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TOPICAL REVIEW

Air-to-land transitions: from wingless animals and plant seeds to shuttlecocks and bio-inspired robots

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Abstract

Recent observations of wingless animals, including jumping nematodes, springtails, insects, and wingless vertebrates like geckos, snakes, and salamanders, have shown that their adaptations and body morphing are essential for rapid self-righting and controlled landing. These skills can reduce the risk of physical damage during collision, minimize recoil during landing, and allow for a quick escape response to minimize predation risk. The size, mass distribution, and speed of an animal determine its self-righting method, with larger animals depending on the conservation of angular momentum and smaller animals primarily using aerodynamic forces. Many animals falling through the air, from nematodes to salamanders, adopt a skydiving posture while descending. Similarly, plant seeds such as dandelions and samaras are able to turn upright in mid-air using aerodynamic forces and produce high decelerations. These aerial capabilities allow for a wide dispersal range, low-impact collisions, and effective landing and settling. Recently, small robots that can right themselves for controlled landings have been designed based on principles of aerial maneuvering in animals. Further research into the effects of unsteady flows on self-righting and landing in small arthropods, particularly those exhibiting explosive catapulting, could reveal how morphological features, flow dynamics, and physical mechanisms contribute to effective mid-air control. More broadly, studying apterygote (wingless insects) landing could also provide insight into the origin of insect flight. These research efforts have the potential to lead to the bio-inspired design of aerial micro-vehicles, sports projectiles, parachutes, and impulsive robots that can land upright in unsteady flow conditions.

1. Introduction

Aerial righting and landing in small wingless animals, from arboreal vertebrates (Jusufi *et al* 2008, Brown *et al* 2022) to specialized jumping hexapods (Ortega-Jimenez *et al* 2022), are performed with extraordinary effectiveness and maneuverability. A favorable landing can mean the difference between life and death for animals. A body colliding inappropriately against the ground may produce transient or permanent physical damage to limbs and vital body structures. Furthermore, landing upside-down can plausibly increase the chance of being targeted and attacked by predators, and reduce the likelihood of escape. Wingless creatures have been improving the art of landing over millions of years through natural selection, making the study of aerial maneuvering and landing in small animals a fertile ground for biomechanical discovery and technological innovation.

Self-righting in wingless animals varies with size. During free fall, large organisms (from humans and cats to geckos and salamanders) exploit inertial forces generated by their limbs, bodies, and elongated tails (when present) to right themselves and to maneuver in midair (McDonald 1960, Jusufi *et al* 2008, Brown *et al* 2022) (figure 1(A)). By contrast, small animals use postural changes with their bodies and legs to generate time-dependent aerodynamic torques, which can induce an upright posture (Yanoviak *et al* 2009, 2010, 2015, Zeng *et al* 2017, Kane *et al* 2021), a more favorable position for absorbing contact and/or gripping with limbs (figure 1(B)). Jumping springtails are a particular case because they regain stability by lowering their center of gravity via body curvature and collecting a water droplet with an adhesive tube-like structure (i.e. the collophore) in their abdomen. Remarkably, self-righting in small animals occurs in a concise time frame -less than 100 ms- among diverse taxa (Jusufi *et al* 2008, Ribak *et al* 2013, Ortega-Jimenez *et al* 2022). Aerial righting also occurs in plant seeds dispersed by the wind, but in contrast with the areal righting seen in animals, it occurs passively without noticeable structural deformation (Cummins *et al* 2018, Ortega-Jimenez *et al* 2019).

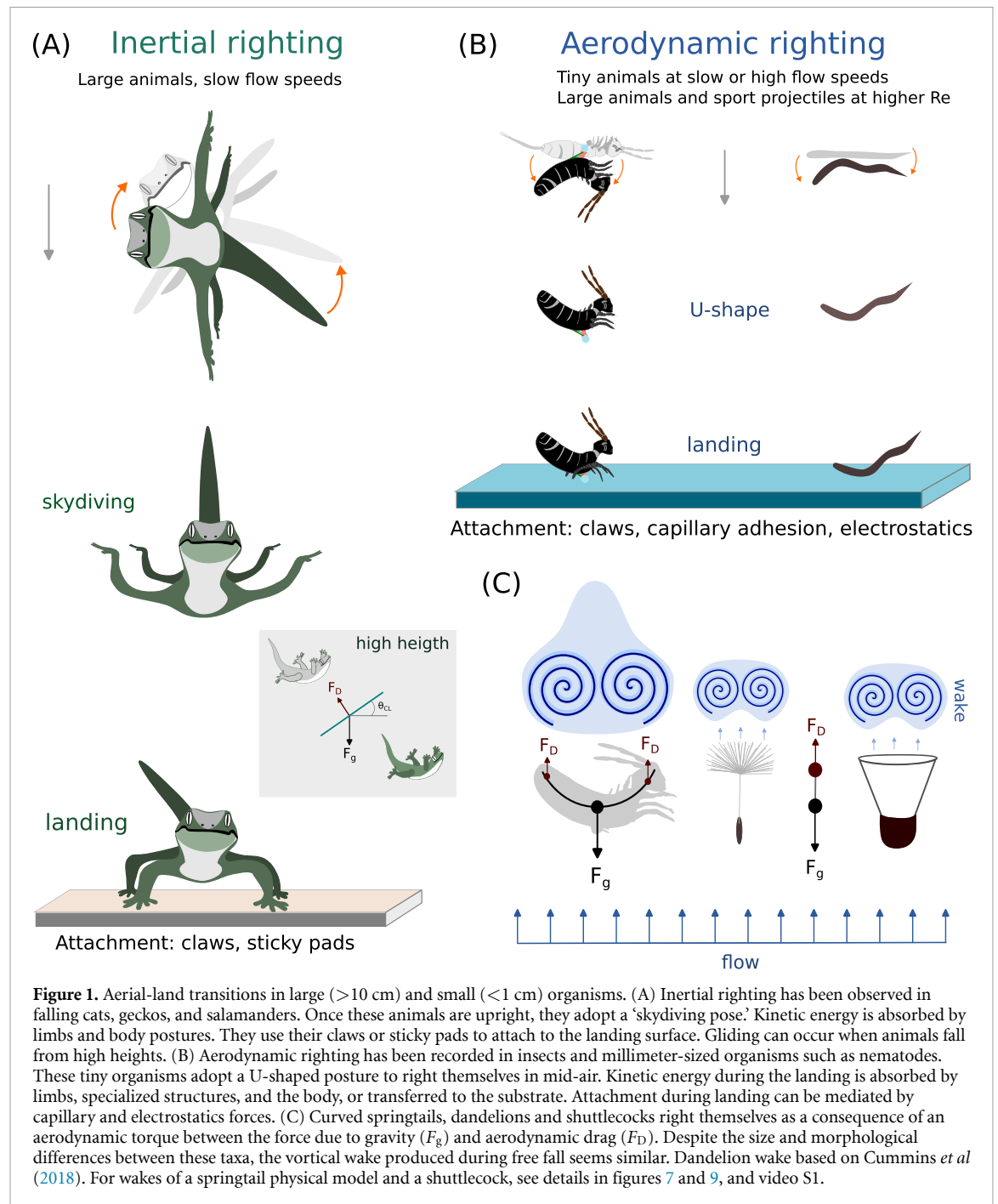
Dandelion seeds can spread a hairy drag-producing structure (the pappus) via changes in water content within minutes (Seale *et al* 2022); however, it is uncertain whether the morphing of the hairs offers aerial control, particularly in turbulent flows. Woody aphids use cotton-like hairs located terminally on their bodies to effect aerial stability (Ristroph *et al* 2013), a drag-based sudden self-righting (Peterson *et al* 1996) that resembles the motion of toy badminton shuttlecocks (Hasegawa *et al* 2013). Aerial righting deserves more research attention because only a few biological groups have been studied, mostly in controlled still air conditions

uncommon in natural environments (McCay 2003). How steady and unsteady flows affect landing performance in animals is an open question that deserves further investigation.

Takeoff height is also an essential factor that affects landing success in animals. For example, in aphids, the probability of an upright landing during free fall increases with height (Ribak *et al* 2013). Notably, the survival of small organisms during impact with the ground seems independent of height, because terminal speed is minimal and is reached quickly during falling. By contrast, in large wingless vertebrates such as felines, the probability of survival is reduced dramatically with height, given the higher speeds reached at impact against a solid substrate (Vnuk *et al* 2004, but see Whitney and Mehlhaff 1987).

Quick attachment or adhesion to the substrate during landing and an appropriate landing orientation is important to preclude bouncing and facilitate a subsequent quick escape. Many terrestrial organisms use their limbs to absorb kinetic energy during the impact. Flying snakes are a particular case because they have no limbs but may contort their bodies prior to impact on the ground and land tail-first, which minimizes risks of head damage (Socha 2011). Several animals use claws (Salerno *et al* 2023) or sticky pads located on their limbs (Zurek *et al* 2015, Palecek *et al* 2022) or body regions (Chen *et al* 2019) to attach firmly to the substrate and to minimize bouncing. Semiaquatic invertebrates such as springtails use their collophore structure to adhere to the water surface, thus minimizing rebound after landing. At the same time, these arthropods produce capillary waves on the water surface that dissipate kinetic energy during the collision. At smaller scales, jumping nematodes, whose cuticle is highly adhesive, descend head-first when falling and then attach firmly to their host.

Technologically, robots that can catapult themselves into the air, albeit with no control mechanism, have been designed based on research on animal jumping performance (Noh 2012, Koh *et al* 2015). Despite these technological advances for fast catapulting, there is little work on aerial self-righting and landing in those jumping devices. Recently, bio-inspired robots with the ability to right aurally and then land upright have been designed based on the aerial responses of geckos and springtails (Jusufi *et al* 2008, Ma *et al* 2021, Ortega-Jimenez *et al* 2022). The gecko bot, for example, exploits inertia produced by a tail-like structure to right itself and land successfully on a vertical surface (Jusufi *et al* 2008). The springtail bot uses drag flaps and an extra weight located ventrally to create aerodynamic torque and to land upright on the ground (Ortega-Jimenez *et al* 2022). Surface attachment in the gecko bot is enhanced by



Velcro on its feet and the landing surface (Jusufi *et al* 2008). Nevertheless, there is ample room for improvement in the design of landing robots. For example, the deployment timing of drag-generating structures can be upgraded to avoid initial drag penalization and consequently favor peak heights reached by the springtail robot. Also, detachment and reattachment from surfaces during takeoff and landing must be implemented. Rapid body morphing during aerial maneuvering is also desirable to mimic the mid-air control shown by millimeter-sized arthropods.

In this review, we examine the current state of the art for aerial righting and landing maneuvers in

wingless organisms, plant seeds, sports projectiles, and robots. Our goal is to inspire new research on wingless organisms that can right themselves in mid-air, particularly under non-steady flow conditions. Such findings could aid in the design of bio-inspired robots, parachute-like decelerators, and micro-aerial vehicles that can recover from unfavorable orientations (such as in turbulent air or rain) and land safely. This paper is organized as follows: section 2 describes how wingless organisms right themselves in midair, focusing on size dependencies in terms of aerodynamic and inertial forces; section 3 investigates how wingless vertebrates and invertebrates leverage their

morphological adaptations for successful landing and anchoring; section 4 examines bio-inspired wingless robots with the ability to catapult themselves through the air, emphasizing those that can correct their position in midair and, therefore, land upright. Finally, in section 5, we conclude by identifying future research opportunities on aerial control and landing in wingless animals experiencing unsteady flows.

