamped systems taking longer to reach the \(\pm 1\) BL envelope around equilibrium and highly underdamped systems fluctuating with large amplitudes around the equilibrium point.
Table 3.1: Summary of the parameter outputs of simulations 1 and 2.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Field data</th>
<th>Simulation 1</th>
<th>Rel. error %</th>
<th>Simulation 2</th>
<th>Rel. error %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rise time, $t_r$</td>
<td>9.48 ms</td>
<td>9.6 ms</td>
<td>1.25%</td>
<td>9.6 ms</td>
<td>1.25%</td>
</tr>
<tr>
<td>Peak, $y_{max}$</td>
<td>14.58 mm</td>
<td>15.07 mm</td>
<td>3.36%</td>
<td>14.81 mm</td>
<td>1.57%</td>
</tr>
<tr>
<td>Peak time, $t_p$</td>
<td>20.81 ms</td>
<td>20.25 ms</td>
<td>2.76%</td>
<td>20.5 ms</td>
<td>1.53%</td>
</tr>
<tr>
<td>Overshoot %</td>
<td>17.93 %</td>
<td>30.5 %</td>
<td>12.57%</td>
<td>23.89 %</td>
<td>5.96%</td>
</tr>
<tr>
<td>Settling time, $t_s$</td>
<td>37.84 ms</td>
<td>60 ms</td>
<td>58.5%</td>
<td>40 ms</td>
<td>5.71%</td>
</tr>
</tbody>
</table>

3.3.5 Model Limitations and Future Work

Our study aims to offer a simplified approach to modeling the complex dynamics of slingshot spider webs. However, certain assumptions in our model could be further refined in future research.

*Dissipation due to aerodynamic drag and molecular friction*

The model demonstrates that aerodynamic drag at intermediate to low Reynolds numbers sufficiently describes the damping experienced by the spider and its web. The model doesn’t account for the potential contribution of viscous dissipation within the viscoelastic spider threads. The relative impact of these two dissipation sources in oscillating spider webs is poorly understood and remains an active research area. Previous studies emphasized the significance of aerodynamic drag for ballooning spiders and orb weaver webs stopping flying insects. In contrast, other research has dismissed aerodynamic drag and attributed dissipation mainly to internal viscous damping. A summary of studies exploring dissipation, both internal and external, is provided in Table A.3.

Due to the thinness of spider silk ($< 4$ in diameter), mechanical property characterization has primarily relied on tensiometry or impulsive loading at lower strain rates. However, replicating the high strain rates encountered by the slingshot spider webs in this study ($> 60 \text{ s}^{-1}$) is experimentally challenging. Moreover, spider silk’s mechanical properties and structural geometries are heavily influenced by environmental factors such as temperature, humidity, wind conditions, water content, and surrounding conditions like substrate location and flexibility. This adds further complexity to experimentally examining spider silk’s mechanical properties under native conditions. Our model shows that viscous damping in silk is not necessary to capture the slingshot spider’s underdamped behavior, but it could still be important and will be the focus of future work.
Geometrical constraints

Our simulations also assume no coupling between parameters. For example, orb webs exhibit significant variations across species in the number of radii and rows of capture spirals. In contrast, slingshot spider webs are relatively similar, having few radii and approximately ten rows of capture silk. This might suggest geometric constraints on slingshot spider web topology and dimensions. Therefore, this model could be extended to investigate other web topologies and silk dimensions to test the hypothesis that the evolution of theridiosomatid web architecture is partly limited by optimizing aerial damping during slingshot motion.

3.4 Conclusion

We have created a 2D mathematical model that simulates the dynamic behavior of the slingshot spider, driven by its conical web geometry and tension line. Our model is validated through experimental results and explores the influence of various physical factors that dictate the dynamics of the slingshot spider, including web forces (radial lines and tension lines) and external forces such as aerodynamic drag. Our research shows that the web parameters are finely tuned to produce an underdamped oscillating web, allowing the spider to move quickly across short distances while minimizing residual web oscillations. Owing to both aerial drag and the tension line, the unique web design may allow the spider to utilize a risky hunting strategy by capturing airborne insects while reducing web oscillations caused by its rapid motion.

While our study provides an initial approach to understanding the fascinating slingshot spider dynamics, there remain unanswered questions about the molecular structure of the radial silk and tension line, as well as the 3D-web topology that enables their agile and powerful performance. These research inquiries offer ample opportunities for interdisciplinary investigation, further enriching our knowledge and appreciation of arachnids and their innovative engineering strategies for movement and survival.
Figure 3.6: **Examining web dynamics based on model parameters.** We investigate the influence of various forces on the slingshot dynamics derived from Simulation 2. The output displacements are normalized by the spider body length (BL) and parameters ($K_{r,ss}$, $K_{r,ss}$, and $C_{w,ss}$) from Simulation 2 (Figure 3.5 a) as a reference. 

- **a** Increasing the stiffness of the radial line $K_r$ results in both a faster initial displacement increase and higher overshoots (approximately 4 BL above equilibrium), along with subsequent larger amplitude vibrations around the equilibrium point. Reducing the radial lines stiffness by an order of magnitude gradually causes the system to approach the equilibrium point without any observable overshoot.

- **b** Altering the tension line stiffness $K_t$ only impacts the dynamics beyond the equilibrium line. Without any tension force, the system achieves a higher overshoot and more subsequent vibrations. As the tension line stiffness increases, the vibration peaks become sharper above the equilibrium with larger and slower undershoots.

- **c** The model demonstrates high sensitivity to web drag $C_w$. Halving the damping coefficient causes the system to vibrate significantly over two body lengths around the equilibrium line. Doubling the damping coefficient results in a small overshoot as the system quickly approaches equilibrium without noticeable oscillations, similar to a critically damped oscillator.
Figure 3.7: **Overview of web dynamics based on model parameters.** We quantify the changes in various simulations by focusing on the percentage overshoot, peak time ($t_p$), and settling time ($t_s$). We highlight the reference values in red. 

**a.** The overshoot increases monotonically from 0 (no peak) to 80% with the increase in $K_{r,ss}$. At low $K_{r,ss}$, the system does not vibrate around the equilibrium point, causing $t_p$ and $t_s$ to exceed the maximum simulation time of 200 ms. This behavior resembles an overdamped dynamical system, as the damping forces overcome the spring forces.

**b.** The overshoot decreases by almost 35% as $K_t$ increases from 0.01 to $100 \times K_t$. Similarly, the peak time $t_p$ slightly decreases from 24 ms to 15 ms as $K_t$ increases. Interestingly, the settling time ($t_s$) decreases to a minimum of 40 ms around the reference value of $K_t$ before sharply increasing. This is mainly due to the larger undershoot caused by a higher $K_t$.

**c.** The simulation is highly sensitive to the damping coefficient. The overshoot decreases from around 60% to almost no overshoot as damping increases. The settling time shows a minimum around the reference point, as low drag causes the system to oscillate violently around the equilibrium point. In contrast, high drag causes it to approach equilibrium slowly. Both effects increase in the settling time.
4.1 Introduction

Springtails (Arthropoda: Collembola) constitute the most widespread, abundant, and diverse group of non-insect hexapods globally, renowned for their significant contributions to soil ecology and their exceptional ability to catapult themselves into the air [99]. Studies on Collembolans’ jumping performance have spanned various fields such as locomotion [100, 11, 101], morphology [102, 101, 103], behavior [104, 105, 106], energetics [107], and computational modeling [108], inspiring the development of mechanical jumpers [109, 110] and robots [111].

Although earlier biomechanical research suggests that springtails’ jumping and landing might be uncontrollable and unpredictable [100, 109], given their ability to achieve remarkable body rotations in mid-air (approximately 500 Hz [110]), behavioral and ecological studies indicate that these minute arthropods are capable of executing sophisticated maneuvers, navigation, and consistent landing. For instance, directed leaping and controlled landing have been observed during the massive, long-distance migration (up to 300,000 bodies per day) of snow-dwelling springtails [112].

Moreover, recent scanning microscope images propose that the collophore could be employed for adhesion to the water surface, cleaning, and nutrient absorption [103], playing a pivotal role in governing takeoff direction and trajectory [113]. Similarly, a previous mathematical analysis and computational model indicate that adjusting the furcula’s length may impact the vertical and horizontal range achieved during jumping [108]. Despite these observations and conjectures, it remains unclear how springtails manage to control their jumping and landing using the collophore, the furcula, and slender bodies (i.e., entomobryomorpha).