2. Skydiving without wings

From small vertebrates to millimeter-sized arthropods, non-volant animals are commonly challenged to move through the air and against gravity for multiple biological reasons. Vertebrates and invertebrates that live on vegetation or rocks can drop to reach lower terrain (or even water) to escape predators, obtain prey, or access nutritional resources. Moreover, animals and plant seeds can be detached by the wind and drift for long distances. For example, light air currents can lift millimeter-sized thrips and aphids upward, resulting in a long-range dispersal (Hardy and Milne 1938, McLaren *et al* 2010). Aerial lifeforms drifting in the atmosphere are so diverse and numerous that they may even have a role in environmental phenomena such as cloud formation and rainfall (Bauer *et al* 2003). Other animals, such as nematodes, springtails, wingless insects, and frogs, easily become airborne by catapulting themselves explosively using spring-like mechanisms. Remarkably, most wingless organisms that move through the air, with distinctive *bauplan* and adaptations, can perform rapid mid-air righting maneuvers, and controlled landings using inertial and/or aerodynamic forces.

2.1. Righting by inertia

2.1.1. Geckos

Various reptiles can control their pitch orientation during aerial maneuvers via inertial forces by simply adjusting the angle of the tail with respect to the body (Jusufi *et al* 2008, 2010, Libby *et al* 2012, Siddall *et al* 2021a). The first aerial righting behavior (in the sense that dorso-ventral righting is conducted from a supine to a prone posture during free fall) in reptiles was observed in the flat-tailed house gecko *Hemidactylus platyurus* (Jusufi *et al* 2008, figures 2(A)–(C)). Analytical modeling demonstrated that tail inertia alone can suffice to reorient the body through the conservation of momentum (Jusufi *et al* 2010, 2011). Aerial righting in flat-tailed house geckos (both tail and body length ~ 5 cm, mass ~ 3 g) is mediated by a counter-rotation of the tail relative to the body (Jusufi *et al* 2010, 2011). This corrective maneuver is completed within ~ 100 ms after the start of free fall. The aerial righting response observed in geckos occurs some 46 ms after falling from rest in upside down posture on the underside of a perch

(figures 1(A), 2(A)), with the geckos not achieving significant velocity before the aerial righting maneuver was executed. Three dimensional modeling of the dynamics of righting revealed that aerodynamic drag torque would account for under 4% of the body rotation observed in the aerial righting response during free fall (Jusufi *et al* 2010), therefore inertia predominates in this behavior. Geckos take 400–600 ms to reach their terminal velocity of ~ 6 m s $^{-1}$ when in free fall (Siddall *et al* 2021b). As a result, these reptiles rely on inertial rather than aerodynamic reaction forces to reorient initially.

However, during subsequent descent and gliding post righting to prone poster, geckos can exhibit considerable aerodynamic authority (figure 3, wind tunnel experiments in Jusufi *et al* 2008, 2010, followed up by field work Siddall *et al* 2021b), being able to successfully alight on a target tree after gliding distances of over ~ 7 m (~ 140 snoutvent lengths), despite lacking the specialized morphological features of other gecko species (e.g. skin flaps of *Ptychozoon kuhli*). In the air, geckos keep a stable orientation using active motions of the tail and legs and by keeping the body curved dorsoventrally with the legs spread and elevated in a ‘skydiving’ posture (Jusufi *et al* 2008, figures 3(A)–(C)). At terminal velocity, geckos move their tails in a circular fashion, combining both inertial and aerodynamic torques to stabilize yaw and pitch (Jusufi *et al* 2010, Siddall *et al* 2021a). Inertial reaction forces in the tail develop larger torques than aerodynamic forces but are limited by the motion range of the tail, so a combination must be used to maintain stability over long glide trajectories (Siddall *et al* 2021a).

2.1.2. Squirrels

Squirrels (Sciuridae) are widespread in arboreal habitats found in temperate latitudes and are specialized for rapid locomotion through the tree canopy. Eastern Gray Squirrels (*Sciurus carolinensis* ~ 0.4 m and ~ 0.2 m body and tail length, respectively, mass ~ 400 g) employ complex dynamic jumps to move through their environment (Hunt *et al* 2021) (figure 2(D)), and arboreal species display a higher encephalization quotient (i.e. relative brain size) than other rodent taxa (Krubitzer *et al* 2011). Although limited data are available on the aerial righting reflex in squirrels, aerial righting in rats (another rodent of comparable size) is widely studied (Altman and Sudarshan 1975), and follows a similar pattern to the well-known righting response of cats (Marey 1894). Anecdotal observations of falling squirrels (Fukushima *et al* 2021) indicate that rather than relying on body motion, squirrels prioritize head orientation and visibility of their landing site and instead rely on tail motion for stability (figure 2(D)). Despite squirrels having considerably lighter tails than geckos ($\sim 1\%$ body mass in squirrels compared to $\sim 10\%$

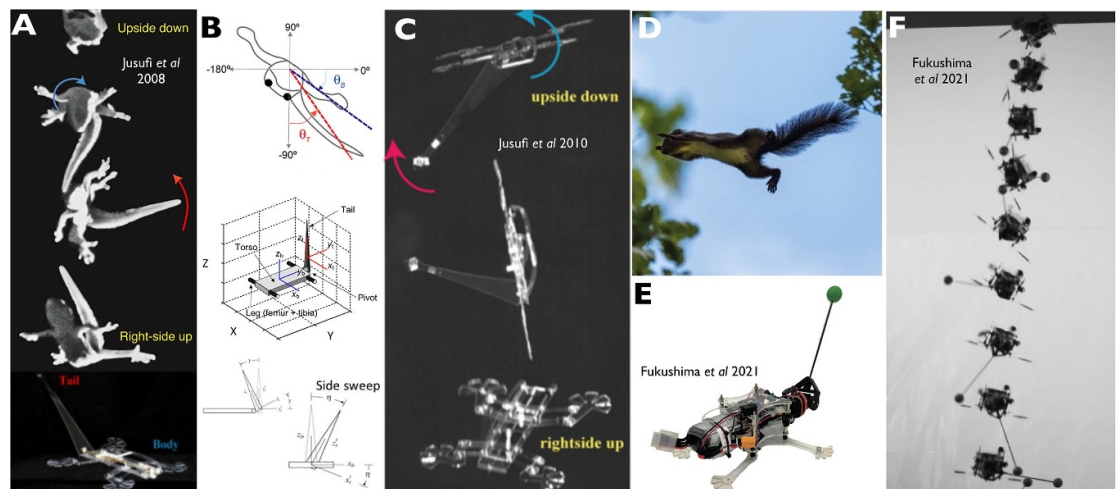


Figure 2. Free fall experiments with dorsoventral aerial righting from supine to prone posture with no external forces acting on the system except gravity and aerodynamics. (A) At takeoff, geckos (body and tail size 54 mm and 50 mm, respectively) were released from an upside down (supine) posture. Counterclockwise tail rotation induced a clockwise rotation of the body. As the geckos' bodies attained right-side up (prone) posture, the tail stopped rotating. Jusufi *et al* (2008). © 2008 by The National Academy of Sciences of the USA. Freely available online through the PNAS open access option. (B) Schematic of a supine gecko falling to show angle convention, and a 3D mathematical model of its dynamics. Jusufi *et al* (2010, 2011). © 2010, 2011 IOP Publishing. Reproduced with permission. All rights reserved. (C) Aerial righting maneuver performed by the robot prototype RightingBot. The tail was rotated about the robot's longitudinal axis. Jusufi *et al* (2010). © 2010 IOP Publishing. Reproduced with permission. All rights reserved. (D) Squirrel jumping from branch to branch. Image credit: Joachim Dobler (CC BY-ND 2.0). (E) Bio-inspired squirrel-like robotic platform, able to self-right, with tail length of 175 mm and body length of 190 mm. Reproduced from Fukushima *et al* (2021). CC BY 4.0. (F) A sequential photo of the dropping robot. After onset of tail rotation, the body rotation speed decreased.

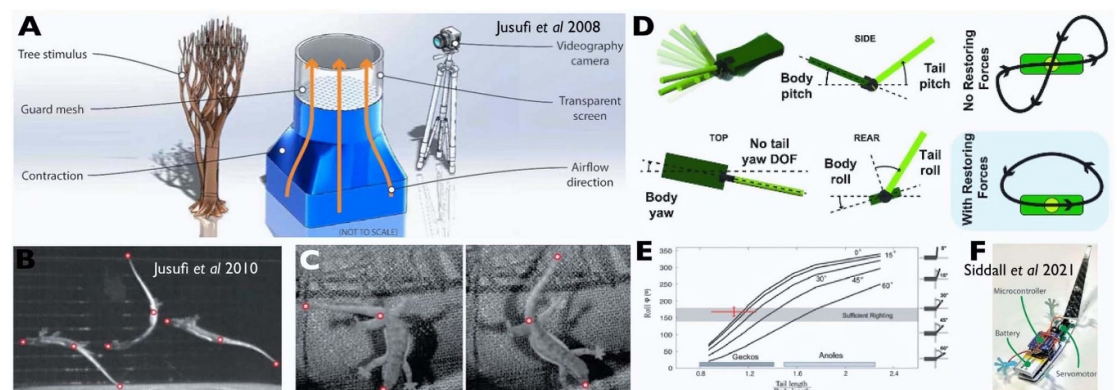


Figure 3. Gliding geckos and robots. (A) Equilibrium gecko gliding experiment with vertical wind tunnel. Jusufi *et al* (2008). © 2008 by The National Academy of Sciences of the USA. Freely available online through the PNAS open access option. (B) Geckos exhibiting translation. (C) Turning associated with tail rotations. (D) Trajectory optimization of tail motion to produce a body yaw, with and without external aerodynamic reactions. (E) Righting effectiveness landscape in comparative analysis of anoles and geckos. Jusufi *et al* (2010). © 2010 IOP Publishing. Reproduced with permission. All rights reserved. (F) At-scale robot drop tests with an active tail to determine aerodynamic versus inertial effects from tail motion. Reproduced from Siddall *et al* (2021a). CC BY 4.0.

in geckos), tests with physical models (figures 2(E) and (F)) have shown that the tail can produce a sufficient inertial effect to correct large body rotations (Fukushima *et al* 2021). When compared to flying squirrels with specialized gliding patagia for aerial maneuvering, non-volant squirrels display a raised tail posture when jumping from a perch (Essner 2002), suggestive of preparation for an inertial pitch correction. The fur present on squirrel tails provides a significant increase in the size of the tail (figure 2(D)), but it has yet to be established experimentally how

strong an aerodynamic role this fur plays in aerial maneuvering. The larger size of squirrels compared to other animals which use tails for aerial maneuvering (e.g. geckos and salamanders) suggests a greater use of aerodynamic forces (Siddall *et al* 2021a).