This study investigates how wingless springtails achieve precise control during landing. We focus on semiaquatic springtails, *Isotomurus retardatus* [114], which live on the water surface where maintaining control and maneuvering are crucial for survival due to the constant presence of numerous predators [99]. Using high-speed videography, kinematic analysis, and mathematical modeling, we examine the locomotion control abilities of these tiny, wingless arthropods living at the air-water interface.
Figure 4.1: **Semiaquatic Springtail Isotomorus retardatus.** (a) Notice the manubrium-furcula and collophore highlighted in green and red, respectively. Image composites are from recordings of springtails taking off (b) and landing (c). (b) Details of the collophore’s water adhesion and the droplet collected after detaching from the water surface are shown above their respective frames. (c) Notice that during a successful landing, springtails attach to the water surface using the collophore.
Our findings reveal that springtails utilize their unique morphology, specifically a specialized hydrophilic structure called the collophore, not only to aid in their take-off from the air-water interface and control their mid-air orientation but also to dampen their landing back on the water’s surface effectively. We observe that individuals approach the water surface with their ventral part directed downwards, which subsequently attaches to the water surface using the collophore. This action effectively absorbs the momentum during the impact by producing capillary waves. In contrast, individuals landing on their backs or laterally bounced uncontrollably on the water until they corrected their position on the water’s surface using their legs.

To confirm the role played by the capillary adhesion of the collophore, we removed the water from the collophore of a few individuals and allowed them to land on a dry solid substrate. Despite landing ventrally on the dry collophore, they bounced several times due to the inability of the collophore to stabilize their landing. Individuals landing on their backs on the water surface took ~10 times longer to correct their position and adhere at the interface with the collophore than those that landed ventrally in the first place (44 ms vs. ~44 ms, respectively).

4.2 Methodology

4.2.1 Data collection: springtails landing on water

High speed videography

In this study, led by Dr. Victor Ortega-Jimenez, we aimed to examine the landing of springtails on water’s surface. We recorded 10 specimens landing ventrally on the water’s surface at 10,000 fps, using their collophore to attach to the surface. For comparison, we filmed 3 individuals landing on their backs and bouncing. Additionally, we recorded a pair of springtails landing ventrally on a solid surface (plexiglass) without sufficient water for collophore attachment. These springtails were placed in a dry plastic container for approximately 7 minutes without water access. We determined the body centroid using the recorded sequences and calculated the trajectory and speed over time. We then assessed the duration from the impact until the vertical bouncing on the water or solid surface stopped.
Data analysis

4.2.2 Mathematical model of springtails landing

To analyze the controlled landing of springtails, we developed a reduced order mathematical model inspired by Aristoff et al. [115], Vella et al. [116] and recently by Zhao et al. [23]. We observed that before landing, springtails adjust their body posture into a U-shape to land mainly on their collophore. Collophore geometry was assumed as a cylinder with a hemisphere at its end $R_c$ (diameter $D_c$) (Figure 4.2 d). We ignored any geometrical effects that may arise due to the arched posture of the springtails as it remains constant during landing. We also assumed that the motion is primarily in 1D in the vertical direction. This approximation is valid since the angle between the velocity vector of the free-falling springtail right before impact and the horizontal free surface of the water is $84.64^\circ \pm 3.78$ ($N = 9$).

We applied Newton’s second law to estimate the motion of the cylinder over time. Upon impact with the surface of water ($\rho = 1000\ \text{kg/m}^3$, $\mu = 1\ \text{mPa.s}$, $\gamma = 72\ \text{mN/m}$), a hemisphere sphere of diameter $D_c$ generates hydrodynamic forces that include form drag $F_{d,f} \propto -\rho D_c^2 \dot{z}^2$ within the water phase, surface tension $F_s \propto \gamma (S/lc)$ (where $S$ is the perimeter of the collophore), and buoyancy force $F_b \propto \rho g (D_c)^2$, added mass (inertia) $F_i \propto \rho g (D_c)^3$ where $g$ is the gravitational constant and $z$ is the distance between the center of gravity of the cylinder and the undisturbed surface of the water, and maximum depth $z_{\text{max}}$ is $0.2 \pm 0.07\ \text{mm}$ (Figure 4.2) [116, 117].

We write the following equation of motion [23, 117]:

$$m_s \ddot{z}(t) = -m_s g + F_b + F_{d,c} + F_{d,f} + F_{ST} + F_i \quad (4.1)$$

Simplifications and governing forces

To simplify the equations, we assume that the system starts at $t = 0$ with the hemisphere submerged in water ($z_o = 0$) and a downward velocity equal to the impact velocity of $u = 0.7\ \text{m/s}$. With these assumptions, the equations can be simplified as follows: $F_b = \frac{1}{4} \rho g \pi D_c^2 (D_c/3 - z)$, $F_{d,c} = -(1/8)C_d$, $F_{d,f} = -(1/8)C_d \rho \pi D_c^2 \dot{z}^2$, $F_{ST} = \gamma (\pi D_c/lc) z$, and $F_i = \frac{1}{12} \pi D_c^3 \rho f$.

What determines the dynamics of springtails impacting the water’s surface? We address this question by estimating the relative contribution of these hydrodynamic forces through dimensional
analysis. Assuming that the springtails do not penetrate the water’s surface, given their size \((L \sim 1.5 \times 10^{-3}, D_a \sim 0.5 \times 10^{-3}, D_c \sim 0.125 \times 10^{-3})\) and impact velocity \((u \sim 0.5 - 1 \text{ m/s})\), the surface tension force is dominant, as summarized in Table A.4. This conclusion can also be supported by the force ratios, which scale as \(F_b/F_{ST} \sim 10^{-3}, F_{d,f}/F_{ST} \sim 10^{-1}\), and \(F_i/F_{ST} \sim 10^{-3}\).

Given that the Ohnesorge number \(Oh = \frac{\nu}{\sqrt{\rho \gamma D_c}}\) is calculated as \(Oh \approx 0.003 \ll 1\), it suggests that viscosity plays a minor role in determining the oscillations of springtails landing on water. Zhao et al. [23] demonstrated that under such conditions, energy dissipation primarily occurs through capillary waves \(F_{d,c} \propto (\gamma D_c/c) \ddot{z}\), where \(c \sim (gl_c)^{1/2}\) is the speed of the capillary wave and \(l_c\) is the capillary length \((\sim 2.7 \text{ mm} \text{ for water})\). This is further corroborated by video evidence showing the onset of capillary waves after springtails impact the water’s surface Figure 4.2d. Additionally, the Heaviside function \(H(\dot{z})\) is used since we assume that energy is mainly dissipated due to capillary waves when the system travels downwards, i.e., when the system is below the undisturbed water-air interface.

To assess the role of collophore adhesion, we solve these equations of motion with and without the added capillary adhesive force of the collophore \(F_c\). In this case, \(F_c = \pi D_c \gamma H(\dot{z})\), where \(D_c\) is the collophore diameter and \(H(\dot{z})\) is the Heaviside function since capillary adhesion is activated only when the body is traveling upwards.

**Solving the equations of motion**

The equation of motion is solved numerically using the 4th-order Runge-Kutta solver (ode45) in MATLAB. A list of all parameters is summarized in Table A.5. The simulation results were fit with a focus on the time scale of the springtail \((4 - 6 \text{ ms})\) and the normalized maximum depth of the springtails \(\bar{z} = (z(t) - z_{t \to \infty})/D_s\). The restoring force of surface tension primarily determines the maximum depth. Meanwhile, the time scale depends on both the amount of dissipation due to capillary and viscous damping, and the value of the restoring force. We note that \(a_1 = -1.25\) and \(a_2 = 6\) are pre-factors for the surface tension and capillary drag forces, respectively, that best matched the experimental data.
4.3 Results and discussion

Springtails land on water surfaces while minimizing undesirable bouncing and uncontrolled tumbling. Our analysis of their landing dynamics is compared to a simplified hydrodynamic model. Springtails land on water at an impact speed of \( u = 0.54 \pm 0.12 \, \text{m/s} \) \((N = 9)\), momentarily submerging to a maximum depth of about 0.2 \( \text{mm} \) (approximately 60\% of their body width \( D_s \)) and resurfacing within 3 – 5 \( \text{ms} \). The springtails’ morphology heavily influences the landing outcome upon impact.

When landing on their ventral side, referred to as ‘collophore landing,’ their arched U-shaped body allows the collophore to be the first point of contact with the water surface (Figure 4.2 a). This results in quick stabilization and anchoring on the water surface (Figure 4.2 b). On the other hand, landing on their peripheral or dorsal side causes springtails to bounce off the water’s surface.

We use a mathematical model to describe the collophore’s interaction with the water-air interface, approximating its geometry as a cylinder with a hemispherical end of radius \( R_c \) (diameter \( D_c \)) (Figure 4.2 d). We assume that the motion primarily occurs in the 1D vertical dimension, where \( z(t) \) signifies the displacement of the collophore’s hemispherical center relative to the undisturbed water surface.