2.1.3. Frogs and salamanders

Amphibians occupy a wide range of ecological habitats and exhibit diverse morphologies. Some taxa, such as frogs and toads (Order: Anura) have evolved

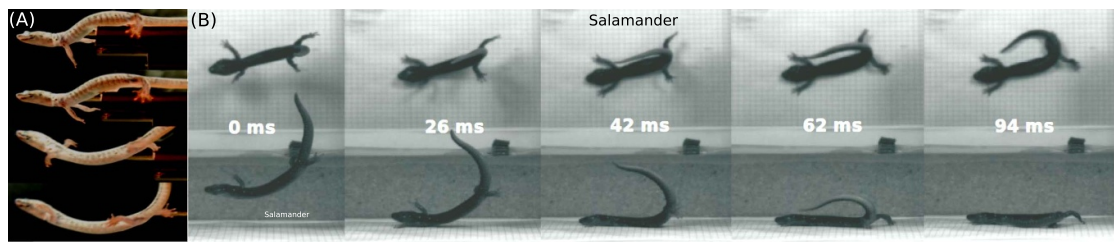


Figure 4. Aerial movements of salamanders. (A) Color image sequence (viewed from top to bottom) representative of a typical jump in an arboreal salamander (*Aneides lugubris*) (mass, body length, and tail length 9 g, 8 cm, and 7 cm, respectively). Reprinted from Brown and Deban (2020), Copyright (2020), with permission from Elsevier. (B) Black and white image sequence (viewed from left to right) representative of a typical landing for an arboreal salamander (*A. lugubris*) after jumping from a perch 75 mm above. Each frame shown (0, 26, 42, 62, and 94 ms) depicts *A. lugubris* through the same trial from both the dorsal (top) and lateral (bottom) views, which were imaged from a single lateral camera perspective using a mirror angled at 45° to capture the dorsal view. Scale: each square on the grid paper is 5 × 5 mm.

specialized self-catapulting systems that enable controlled airborne flight and landing (Gans and Parsons 1966, Marsh and John-Alder 1994, Peplowski and Marsh 1997). Except New Zealand primitive frogs (Leiopelmatidae), most anurans (Lalagobatrachia) use their hindlimbs for catapulting and self-righting. To control landing, anurans protract and adduct the forelimbs, which allows for rapid postural recovery during landing and enables consecutive jumps (Nauwelaerts and Aerts 2006, Essner *et al* 2010, Reilly *et al* 2016). Similarly, toads exhibit highly coordinated landings in which they match forelimb angle and muscle recruitment to jump height and distance, and use their forelimbs to stabilize the body as their hindlimbs touch down (Gillis *et al* 2014, Cox and Gillis 2015). Cricket frogs extend both sets of limbs when conducting air-water interfacial locomotion, effectively porpoising in and out of the water (Weiss 2022 dissertation). The hindlimb extension results from the propulsive phase of jumping; the forelimb extension may control pitch orientation in the air, but modeling needs to be conducted to test this hypothesis.

One of the earliest recorded examples of aerial control in wingless animals is the tree frog *Rhacophorus nigropalmatus*, described by Alfred Russell Wallace in 1855. Wallace noted on the back of a watercolor sketch that this newly described species of frog from Borneo ‘descended from a high tree as if flying’ (Yandell 2013). The morphological adaptations of arboreal amphibians allow them to cope with a range of daily biological and locomotor challenges, including the risk of longer flights from greater heights and more precarious starting positions compared to those found in terrestrial frogs. Upside-down or head-down tree frogs use rapid hindlimb movements to perform aerial righting. First, they extend their hindlimbs laterally and posteriorly, followed quickly by a swing about the body axis, leading to a body counter-rotation before finally retracting their hindlimbs. This entire maneuver happens in about 42 ms and generates enough inertial forces for the frog to rotate its body while conserving angular

momentum (Wang *et al* 2013, 2022). Tree frogs move their limbs next to or above the body and constantly maneuver to maintain position while descending (McKay 2001), utilizing their interdigital webbing to increase drag and descend more efficiently (Wu *et al* 2022).

Jumping and arboreality are not exclusive to frogs and toads among amphibians. Many lungless salamanders (Plethodontidae) can jump effectively by rapidly bending and unbending their bodies in a maneuver similar to the C-start propulsion used by fish and worms (Ryerson 2013, Brown and Deban 2020). Nearly half of lungless salamander species are either facultative or obligately arboreal (McEntire 2016). The genus *Aneides*, in particular, exhibits unique jumping behaviors, such as frequently toeing off with both feet simultaneously with lower takeoff velocities (Brown and Deban 2020). This symmetrical jumping strategy minimizes axial body rotation, facilitating aerial maneuvering and landing control. In addition, *Aneides* assumes a characteristic skydiving posture significantly faster than other plethodontids (Brown and Deban 2020). To do so, they extend their limbs perpendicularly to the trunk while positioning the head and tail above the body to form a characteristic U-shape. Less than 100 ms after toe-off, they rotate the feet ventral-side-down while maintaining this skydiving pose (figure 4(B)).

Accidental falls are a common occurrence in climbing salamanders, particularly for *Aneides vagrans* which live in tree crowns (personal observation, CB). These salamanders can slip and fall from the canopy, or experience foot slipping or tail dragging while jumping, resulting in them being upside-down or head-down in the air up to 100 m above the ground. To right themselves, these salamanders extend all four limbs dorsolaterally while rapidly rotating the tail causing the body to counter-rotate, followed by a skydiving posture in which the tail is held above the body. This entire maneuver takes only 116 ± 56 ms (average ± 1 sd) to complete (Brown *et al* 2022).

Morphologically, climbing salamanders and ‘flying’ tree frogs are somewhat similar, as both groups

possess relatively long hindlimbs and greater interdigital webbing compared to non-arboreal species within their respective genera. Behaviorally, these salamanders employ postures similar to those of tree frogs that facilitate aerial control. Furthermore, computational fluid dynamic simulations suggest that such morphological changes and postures in salamanders contribute to higher lift:drag ratios (Brown and Kirk 2023), which can be harnessed to glide laterally when paired with repeated parasagittal undulations of the tail (Brown *et al* 2022). This strategy is also seen in various gliding reptiles such as geckos (Jusufi *et al* 2008). Despite stark differences in tail morphology, salamanders and tree frogs appear to achieve convergent aerial maneuvering and control by extending and rotating appendages behind the body to initiate counter rotations of the body.

2.1.4. Snakes

Flying snakes (genus: *Chrysopelea*) are a small group of arboreal snakes found in lowland forests of South and Southeast Asia. As gliders, they jump from a perch, create aerodynamic forces (Miklasz *et al* 2010, Holden *et al* 2014, Krishnan *et al* 2014, Hong *et al* 2022) that both slow their descent and promote horizontal travel, and land on the ground or another vegetative substrate (Socha 2011). Once airborne, they appear to ‘swim’ through the air using aerial undulation (Socha *et al* 2005), a complex three-dimensional movement that involves large horizontal waves as well as smaller vertical ones (Yeaton *et al* 2020). As has been hypothesized for all other terrestrial gliding taxa (Dudley and Yanoviak 2011), aerial righting presumably played a significant role in the evolution of gliding in snakes, but aerial righting has not been studied in this group.

A few lines of evidence, direct and indirect, suggest that flying snakes can actively control aerial righting. First, no flying snake has been observed to lose control in the air during takeoff, gliding, or landing across hundreds of experimental trials under different conditions (Socha 2002, Socha and LaBarbera 2005, Socha *et al* 2005, 2010, Yeaton *et al* 2020). Mathematical models of the snake’s dynamics suggest that the snake requires active control to remain stable in the air (Jafari *et al* 2014, 2017, Yeaton *et al* 2020); such mechanisms for control are unknown, but could be employed to effect righting. Second, one species (*Chrysopelea paradisi*) is capable of volitional turning in the air (Socha 2002, Socha *et al* 2005, 2010, Yeaton *et al* 2020), demonstrating that stability characteristics could be manipulated to effectuate aerial rotation. Lastly, although aerial righting has not been specifically studied, one snake that was induced to fall in a preliminary study quickly righted itself, began undulating, and obtained horizontal distance in the

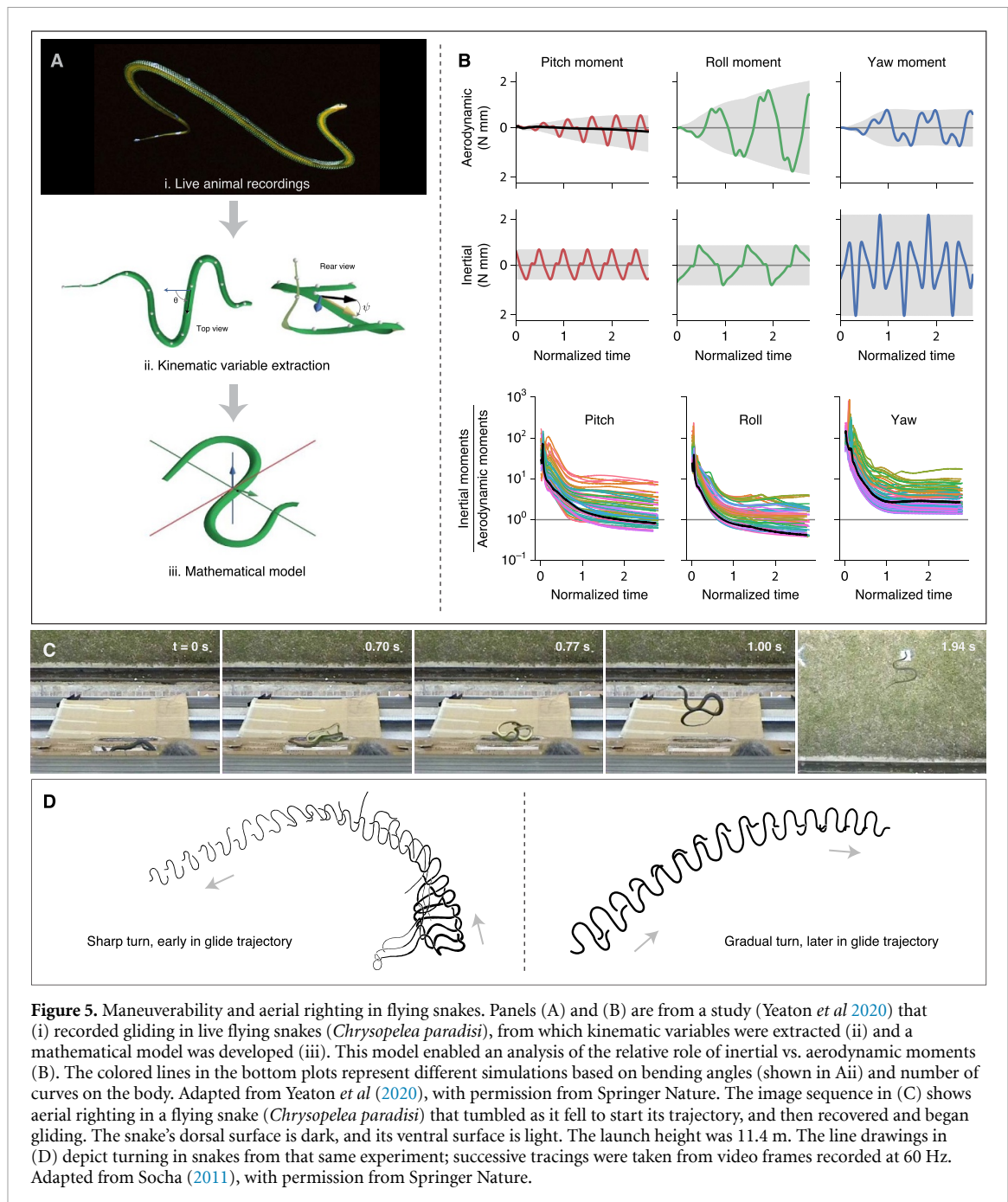
air (figure 5), providing a hint of its capabilities in this regard.

The body plan of a flying snake is conducive for inertial control of aerial righting; in effect, it is a long, flexible cylinder. The tails of other species are known to employ angular momentum conservation for righting, but the snake itself could be considered as one long tail. Its mass distribution varies along its length, with the greatest mass at mid-body and only a small percentage in its tail (Yeaton *et al* 2020), so in contrast to other limbed animals that use their tail to drive righting rotations, the snake’s most important inertial mechanism should derive from its trunk (the snout-to-vent region). A recent mathematical model of gliding in flying snakes (Yeaton *et al* 2020) examined the relative contributions of inertia vs. aerodynamic moments in the snake’s trunk. In the pitch axis, these moments contributed roughly equally. However, in the roll axis, inertial moments were slightly greater than aerodynamic moments, and in the yaw axis they were about an order of magnitude greater (figure 5). These results were used to suggest that inertial forces could be used to effectuate turns, but they could also be employed for aerial righting. Modeling that specifically addresses righting, and new experimental work on live animals akin to previous work on geckos (Jusufi *et al* 2008), is needed to address this hypothesis in snakes.