Various hydrodynamic forces are generated during impact, such as form drag, buoyancy, added mass, surface tension, and dissipation through capillary waves. Our analysis reveals that the interplay between capillary and inertial forces dictates landing dynamics, while buoyancy and viscous forces are negligible. We assume inertial forces transform into surface deformation and dissipate as capillary waves. Similar assumptions were employed in a study on water striders’ landing.

To evaluate the hydrophilic collophore’s influence on springtail landing dynamics, we incorporate a capillary adhesion force, which only slows the springtail’s upward movement. Simulations indicate that without this force, springtails would bounce upwards, albeit with an overestimated velocity and trajectory due to factors like impact geometry and other kinematic parameters. With the capillary adhesion force, springtails are rapidly halted and reach equilibrium within approximately 6 milliseconds. Notably, the maximum capillary force calculated by the model is close to the maximum values obtained in rotating disk experiments.

We plot the force time series during impact (Figure 4.2 e), showing that surface tension force
$F_{ST}$ is dominant, increasing up to a maximum of $38 \ \mu N$ as the springtail deforms the water surface. Concurrently, the capillary drag $F_{d,c}$ reduces from a maximum of $36 \ \mu N$ to zero as the system reverses direction and begins vibrating back. The maximum surface tension force per unit length (wetted collophore perimeter) is about $100 \ mN/m$, less than the theoretical force per unit length needed to break the water’s surface is around $144 \ mN/m$ [117].
Figure 4.2: **Springtails adhesive landing on the air-water interface**

(a) Before impact, springtails bend their bodies to extend their collophore further as they come into contact with the water surface. The collophore primarily interacts with the water surface during this impact. (b) The body orientation of the springtail is crucial for a successful landing. A controlled landing occurs when the collophore quickly adheres to the water’s surface. Post-impact capillary waves are observed as the organism stabilizes. However, if the springtail lands in other configurations (such as on its side or back), it experiences uncontrolled rebounding. (c) The progression of hydrodynamic forces over time shows that collophore adhesion helps slow the springtail’s upward movement after reaching its maximum depth. (d) We create a simplified mathematical model to analyze the influence of collophore adhesion on springtail landing dynamics. The hydrodynamic forces involved include weight, drag, surface tension, and collophore adhesion. Both experimental and theoretical outcomes of the normalized displacement $\bar{z} = (z(t) - z_{t\to\infty})/D_s$ demonstrate the significance of collophore adhesion in rapidly halting the springtail’s landing dynamics. The springtail would be propelled off the water’s surface without the collophore force.
Numerous organisms have evolved remarkable strategies to manipulate and leverage their fluidic environment to fulfill their biological necessities. The term “controllability” in this context primarily refers to the ability to navigate the external forces imposed by fluids, specifically, how to initiate and halt movement and enhance propulsion. Fluids can function as a damper to dissipate energy, but they can also serve as a catalyst to augment movement. In sharpshooters, superpropulsion allows these insects to leverage the elasticity of a liquid droplet mediated by surface tension. This strategy enables them to enhance energy transfer and catapult an elastic projectile at a velocity exceeding that of an actuator. It effectively helps them overcome the energy challenges associated with high-speed jet propulsion. In principle, superpropulsion relies on tuning between elastic structures and is not confined to droplets. This naturally leads to the question of whether other impulsive organisms also harness this phenomenon to amplify their movements. Might superpropulsion manifest differently, especially given that many biological systems employ spatially heterogeneous, non-linear springs? Could there be a hierarchical and cascading array of springs facilitating such a strategy?

In the case of slingshot spiders, we demonstrate how these arachnids utilize specialized structures, specifically tension lines, along with viscous air drag to regulate their impulsive motion. Our mathematical model emphasizes the crucial need for balance – steering clear of excessive damping (overdamping) while maintaining their webs in a slightly underdamped state. A question that arises from this is: how do slingshot spiders adjust to fluctuating environmental conditions such as temperature and humidity when constructing their webs?

We demonstrate in semi-aquatic springtails how these organisms exploit a unique hydrophilic structure called the ‘collothor’ to rapidly anchor themselves on the water surface. We also pose the question: what other factors, such as body posture and the horizontal and vertical components of impact speed, affect their landing?

The intricate interplay between control and adaptation illuminates the complex relationship be-
tween biology and physics in the natural world. Biological systems exhibit a multitude of detailed and innovative adaptations that evolved over time to meet specific environmental needs and perform designated tasks. These biological systems, while inspiring awe, also serve as a rich source of ideas for engineering solutions. Through careful study and understanding of these mechanisms, we can translate these biological strategies into bioinspired applications. This process can lead to the solution of complex engineering problems, thereby catalyzing a realm of innovation and technological advancements.
Appendices
Table A.1: Summary of kinematic properties of GWSS, GWSS hairless, BGSS, RBSS. Maximum values are calculated for the tip of the stylus.
Table A.2: Summary of calculated pressure contributions in glassy-winged sharpshooters from inertial, viscous, and surface tension forces in flow through pipe and out of nozzle at low Re

<table>
<thead>
<tr>
<th>Dynamic Pressure, $P_i = \rho u^2/2$</th>
<th>Surface Tension, $P_{ST} = 4\gamma/d$</th>
<th>Viscous Pressure, $P_{viscous} = 32\mu u/d^2$</th>
<th>Total Pressure</th>
</tr>
</thead>
<tbody>
<tr>
<td>21</td>
<td>4095</td>
<td>1977</td>
<td>6093</td>
</tr>
<tr>
<td>50</td>
<td>4874</td>
<td>4340</td>
<td>9264</td>
</tr>
<tr>
<td>84</td>
<td>5037</td>
<td>6031</td>
<td>11152</td>
</tr>
<tr>
<td>77</td>
<td>5167</td>
<td>6082</td>
<td>11327</td>
</tr>
<tr>
<td>60</td>
<td>4928</td>
<td>4874</td>
<td>9861</td>
</tr>
<tr>
<td>317</td>
<td>5007</td>
<td>11582</td>
<td>16907</td>
</tr>
<tr>
<td>74</td>
<td>4788</td>
<td>5111</td>
<td>9973</td>
</tr>
<tr>
<td>70</td>
<td>4845</td>
<td>5087</td>
<td>10002</td>
</tr>
<tr>
<td>176</td>
<td>7641</td>
<td>20075</td>
<td>27892</td>
</tr>
<tr>
<td>75</td>
<td>5772</td>
<td>7465</td>
<td>13312</td>
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<tr>
<td>71</td>
<td>5907</td>
<td>7605</td>
<td>13583</td>
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<tr>
<td>129</td>
<td>6678</td>
<td>13157</td>
<td>19964</td>
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<td>57</td>
<td>5930</td>
<td>6896</td>
<td>12884</td>
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<td>94</td>
<td>6687</td>
<td>11221</td>
<td>18001</td>
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<td>93</td>
<td>6358</td>
<td>10097</td>
<td>16548</td>
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<tr>
<td>85</td>
<td>6358</td>
<td>9678</td>
<td>16122</td>
</tr>
<tr>
<td>10</td>
<td>4972</td>
<td>1997</td>
<td>6979</td>
</tr>
<tr>
<td>12</td>
<td>4972</td>
<td>2250</td>
<td>7235</td>
</tr>
<tr>
<td>60</td>
<td>5841</td>
<td>6874</td>
<td>12776</td>
</tr>
<tr>
<td>62</td>
<td>5841</td>
<td>6940</td>
<td>12842</td>
</tr>
<tr>
<td>53</td>
<td>5841</td>
<td>6437</td>
<td>12331</td>
</tr>
<tr>
<td>50</td>
<td>5841</td>
<td>6253</td>
<td>12144</td>
</tr>
</tbody>
</table>