2.2. Righting by aerodynamics

2.2.1. Arboreal insects and spiders

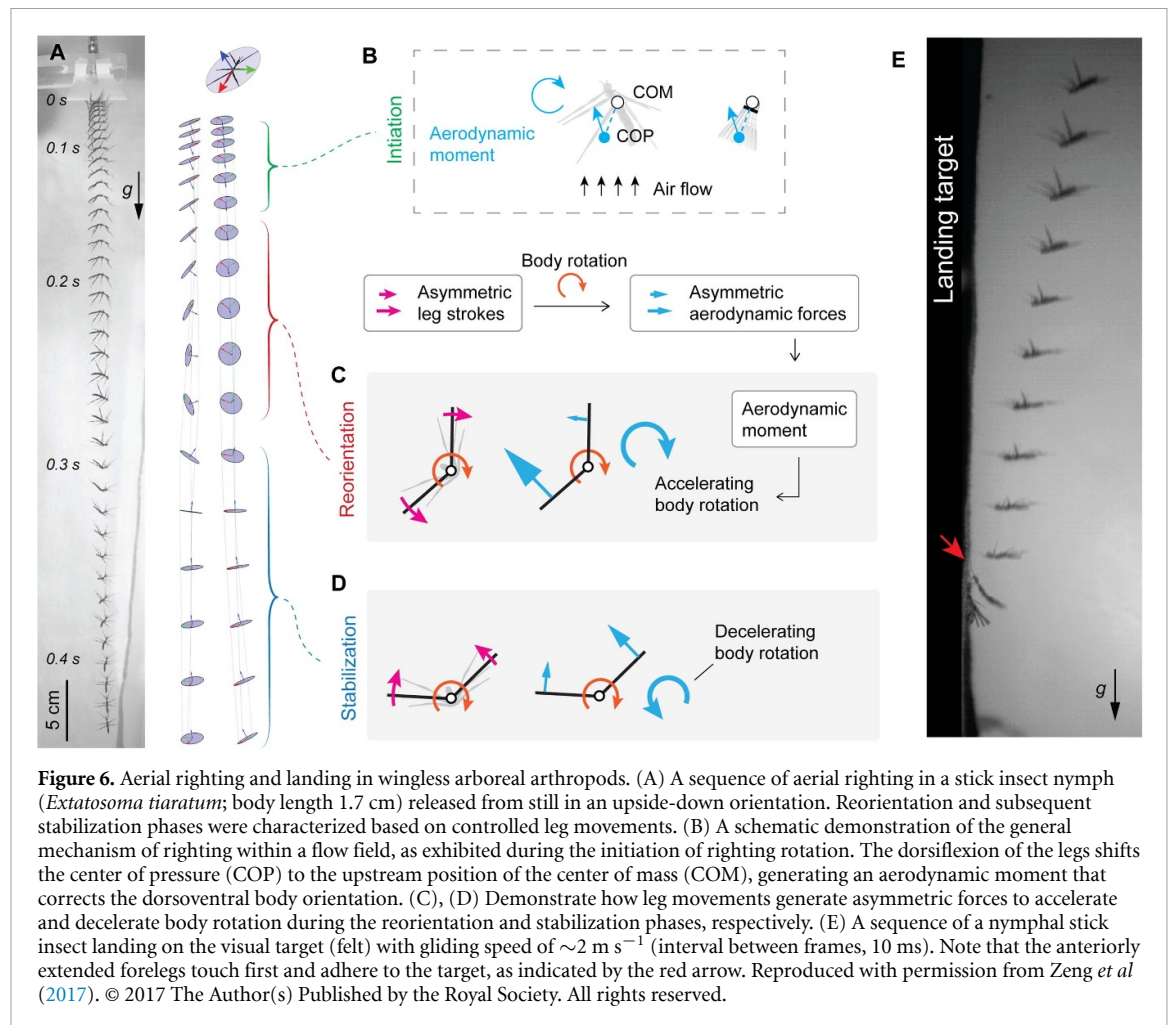
Wingless arthropods dominate the arboreal fauna and exhibit sophisticated aerial and landing responses that can compete with those of animal fliers. The ability to glide has been demonstrated in arachnids and at least ten hexapod orders, such as bristletails, ants, and stick insects (Dudley and Yanoviak 2011, Yanoviak *et al* 2015). This aerial behavior seems to be used to avoid predation and potential threats or simply as a result of adverse environmental conditions such as intense winds or heavy precipitation. For example, arboreal stick insect nymphs jump to cross air gaps and use a self-dropping reflex to evade threats or perturbation, and they become airborne after self-dropping or missed landing (Zeng *et al* 2020). Once airborne, these arthropods can change their body orientation and control the direction of descent while gliding, allowing them to redirect their landings towards preferred vegetational structures. These behaviors can indirectly reduce the energy and time required for climbing, as well as enabling them to avoid unfamiliar habitats or potential threats within the understory. The ecological contexts of gliding and associated behaviors are specific to each taxon. For example, in foraging workers of *Cephalotes* ants, gliding helps them stay close to home trees and to avoid predation, including threats in the sometimes



flooded understory (Yanoviak *et al* 2011). In newly hatched stick insect nymphs (*Extatosoma tiaratum*), which disperse upward from the understory towards the canopy, gliding can be used during diurnal dispersal, when inadvertently falling, and while searching for host plants (Zeng *et al* 2020).

An aerodynamically-driven righting mechanism is present across wingless arthropods of different sizes. Field research in various ants (mass, 10–80 mg) and spiders (mass, 2–700 mg) have demonstrated an aerial righting phase during the initial fall (Yanoviak *et al* 2005, 2015). More detailed body and leg kinematics have been studied under controlled laboratory conditions, specifically in aphids and nymphal stick insects during free fall (Ribak *et al* 2013, Zeng

et al 2017). In general, aerial righting of an arthropod is powered by the aerodynamic moment induced by a stereotypic leg and abdomen posture, typically via dorsiflexion (i.e. elevating dorsally). This postural change shifts the center of aerodynamic pressure to an upstream position relative to the center of mass, creating an aerodynamically unstable configuration. For example, falling aphids (body length, 4.2 mm; mass, 4.2 mg) adopt such a stereotypical posture and complete righting within ~170 ms and with <20 cm height loss (Ribak *et al* 2013). More complex leg movements were observed in stick insect nymphs (body length, 1.7 cm; mass, 25 mg), which attain righting within 200 ms and with ~30 cm height loss. They adopt bilaterally asymmetric leg



strokes to effect body rotation during righting and subsequently decelerate body rotation (figures 6 (A)–(D); Zeng *et al* 2017). These righting behaviors are initiated as reflexes using various sensory modalities, such as tactile cues on the tarsus and from air flow (Meresman *et al* 2014). As noted in experiments on aphids (Ribak *et al* 2013), the sequence and timing of righting maneuvers, in general depends on the initial condition (e.g. body orientation).

2.2.2. Collembolans

Springtails are an abundant group of tiny hexapods that play a fundamental role in the formation, microstructure, and nutrient recycling of soil, as well as in the trophic maintenance of meso- and microfauna. Collembolans are also famous for their ability to jump in such a way that through our eyes, they seem to vanish when catapulting into the air. Because of such explosive performances following even minuscule perturbations, springtails have traditionally been considered uncontrollable jumpers. Recent evidence has challenged this assumption, and we now know that these wingless hexapods exert tight control over all stages of a jump, from takeoff and

mid-air displacement to landing and final surface attachment (Ortega-Jimenez *et al* 2022).

In general, springtails ($\sim 1 \text{ mm}$ length and 0.1 mg mass) launch themselves into the air by rapidly unfolding and impacting their tail-like appendage (furcula) against the ground (or water surface) while anchoring to the surface using an adhesive tube-like organ located in the abdomen (the collophore), which acts via capillary action. During takeoff, semiaquatic springtails control their jumping directionality by simply changing the body angle with respect to the surface, in a similar way as an artillery cannon controls projectile elevation. Thus, collembolans can perform either vertical or horizontal jumps by maintaining positive or negative body angles, respectively (figure 7(A)). The furcula's stroke duration controls takeoff speed in semiaquatic springtails. A shorter stroke duration results in faster jumping. Impressively, individuals performing fast vertical jumps over the water can reach heights and horizontal distances up to ~ 20 and ~ 50 times the body length, respectively (Ortega-Jimenez *et al* 2022). It is worth noting that the collophore, which initially remains attached to the surface, acts as a stand, which

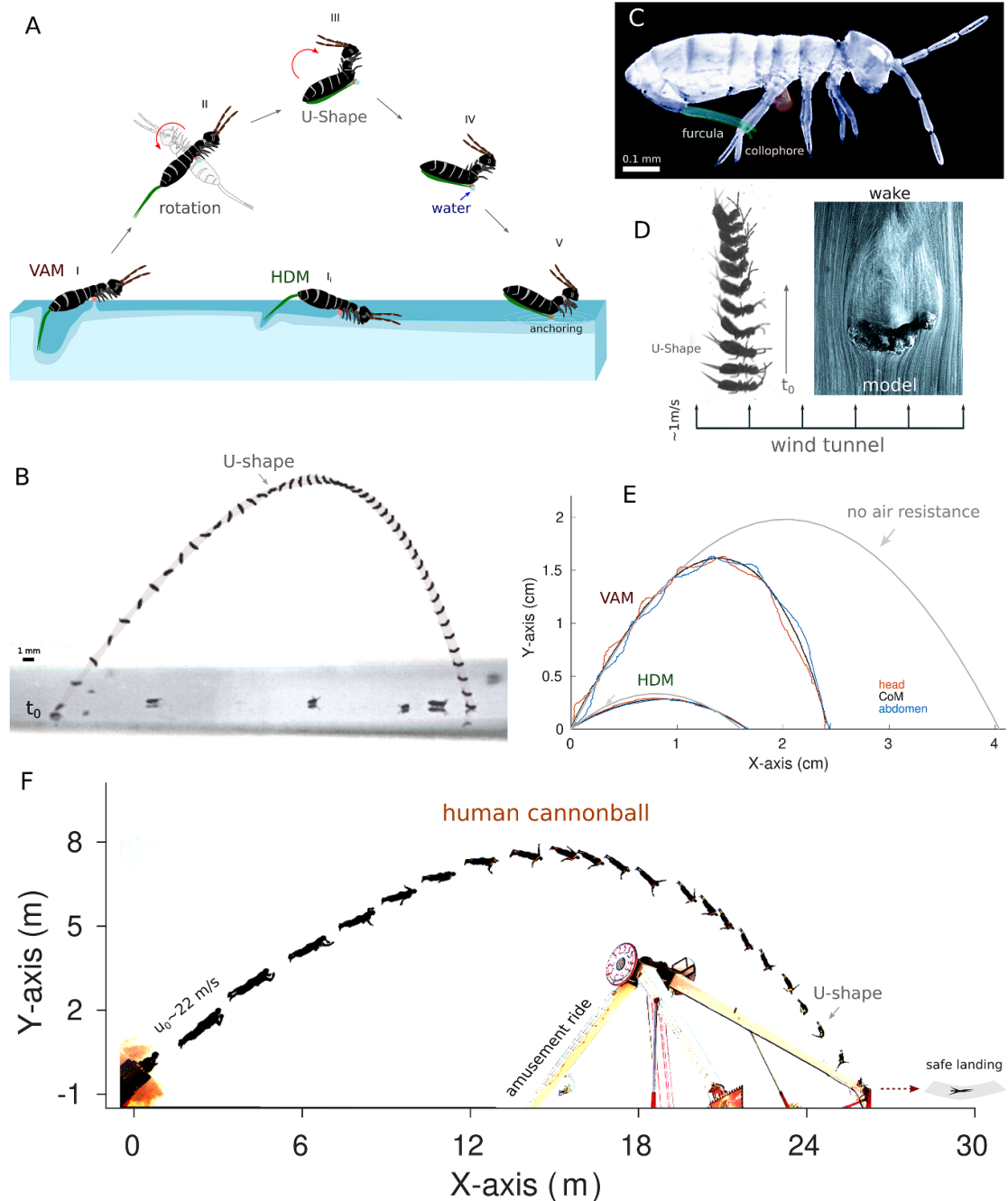


Figure 7. Springtails and human cannonball trajectories. (A) Drawing of a springtail showing all stages of vertical aerial motion (VAM): takeoff and water collected by the collophore (I), body rotation (II), U-shape formation and self-righting (III and IV) and adhesion landing (V). Horizontal directed motion HDM is shown in I. (B) Merged frames from a video showing how a U-shaped body stops body rotation and induces stable aerial righting. (C) Springtail showing furcula (green) and collophore (red). (D) Left: frame-by-frame image of a springtail recovering from an upside-down position in a vertical wind tunnel. Interval between frames is 1.2 ms. Right: wake produced by a physical model. (E) VAM and HDM jumping trajectories of the head (red), center of mass (black) and abdomen (blue). Gray lines show ballistic trajectories (with no air resistance), for VAM and HDM, with initial speeds of 0.7 and 0.4 m s⁻¹, as well as takeoff angles of 60° and 40°, respectively. Notice the marked differences between real and ballistic trajectories for VAM. By contrast, for HDM the difference is minimal. Ortega-Jimenez *et al* (2022). Copyright © 2022 the Author(s). Published by PNAS. This article is distributed under Creative Commons Attribution-Non Commercial-No Derivatives License 4.0 (CC BY-NC-ND). (F) Human cannonball David Smith launching at 22 m s⁻¹ and landing safely on his back. Filmed by VMO-J at the North Georgia State Fair 2022. Notice that David Smith curves his body just before landing similarly to the springtails despite the associated higher Re.

can also help to maximize the tension of the furcula against the water surface. By controlling their launching directionality and impulse in this way, these springtails can move horizontally or vertically at will

(figures 7(A), (B), and (E)). Springtails moving horizontally can practically glide over the water's surface, even without detaching their ventral tube. These organisms can skate over the water surface at similar

rates and produce similar vortical wakes as juvenile water striders (Gerridae).

Once airborne, springtails have been observed to spin in the air at high rates similar to the wing flapping rates of insects. Remarkably, these small wingless animals can stop their body rotation and right themselves in mid-air by adopting a U-shaped posture. Experiments in a vertical wind tunnel have shown that this sudden postural change allows them to produce aerial righting in less than 20 ms, the fastest such righting ever measured in wingless animals (figure 7(D)). It is worth noting that during the takeoff, the colophore (organ on the underside of the springtail's body) retains water equivalent to $\sim 3\%$ of the body mass, which further lowers the center of gravity and contributes to the stability provided by the U-shaped posture. This combination of posture and retained water allows springtails to quickly and effectively right themselves and maintain postural stability in the air.

2.3. Aerial righting in nematodes

Entomopathogenic nematodes are small and highly specialized jumpers widely used in agriculture to control specific pest populations. These nematodes are ambush predators that can stand upright on the soil, but can also catapult themselves into the air in response to certain stimuli to reach their insect host (Hallem et al 2011, Baiocchi et al 2017). While much research has been conducted on the first stages of takeoff in these nematodes (Reed et al 1965, Campbell et al 1999, Dillman et al 2021), their aerial and landing phases were largely previously unexplored. Here we briefly describe our findings on the landing phase of these entomopathogenic nematodes (data are shown as average $\pm$ one sd, with $n = 6$).

Steinernema carpocapsae nematodes have a length of 0.5 ± 0.1 mm and a diameter of 28 ± 5 μm . After takeoff, they can rotate in the air at very high rates of ~ 1 kHz (figure 8). In only 17 ± 3 ms, they reach a maximum height (h_{max}) of up to ~ 16 times their body length. While airborne, these nematodes maintain a curved body posture, with the head at $\sim 80^\circ$ relative to the longitudinal body axis, resembling the U-shaped posture of skydiving springtails (figure 7(A)). The spinning rate of the nematodes decreases significantly before they enter a period of free fall (figure 8(A)). In less than 40 ms during this free fall, the nematode reaches a constant posture angle θ_{CL} of $130 \pm 12^\circ$ and a terminal velocity (V_{term}) of 150 ± 40 mm s^{-1} (figures 8(B) and (C)). This speed is three times slower than that reached by falling dandelion seeds (Cummins et al 2018). In all recorded sequences, the nematodes land head-first while maintaining this postural angle (θ_{CL}) (figure 8(C)). The free fall takes 80 ± 20 ms to reach the ground. Interestingly, if we use the equation of

motion $h = ut + 0.5gt^2$, where h is height, u is initial velocity, g is the acceleration due to gravity, and t_{Lt} is time, the theoretical landing time t_{Lt} would be about half the duration of the actual landing time (t_{L}) for the descending nematode. Since the equation ignores air friction, this result suggests that aerodynamic drag forces on the nematode's body increase the landing duration, which may serve to reduce impact force and also enhance aerial dispersion in the presence of horizontal air currents. The role of aerodynamic drag during landing can be further reinforced by calculating the dimensionless Reynolds number Re , the ratio of inertial to viscous forces. Taking the kinematic viscosity of air as $1.5 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$, the terminal velocity as $150 \pm 40 \text{ mm s}^{-1}$, and the body diameter of the worm as $30 \mu\text{m}$, we obtain $Re \sim 0.1\text{--}0.3$ indicating that viscous forces dominate the nematode's free fall. All landing experiments were conducted in a small fully enclosed chamber with no ambient airflow.

We also observe that during landing, the nematodes drift horizontally from their expected landing position, as shown in figures 8(A) and (B). To understand the physical origin of this drifting behavior, we model these nematodes using slender-body theory, approximating the nematode as a slanted axisymmetric rod translating in a quiescent viscous fluid. When a slanted rod is in motion with a velocity U and an angle β , it experiences two forces: a downward body force (F_b) and an opposing drag force (F_D) (Leal 1975). Following Leal (1975), the forces in the direction of landing can be used to estimate the horizontal landing drift of the nematodes theoretically.

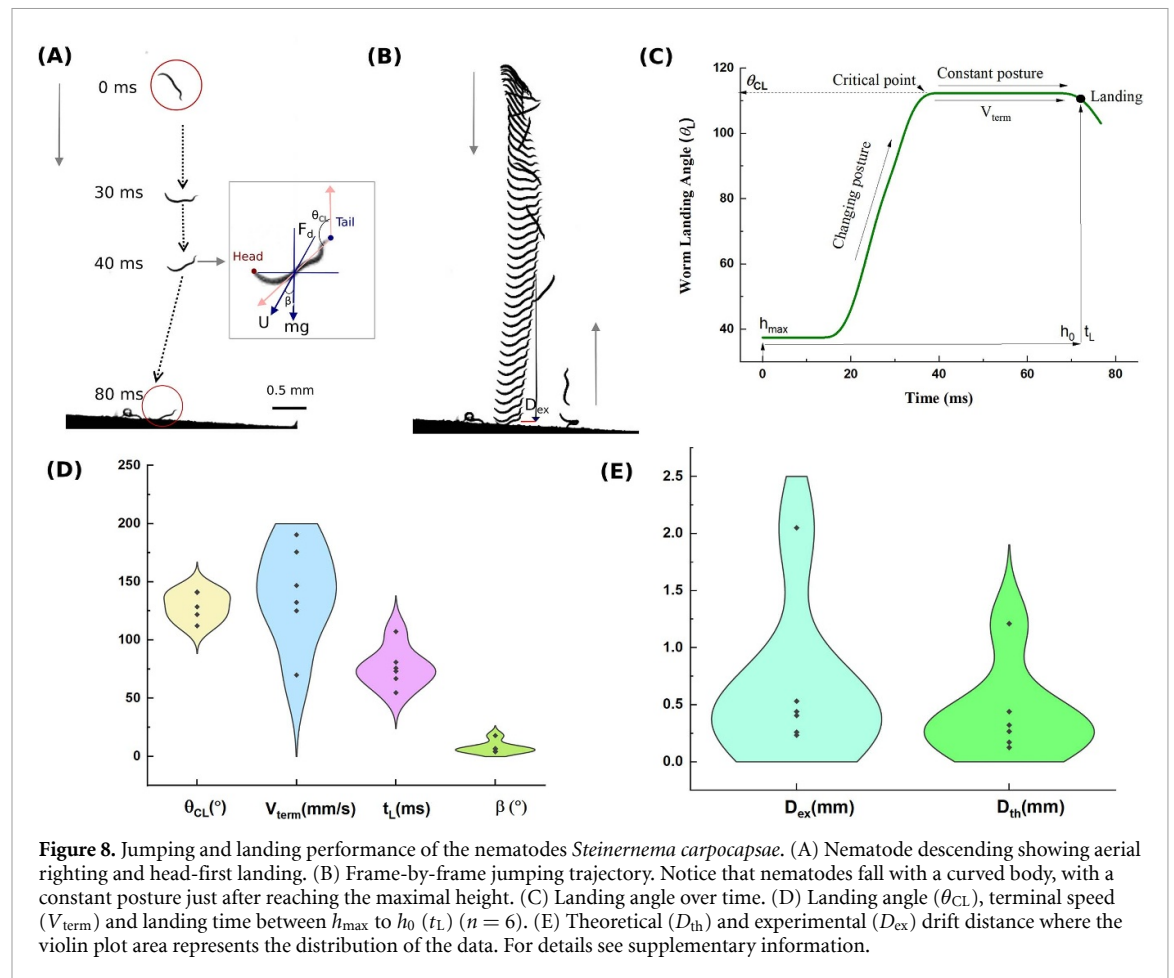
$$F_D = F_b \cos \beta \quad (1)$$

$$F_D = \frac{4\pi L \mu U}{\ln(\epsilon)} \quad (2)$$

where ϵ is the ratio of a/L , a is diameter and L is length, μ is air viscosity, U is terminal landing velocity in the direction of motion, and m is the mass of the nematode (2.18×10^{-10} kg).

$$\frac{4\pi L \mu U}{\ln(\epsilon)} = mg \cdot \cos \beta. \quad (3)$$

The theoretical terminal landing velocity (U) is calculated by equation (3) in the direction of motion and is approximately 51.5 mm s^{-1} , within the range of the measured settling velocity of the nematode (figure 8(D)). Using U and the range of β 's measured ($7.8^\circ \pm 5.1^\circ$), the theoretical drift distance (D_{th}) is calculated using $D_{\text{th}} = t \cdot U \cdot \sin \beta$. The resulting theoretical drift distance is in good agreement with the experimental results shown in figure 8(E). It is worth noting that the drift of nematodes is likely to be relatively small compared to larger organisms due to their small size and mass. However, drift can still



play a role in the movement of nematodes through the air and may be important to consider in specific applications involving nematodes, such as pest control and microscale aerodynamics. Additionally, nematodes often land headfirst and without rebound (due to their sticky cuticle), allowing them to immediately parasitize target insects. Our results reveal how the high aspect ratio of the nematode's body, their slanted posture, and the consequent viscous air drag influence the landing dynamics of these entomopathogenic nematodes.

2.4. Aerial righting in plant seeds

Plants may have evolved flight capabilities even earlier than insect fliers, particularly to aid in seed dispersal. Anemochory, the dispersal of seeds by wind, can sometimes span hundreds of kilometers (Seale *et al* 2022). For example, aerial seeds such as those of dandelions and samaras (e.g. pine and maple) have structures that allow them to generate aerodynamic forces and recover from upside-down positions during free fall (Ortega-Jimenez *et al* 2019, Seale *et al* 2022). Dandelion seeds have a feather-like structure called a pappus that allows them to travel great distances. In contrast, samaras have wing-like structures attached

to their nuts enabling them to autorotate like an autogyro helicopter. Dandelion, pine, and maple seeds are able to recover from an upside-down position in less than 80 ms, 120 ms, and 150 ms, respectively.