Table A.3: Summary of the geometrical parameters and physical properties used in the simulation. The source of these parameters is either from literature or measured from field data. The results of simulations 1 and 2 are shown in Figure 3.5 a and Figure 3.6 a, respectively.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Simulation 1</th>
<th>Simulation 2</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Spider</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mass, $m_s$ (Kg)</td>
<td>$1.6 \times 10^{-3}$</td>
<td>$1.6 \times 10^{-3}$</td>
<td>Measured</td>
</tr>
<tr>
<td>Characteristic Length, $D_s$ (m)</td>
<td>$1.3 \times 10^{-3}$</td>
<td>$1.3 \times 10^{-3}$</td>
<td>Measured</td>
</tr>
<tr>
<td>Body Length, BL (m)</td>
<td>$1.75 \times 10^{-3}$</td>
<td>$1.75 \times 10^{-3}$</td>
<td>Measured</td>
</tr>
<tr>
<td>Damping coefficient, $C_s$ (Kg/s)</td>
<td>$8.3 \times 10^{-7}$</td>
<td>$8.3 \times 10^{-7}$</td>
<td>Calculated</td>
</tr>
<tr>
<td><strong>Radial lines</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number, $N_r$</td>
<td>8</td>
<td>8</td>
<td>Field Data</td>
</tr>
<tr>
<td>Young’s Modulus, $E_r$ (Pa)</td>
<td>$0.35 \times 10^{10}$</td>
<td>$0.45 \times 10^{10}$</td>
<td>[93]</td>
</tr>
<tr>
<td>Diameter, $D_r$ (m)</td>
<td>$1 \times 10^{-6}$</td>
<td>$1 \times 10^{-6}$</td>
<td>SEM</td>
</tr>
<tr>
<td>Length, $L_r$ (m)</td>
<td>$4.5 \times 10^{-2}$</td>
<td>$4.5 \times 10^{-2}$</td>
<td>Measured</td>
</tr>
<tr>
<td>Equilibrium Length, $L_{r,eq}$ (m)</td>
<td>$2.34 \times 10^{-2}$</td>
<td>$2.34 \times 10^{-2}$</td>
<td>Measured</td>
</tr>
<tr>
<td><strong>Tension line</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Young’s Modulus, $E_t$ (Pa)</td>
<td>$0.35 \times 10^{10}$</td>
<td>$0.45 \times 10^{10}$</td>
<td>[93]</td>
</tr>
<tr>
<td>Diameter, $D_t$ (m)</td>
<td>$1 \times 10^{-6}$</td>
<td>$1 \times 10^{-6}$</td>
<td>SEM</td>
</tr>
<tr>
<td>Length, $L_t$ (m)</td>
<td>$4 \times 10^{-2}$</td>
<td>$4 \times 10^{-2}$</td>
<td>Measured</td>
</tr>
<tr>
<td>Equilibrium Length, $L_{t,eq}$ (m)</td>
<td>$6 \times 10^{-2}$</td>
<td>$6 \times 10^{-2}$</td>
<td>Measured</td>
</tr>
<tr>
<td><strong>Capture lines</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number per radial line</td>
<td>13</td>
<td>13</td>
<td>Measured</td>
</tr>
<tr>
<td>Length, $L_c$ (m)</td>
<td>$6.5 \times 10^{-3}$</td>
<td>$6.5 \times 10^{-3}$</td>
<td>Calculated</td>
</tr>
<tr>
<td><strong>Total web lines</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Length, $L_w$ (m)</td>
<td>1.03</td>
<td>1.03</td>
<td>Calculated</td>
</tr>
<tr>
<td>Damping coefficient, $C_w$ (Kg/s)</td>
<td>$2.41 \times 10^{-4}$</td>
<td>$2.41 \times 10^{-4}$</td>
<td>Calculated</td>
</tr>
<tr>
<td><strong>Initial Conditions</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$x_o$ (m)</td>
<td>$-4.5 \times 10^{-4}$</td>
<td>$-18.5 \times 10^{-4}$</td>
<td></td>
</tr>
<tr>
<td>$y_o$ (m)</td>
<td>$-12 \times 10^{-3}$</td>
<td>$-12 \times 10^{-3}$</td>
<td></td>
</tr>
</tbody>
</table>