Recently, millimeter-sized porous disks based on dandelion seeds have been developed that are solar-powered and capable of measuring environmental parameters (e.g. temperature, humidity, and pressure). These flat devices can land upright 95% of the time and reach similar rates of descent to their biological counterparts (Iyer *et al* 2022).

2.5. Aerial righting in humans

Similarly to cats and geckos, human gymnasts use their bodies and limbs to correct their orientation in mid-air. However, landing can be challenging for gymnasts, responsible for 70% of all gymnastics injuries (Sheets 2007). The ground reaction forces during the collision can be as high as ten times the body weight, while the athlete rotates in mid-air at rates of $\sim 1000^\circ \text{ s}^{-1}$ (Cuk and Marinšek 2013). It is rare for gymnasts to achieve perfect landings during international competitions (Marinšek 2010), which can significantly impact the final rankings. Similar percentages of injuries have been reported for ski jumping (Bessone and Schwirtz 2021) and freestyle

skiing (Fu *et al* 2022), where landing on an inclined slope is performed at speeds of $\sim 20 \text{ m s}^{-1}$.

One extreme example of catapulting in humans is the so-called ‘Human Cannonball’, who must perform safe landings after being launched through the air. VMO-J had the opportunity to film the Human Cannonball (David Smith), who was launched at $\sim 22 \text{ m s}^{-1}$ and $\sim 10 \text{ m}$ in height over the amusement rides at the North Georgia State Fair 2022. He seemed to use extended arms moving in circles for stabilization, similar to the movements of stick insects and amphibians. Interestingly, before he reached the safety net located $\sim 30 \text{ m}$ from the cannon, David bent his body like the posture used by springtails, which appears to be effective in changing his head-first vertical orientation to a horizontal posture (figure 7(F)). Thus, it seems that human cannonballs may use a combination of inertial and aerodynamic forces to correct their position in the air, similar to wingless organisms. Landing vertically and head-first could be fatal otherwise. Further research on how humans exploit inertial and aerodynamic forces when launched or descending at high speeds is necessary to fully understand their aerial righting and safe landing performance.

3. Landing success

Landing is traditionally defined as the final phase of a flying animal’s return to the ground or other substrate. Surprisingly, animals without wings can also achieve as high as 90% effectiveness in landing. For example, geckos that were $\sim 9 \text{ cm}$ in size and launched from a height of 7 m landed safely 87% of the time, even when approaching tree trunks head-first at a speed of $\sim 6 \text{ m s}^{-1}$ (Jusufi *et al* 2008). They used their tails to stabilize their descent. Similarly, wingless insects such as pea aphids, which are only 4 mm in size, can land on their feet up to 95% of the time while falling at terminal speeds of $\sim 4 \text{ m s}^{-1}$ (Ribak *et al* 2013). However, landing effectiveness decreases down to 60% at lower heights (Ribak *et al* 2013). Spotted lanternfly nymphs, which are $\sim 1 \text{ cm}$ in body length and fall at terminal speeds of $\sim 3 \text{ m s}^{-1}$, can land upright with a success rate of up to 67% (Kane *et al* 2021). Springtails, which are millimeter-sized animals, can land ventrally with success rates of up to 85% after jumping vertically and hitting the water’s surface at a speed of 1 m s^{-1} (Ortega-Jimenez *et al* 2022). Even uncontrolled landings and subsequent bouncing may allow springtails to escape capture by slower or ambush predators under certain conditions.

3.1. Vertebrates

Landing can be risky for wingless vertebrates because the reaction forces of a collision with the ground can be significantly greater than the animal’s body

weight. In comparison, for animal fliers, such as starlings during perching, landing reaction forces are often only twice their body weight (Bonser and Rayner 1996). To mitigate these risks, wingless animals such as humans and cats (McDonald 1960) use their limbs, joints, and postural changes to absorb kinetic energy during high-impact landings. Many animals also use claws or special sticky pads to anchor themselves upon impact and thus prevent bouncing. For example, tree frogs often land on their soft bellies unless landing on narrow branches, in which case they use their sticky toe pads (Emerson and Koehl 1990, Bijma *et al* 2016). *Aneides* salamanders maneuver to stay upright until they land via an abdomen-first bellyflop, similar to tree frogs (Brown and Deban 2020). When landing, the region near the pectoral girdle is typically the first to touch down, followed quickly by the trunk and head, the pelvic girdle and hindlimbs, and finally the long tail bent towards the back (figure 4(A)).

In the case of flat-tail geckos, despite their well-documented ability to cling to surfaces using van der Waals forces (Autumn *et al* 2002), they risk becoming dislodged as they land post gliding, relying on their tails not only for midair steering (Jusufi *et al* 2008, 2010), but tails are also found by Ardian Jusufi and colleagues to ultimately be used as a postural stabilizer to cushion hard tree landings (figures 9(A)–(F)). These unspecialized geckos can impact surfaces near terminal velocity ($\sim 6 \text{ m s}^{-1}$) during the ‘Fall Arresting Response’, often without the deceleration observed in some other arboreal gliding animals. Geckos instead employ a mechanically mediated landing strategy involving rolling down a vertical substrate along their ventral surface from head to tail, culminating in a large pitchback with only the tail and hind limbs attached to the tree (Siddall *et al* 2021b). This strategy allows for a more gradual deceleration, with the tail reducing the attachment forces required at the rear feet. Materials and systems relationships are also important aspects for biorobotic experimental validation (Chellapurath *et al* 2022).

Systematic experiments with different torso and tail stiffnesses determined landing performance with soft physical models of gliding geckos *H. platyurus* at scale revealed that a flexible back and a stiff tail as the appropriate combination to allow for landing energy to be dissipated, thus enabling a mechanically and materials mediated landing (figures 9(A)–(F), Chellapurath *et al* 2022).

3.2. Invertebrates

Little attention has been paid to landing reflexes or maneuvers in wingless invertebrates, or their interactions with the substrate during landing. Body size serves as a principal parameter in aerial maneuvering given that larger gliders descend at higher speeds

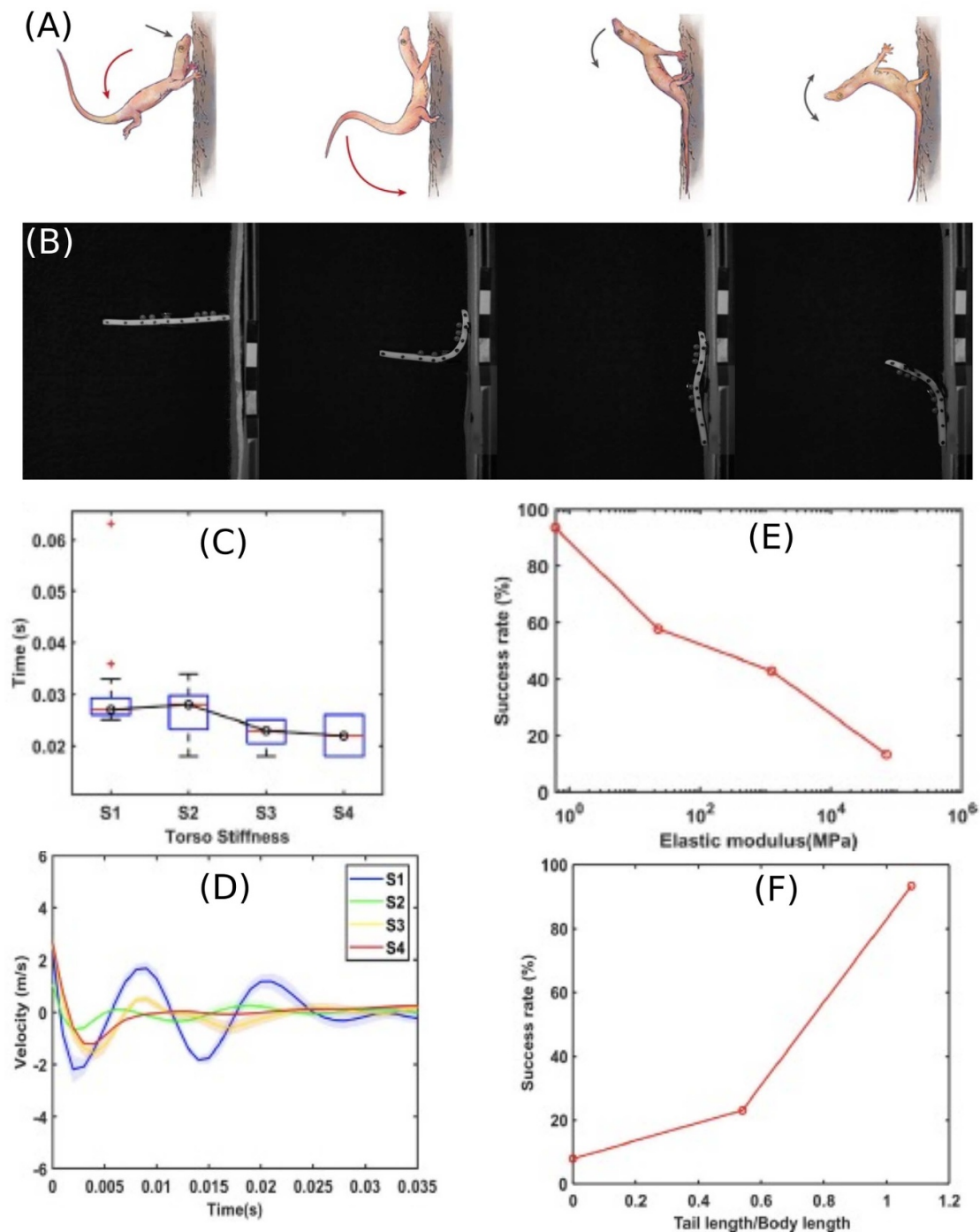


Figure 9. Geckos landing on a vertical surface after a glide using the Fall Arresting Response (FAR). (A) Illustration of Asian Geckos approach their landing site of a rainforest tree trunk at near terminal velocity and collide headfirst. They reduce landing forces by rolling down the tree and pitching backwards, allowing them to dissipate impact energy over a greater window. Adapted from Siddall *et al* (2021b), with permission from Springer Nature. (B) Panels illustrate the postural sequence of the fall arresting response in the gecko inspired soft physical model at scale. Reproduced from Chellapurath *et al* (2022). CC BY 4.0. (C) Time between the collision of head and hindlimbs and the success rate of each torso stiffness model. (D) Velocity profile of gecko inspired soft robotic physical models landing on a wall. Physical model at scale of Asian Flat Tailed gecko. (E) Tail length to body length ratio followed by their perching success rate. (F) Bounce back behavior of the tail for all tail stiffnesses, followed by their perching success rate.

(e.g. McGuire and Dudley 2005). In the field, gliding ants and spiders directly strike the landing target and sometimes bounce off if their first attempt fails (Munk *et al* 2015, Yanoviak *et al* 2015). In contrast, aphids did not exhibit obvious landing maneuvers under laboratory conditions. Gliding stick insects

use their forelegs for contact and adhesion during landing (figure 6(E)). The limited existing evidence suggests that wingless arthropods tend to land with passive shock absorption and adhesion through their appendages, partly due to the mechanical properties of their legs' and body's exoskeleton,

including stiffness and damping (Jayaram *et al* 2018, Schmitt *et al* 2018). Additionally, neuromechanical constraints, such as visual acuity during landing, may, in principle, limit rapid and actively controlled landing responses. Leaves and other flexible vegetational structures may also absorb impact forces during collisions. The interaction between natural landing substrates and the tarsi of arthropods warrants future investigation, particularly regarding how contact dynamics scale with body size.

Semiaquatic springtails have been observed landing and then firmly adhering to the water's surface. The ballistic jump of springtails (suborder Entomobryomorpha) follows a non-parabolic and asymmetric trajectory, traveling almost in a straight line before falling, as if they hit an aerodynamic wall (Cohen *et al* 2014). This 'triangular' trajectory, as described by Tartaglia's studies on artillery ballistics (Cohen *et al* 2014), allows semiaquatic springtails to fall almost vertically onto the water's surface at an angle of 84° , preventing any horizontal skipping (figure 7(E)). As they approach the water's surface, springtails adopt a U-shaped posture, exposing their colophore prior to impact (figure 7(A)). Upon impact with the water (at a speed of $0.5 \pm 0.1 \text{ m s}^{-1}$), springtails generate hydrodynamic forces mainly due to surface tension and inertia (Bond number, $Bo \sim 10^{-2}$, Weber number, $We \sim 1-7$). The inertial impact deforms the water surface without piercing it, generating dissipative capillary waves. Springtails use their hydrophilic colophore to rapidly anchor to the water's surface and to avoid bouncing off due to the recoil of the deformed air–water interface (figures 10(A) and (B)). As a result of this 'colophore landing,' springtails stabilize and quench oscillatory motion within $\sim 5 \text{ ms}$ post-impact (Ortega-Jimenez *et al* 2022). By contrast, in the rare case of a non-colophore landing (i.e. dorsal, lateral, or head-first landings), springtails dramatically bounce off the surface of the water (figure 10(C)). For these failed and uncontrolled landing trials, the reset time for subsequent jumping increases by up to one order of magnitude, increasing the risk of predation.

4. Self-righting robots and technological innovations

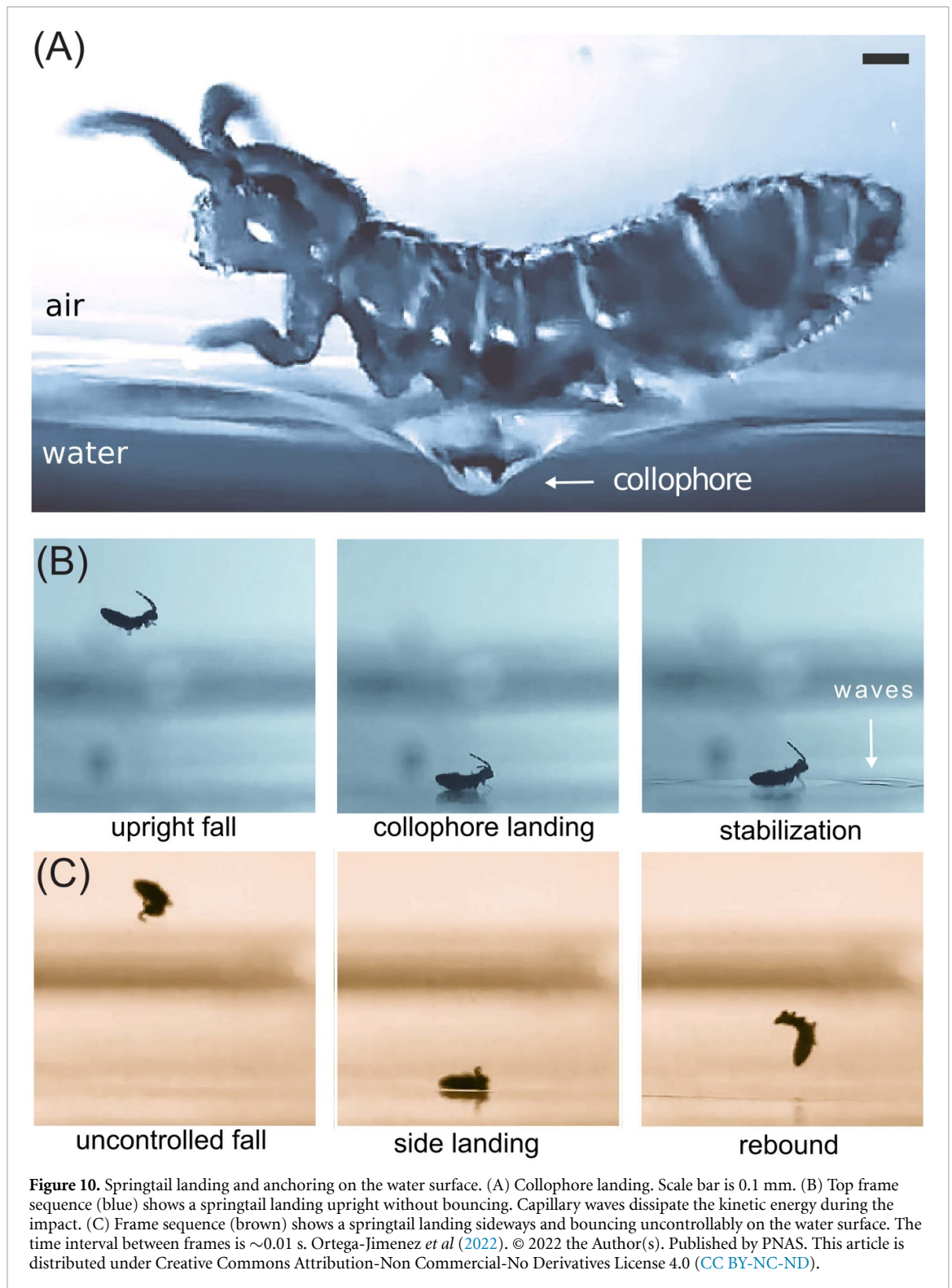
Self-righting physical models have been used to gain insight on how animals reorient from a supine to a prone posture in free fall (Jusufi *et al* 2010, 2011). Self-catapulting robots have been designed in recent decades based on both natural (Hu *et al* 2007, 2010, Noh *et al* 2012, Koh *et al* 2015) and artificial jumping systems (Zhao *et al* 2013, Hawkes *et al* 2022). The most advanced launching device ever created, based on work multiplication (i.e. multiplying the energy that can be stored in a spring), can reach a height of

~ 100 times its length in $\sim 3 \text{ s}$ (Hawkes *et al* 2022). Despite these technological achievements, most bio-inspired catapulting systems lack aerial righting and landing control systems, which are essential for reducing rotation, avoiding structural damage, or simply preparing for the next jump.

Some robotic jumpers can right themselves once on the ground after an upside-down landing. To correct their posture, they use either motorized levelers deployed against the ground (Jung *et al* 2019) or the force due to gravity (Ma *et al* 2021). Robots with the ability to control pitch in mid-air have been successfully designed based on the inertial responses of the tail (Libby *et al* 2012, Haldane *et al* 2016) and the elongated tails of lizards and geckos during jumping and descending, respectively (Jusufi *et al* 2008, 2010, Siddall *et al* 2021a). These tailed robots can tilt their bodies by simply rotating or moving their tails up or down while airborne. Increasingly the biorobotic physical models for the study of bending torsos and appendages in locomotion neuromechanics are leveraging advances from soft active materials (Siddall *et al* 2021c) and sensors (Schwab *et al* 2021, 2022).

4.1. The springtail robot that lands upright

Springtails have long inspired the design of jumping mechanisms in robots, given their impressive jumping performance (Li *et al* 2012, Sudo *et al* 2013, Zhakypov *et al* 2019). Recently, Ortega-Jimenez *et al* (2022) reported that semiaquatic springtails have the ability to right themselves in midair, resulting in near-perfect landing success rates (85%). Based on these findings, a robophysical model capable of postural control while jumping was developed. The robot launches itself using a torque-reversal catapult mechanism and uses drag flaps and additional weight added ventrally to enhance aerial control (figure 11). In general, its jumping performance consists of three phases: (1) a reaction with the ground, which initiates takeoff; (2) an aerial phase; and (3) a landing phase. The robot is less than $\sim 100 \text{ mg}$ (the drag flaps and additional mass weigh $\sim 10 \text{ mg}$ each) and is 20 mm in length. Robots without and with drag flaps and additional mass can jump to heights of ~ 25 and ~ 18 times their size, respectively. By contrast, the robot without additional mass rotates uncontrollably until it lands due to the inertial torque initially generated by directional jumping. Drag flaps only exert a small effect; the rotational speed of the robot with drag flaps only is reduced by $\sim 29\%$ through aerodynamic torque. The jumping robot (with drag flaps + additional mass) can right itself in mid-air in less than 128 ms (figure 11(B)), similar to the postural correction time shown by wingless insects. Additional weight further reduces the rotational speed and turn number of the robot (figure 11(C)), with the added

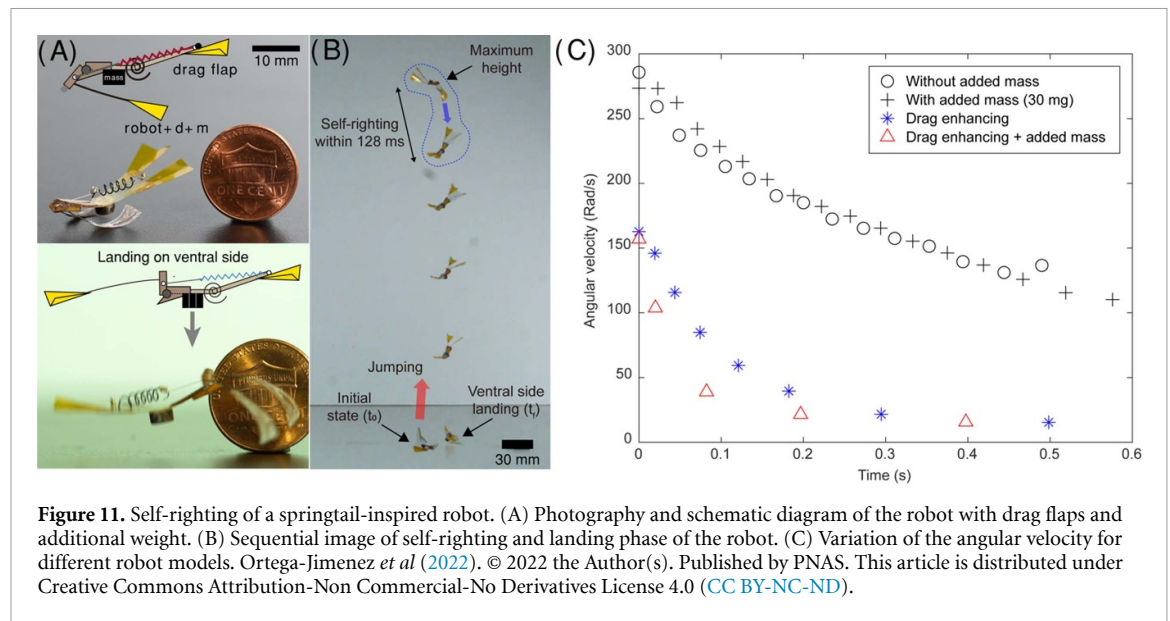


benefit of enhancing the robot's ventral landing by lowering the center of gravity.