Table A.4: Summary of dimensionless numbers in springtails landing on the water surface

<table>
<thead>
<tr>
<th>Dimensionless number</th>
<th>Springtail landing</th>
</tr>
</thead>
<tbody>
<tr>
<td>$Re = \rho u D_s / \mu$</td>
<td>$250 - 500$</td>
</tr>
<tr>
<td>$We = \rho u^2 / D_s$</td>
<td>$1 - 7$</td>
</tr>
<tr>
<td>$Bo = \rho g D_s^2 / \gamma$</td>
<td>$3.5 \times 10^{-2}$</td>
</tr>
<tr>
<td>$Ba = M g / \gamma D_s$</td>
<td>$3.6 \times 10^{-3}$</td>
</tr>
<tr>
<td>$Oh = \mu / \sqrt{\rho \gamma D_s}$</td>
<td>$3 \times 10^{-3}$</td>
</tr>
</tbody>
</table>

Table A.5: Summary of parameters used for landing model

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Description</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$C_d$</td>
<td>Drag coefficient of collophore</td>
<td>0.5</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>Surface tension of air-water surface</td>
<td>$72 \times 10^{-3}$ $N/m$</td>
</tr>
<tr>
<td>$\nu$</td>
<td>Kinematic viscosity of water</td>
<td>$10^{-6}$ $m^2/s$</td>
</tr>
<tr>
<td>$\rho_f, \rho_s$</td>
<td>Density of water and springtail</td>
<td>$10^{-3}$ $kg/m^3$</td>
</tr>
<tr>
<td>$m_s$</td>
<td>Mass of springtail</td>
<td>0.13 $mg$</td>
</tr>
<tr>
<td>$u$</td>
<td>Speed of springtail at impact</td>
<td>$-0.68$ $m/s$</td>
</tr>
<tr>
<td>$D_c$</td>
<td>Collophore diameter</td>
<td>$0.125 \times 10^{-3}$ $m$</td>
</tr>
<tr>
<td>$D_s$</td>
<td>Springtail diameter</td>
<td>$0.5 \times 10^{-3}$ $m$</td>
</tr>
<tr>
<td>$L_s$</td>
<td>Springtail length</td>
<td>$1.5 \times 10^{-3}$ $m$</td>
</tr>
<tr>
<td>$g$</td>
<td>Gravitational acceleration</td>
<td>$10$ $m/s^2$</td>
</tr>
</tbody>
</table>
APPENDIX B
SCHOLARLY ACHIEVEMENTS

B.1 Published Journals


Elio J. Challita, P. Sehgal, R. Krugner, M. S. Bhamla. ”Droplet superpropulsion in an energetically constrained insect.” Nature Communications, 2023

V. M. Ortega-Jimenez, Elio J. Challita, B. Kim, H. Ko, M. Gwon, J. Koh, M. S. Bhamla. ”Directional takeoff, aerial righting and adhesion landing of semiaquatic springtails”. Proceedings of the National Academy of Sciences, 2022


G. Byagathvalli *, Elio J. Challita * & M. S. Bhamla. ”Frugal science powered by curiosity”. Industrial & Engineering Chemistry Research, 2021

B.2 Presentations

2023 Rowland Institute, Harvard University (Invited talk)

2023 Society of Tribologists and Lubrication Engineers, Tribology Frontiers Conference,
"The ultrafast finger snap is mediated by a frictional skin latch" (Invited talk - Postponed)

2023 American Physical Society (APS), March meeting,
"The dynamics of microjet spitting in termite soldiers"

2023 Society of Integrative and Comparative Biology (SICB),
"Viscoelastic spitting of termite soldiers" (Session Chair)

2022 Global and open-source hardware (GOSH) gathering, Panama City, Panama

2022 The Society of Rheology, Tribology Frontiers Conference, 93rd annual Meeting,
"Conehead termites spit predators with large liquid lassos"

2022 Interdisciplinary symposium: Fast Movements, Impacts, and Deformations. MURI

2022 American Physical Society (APS), March Meeting,
"How sharpshooter insects exploit biological superpropulsion to catapult their droplet pee"

2022 American Physical Society (APS), March Meeting,
"Liquid lassos: The defensive spitting of a termite soldier" (Invited focus talk)

2022 Society of Integrative and Comparative Biology (SICB),
"How cicadas pee in powerful fluidic jets"

2021 American Physical Society (APS), Division of fluid mechanics (DFD),
"How sharpshooter insects fling their droplet pee"

2021 Society of Integrative and Comparative Biology (SICB),
"Peeing one drop at a time: How sharpshooter insects use superpropulsion to launch their fluid excreta and why"

2019 Society of Integrative and Comparative Biology (SICB),
"Insect pee: How glassy-winged sharpshooters excrete ultrafast fluid droplets"
REFERENCES


[29] D. Charles R., *On the various contrivances by which british and foreign orchids are fertilised by insects, and on the good effects of intercrossing*, 1862.


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VITA

Elio Joseph Challita was born and raised in Lebanon. In 2010, he received his high school degree from Collège Central in Jounieh (CCJ), Lebanon. He moved to the United States in 2016 to pursue his master’s degree at the University of Georgia, Athens, Georgia, USA working with Professors Eric Freeman and Donald Leo. He met with Professor Saad Bhamla after being introduced by the Bioengineering program coordinator Laura Paige during BioE day in 2018.

He currently resides in Cambridge, MA with his wife Professor Maria Roche.