4.2. Shuttlecocks

Shuttlecocks (or 'birdies') have been used in the sport of badminton since the 19th century. These projectiles, which have a mass of 5 g and a length

of 7 cm, are unique because they consist of a ball (made of cork or rubber) attached to a conical skirt of either natural or synthetic feathers. During free fall, a shuttlecock takes up to ~ 400 ms to right itself. By contrast, righting takes only ~ 100 ms when the shuttlecock is propulsively launched at $\sim 5 \text{ m s}^{-1}$ (figure 12(F)). Because these projectiles are designed



to travel at higher speeds (up to $\sim 117 \text{ m s}^{-1}$) after being struck by the racquet, the righting duration can be as little as 40 ms (Texier *et al* 2012). Shuttlecocks are also impressive in their ability to decelerate, capable of speed reductions of one order of magnitude from $\sim 70 \text{ m s}^{-1}$ to 7 m s^{-1} in less than 0.6 s (Hubbard and Cooke 1997). This reduction is solely an effect of drag production, a function of the shuttlecock's cone porosity (Alam *et al* 2015). The trajectory of these projectiles at high speeds is asymmetrical and resembles a skewed parabola or Tartaglia curve (Cohen *et al* 2014). Shuttlecocks with a skirt made of feathers have 60% larger drag coefficients than those with covered skirts (Alam *et al* 2015). This difference is congruent with recent results on dandelion seed aerodynamics, which show that the porosity of the pappus increases the drag coefficient, which has a stabilizing effect on the vortex ring, in comparison with that of a solid disk (see figure 2 from Cummins *et al* 2018). The wake produced by a shuttlecock, with a skirt made of mesh, placed in a wind tunnel resembles that of a dandelion (figure 12(F), video S1). Given their exceptional righting ability, design inspiration from badminton shuttlecocks could help effectuate rapid aerial righting in future jumping robots.

5. Concluding remarks

In the natural world, it is unsurprising that winged animals universally perform both aerial maneuvering and controllable landings. However, these aerial skills are not exclusive to animal flyers. A growing body of evidence is demonstrating that many organisms without wings, over a range of length scales (from millimeter to meter), are able to correct adverse mid-air body orientations and land successfully in a matter of milliseconds (from 20 ms to $\sim 400 \text{ ms}$) (table 1). Wingless animals have evolved

the ability to control their landings, enabling them to reduce injury, enhance survival against predators, and even disperse.

Slender, rod-like organisms of tiny size, such as parasitic nematodes, are able to suddenly stop their extreme body rotations ($\sim 1 \text{ kHz}$) by maintaining a curved body posture while descending at incredibly low terminal speeds (lower than those of aerial seeds) and finally landing head-first on their host. Springtails, arthropods the size of a grain of sand, can contort their body and use a collected water droplet on their adhesive ventral tube to gain aerial control and land on their feet. Centimeter-sized insect nymphs, such as those of stick insects, adopt a skydiving posture and use their legs to right themselves during free fall.

Small vertebrates with body lengths on the decimeter scale, such as arboreal salamanders and geckos, have a remarkably similar body plan. Both groups demonstrate aerial control using inertial forces based on body posture and corrective movements of their long tails. Flying snakes (length $\sim 1 \text{ m}$) which have no limbs, can correct unfavorable orientations during falling (figure 5(C), video S1), 'swim' through the air, and land tail-first (on the ground). Cats, squirrels, and humans use their appendages and rapid twisting of their bodies to conserve angular momentum while righting themselves during a fall. When artificially catapulted (or launched) into the air at high speeds, humans can bend themselves in mid-air to gain a favorable orientation and land safely using a combination of inertial and aerodynamic forces. Similarly, sport projectiles and plant seeds, such as dandelion seeds, can right themselves passively, without active body deformations, using aerodynamic forces. Powerful jumping robots are a technological achievement, and recent bio-inspired designs can control landings based on mechanisms similar to those used

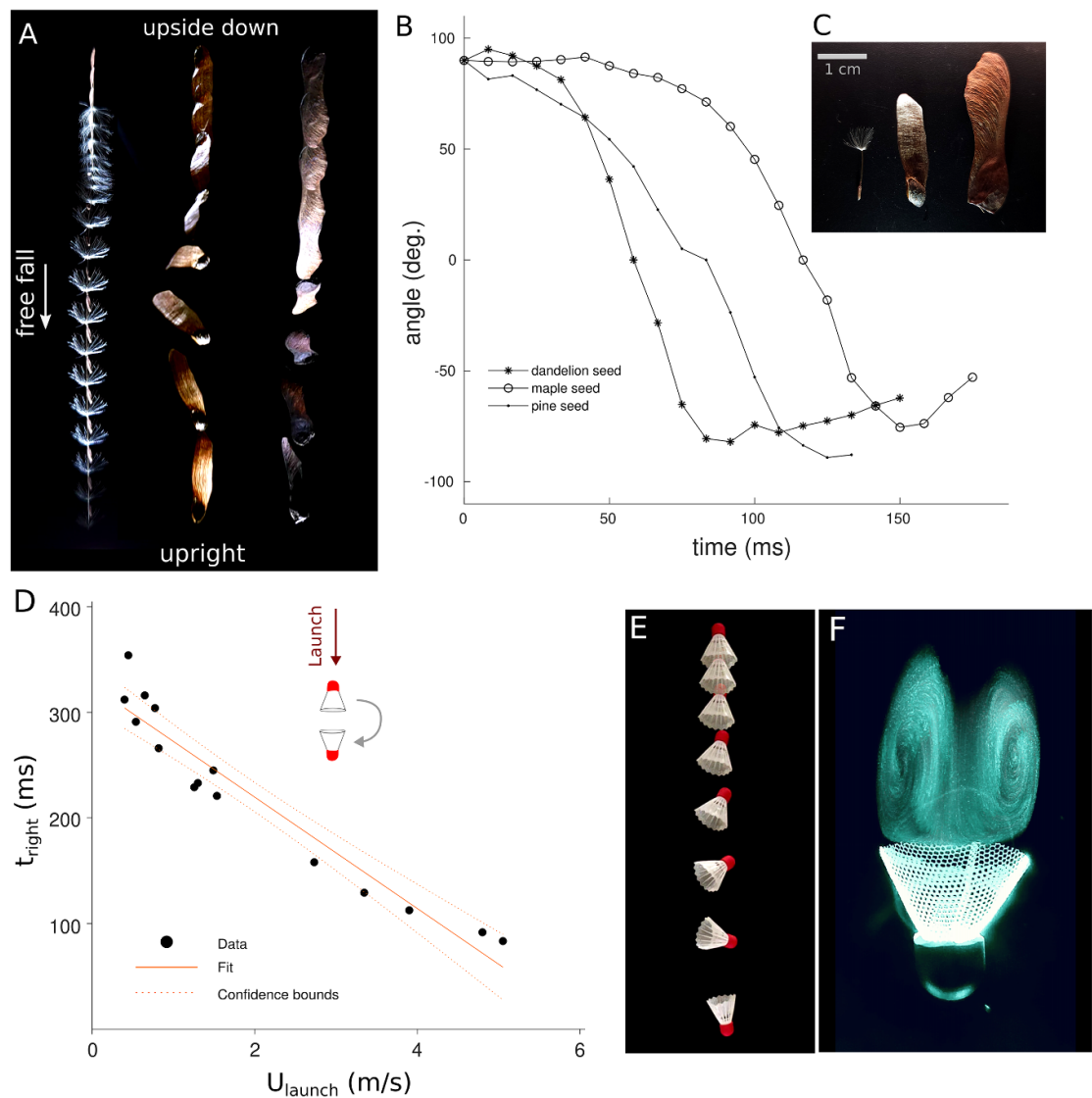


Figure 12. Plant seeds and shuttlecock during free-fall. (A) Frame-by-frame pictures of dandelion, maple, and pine seeds during free fall; the interval between frames is 8.2, 4.3, and 4.3 ms, respectively. Each seed was released with an upside-down orientation. (B) Time series of the seed orientation angle. Upside-down recovery happened at 80, 120, and 150 ms, for the dandelion seed, pine seed and maple seed, respectively. Surprisingly, self-righting in samaras seems faster than that observed in insects. (C) Photograph of the tested seeds. (D) Shuttlecock launched vertically downwards. The plot shows that righting duration decreases with initial launching speed ($t_{\text{right}} = -52 \times U_{\text{launch}} + 325$, $r^2 = 0.92$). The continuous and broken lines represent linear fit and the confidence interval (95% CI), respectively. (E) A shuttlecock (8 cm size) rights itself in 400 ms during free fall. (F) Visualization of a shuttlecock's wake produced in a wind tunnel (see video S1). The skirt of the shuttlecock was made of mesh. For details see supplementary information.

by wingless organisms. Examining aerial stability and controlled landing may help contribute to a new paradigm of robots that can jump repeatedly, covering larger distances and protecting fragile onboard electronics, instead of one-shot jumping systems that impact destructively on landing.

However, these discoveries and technological innovations have not yet been tested under natural environmental conditions. Factors such as wind magnitude, flow turbulence, thermal convection, precipitation, and electrostatic force can all influence the

aerial maneuvering and landing of wingless animals. Therefore, there is still much to be explored and discovered about aerial maneuvering and the effects of environmental conditions. The study of aerial maneuvering, landing, and anchoring in basal insect hexapods can also reveal biomechanical details relevant to the origin of insect flight. Overall, new research on such biological movements will further our understanding of the art of aerial control and landing in animals that seem designed not to fly.

Table 1. Morphological, righting and landing information from wingless organisms, aerial seeds, a sport projectile, and a springtail-bot. Information for the flying snake refers to ground landings only.

ID	Mass	Size	Righting duration	Landing orientation	Attachment	Righting mechanism	References
Nematodes	0.2 μ g	0.5 mm	<40 ms	Head first	Adhesive cuticle	Aerodynamics	Here
Springtails	0.1 mg	1 mm	<20 ms	Ventral	Collophore, legs	Aerodynamics/ Extra mass	Ortega <i>et al</i> (2022)
Aphids	4.2 mg	4.2 mm	170 ms	Ventral	Claws, adhesion	Aerodynamics	Ribak <i>et al</i> (2013), Lees and Hardie (1988)
Stick insect nymphs	25 mg	1.7 cm	200 ms	Head first	Forelegs/ Adhesion	Aerodynamics	Zeng <i>et al</i> (2017)
Climbing salamanders	3–11 g	~8 cm body, ~7 cm tail	116 ms	Ventral	Feet/ Mucous adhesion	Inertia	Brown <i>et al</i> (2022), Hanna <i>et al</i> (2021)
Tree frog	37 g	80 mm body, 127 mm leg	42 ms	Ventral	Adhesive toe pads	Inertia	Meng <i>et al</i> (2019), Wang <i>et al</i> (2013), Wang <i>et al</i> (2022)
Flat-tailed geckos	~3 g	5 cm body, 5 cm tail	100 ms	Head first (tree trunk)	Van der Waals forces of sticky toe pads	Inertia	Jusufi <i>et al</i> (2010, 2011)
Flying snakes	~100 g	1 m	<500 ms	Tail first	N/A	Inertia	Here, Socha (2011)
Gray squirrel	400 g	40 cm body, 20 cm tail	<300 ms	Ventral	Claws	Inertia	Fukushima <i>et al</i> (2021)
Domestic cat	4 kg	50 cm body, 30 cm tail	~300 ms	Ventral	Claws	Inertia	https://doi.org/10.1038/051080a0
Human cannonball	80 kg	1.80 m	800 ms	Horizontal landing	N/A	Inertial/ Aerodynamics	Here
Dandelion seeds	~0.5 mg	1.2 cm	80 ms	Seed first	N/A	Aerodynamics	Here
Pine seeds	17 mg	~2 cm	120 ms	Seed first	N/A	Aerodynamics	Here
Maple seeds	120 mg	~3 cm	150 ms	Seed first	N/A	Aerodynamics	Here
Shuttlecock	5 g	7 cm	400 ms	Ball first	N/A	Aerodynamics	Here
Springtail-bot	100 mg	2 cm	128 ms	Ventral	N/A	Aerodynamics/ Extra mass	Ortega-Jimenez <i>et al</i> (2022)

Data availability statement

All data that support the findings of this study are included within the article (and any supplementary files).

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Conflict of interest

We have no conflicts of interest to disclose.

Ethical statement

All experiments with animals were approved by their respective institutional research ethics committee. See text and references for details.

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