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Link to published version (if available):
10.1073/pnas.1510060112

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BIOLOGICAL SCIENCES: Plant Biology

Mechanism for rapid passive-dynamic prey capture in a pitcher plant

Short title: Passive-dynamic pitcher plant trap

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Abstract

Plants use rapid movements to disperse seed, spores or pollen, and catch animal prey. Most rapid release mechanisms only work once, and if repeatable, regaining the pre-release state is a slow and costly process. We present an encompassing mechanism for a rapid, repeatable, passive-dynamic motion used by a carnivorous pitcher plant to catch prey. *Nepenthes gracilis* utilizes the impact of rain drops to catapult insects from the underside of the canopy-like pitcher lid into the fluid-filled trap below. High-speed video and laser vibrometry revealed that the lid acts as a torsional spring system, driven by rain drops. During the initial downstroke, the tip of the lid reached peak velocities similar to fast animal motion and an order of magnitude faster than the snap traps of Venus flytraps and catapulting tentacles of the sundew *Drosera glanduligera.* In contrast to these active movements, the *N. gracilis* lid oscillation requires neither mechanical pre-loading nor metabolic energy, and its repeatability is only limited by the intensity and duration of rainfall. The underside of the lid is coated with friction-reducing wax crystals, making insects more vulnerable to perturbations. We show that the trapping success of *N. gracilis* relies on the combination of material stiffness adapted for momentum transfer and the anti-adhesive properties of the wax crystal surface. The impact-driven oscillation of the *N. gracilis* lid represents a new kind of rapid plant movement with adaptive function. Our findings establish the existence of a continuum between active and passive trapping mechanisms in carnivorous plants.

Significance

Carnivorous pitcher plants were thus far considered a classic example of passive, motionless pitfall traps. Here, we describe a rapid, passive-dynamic movement used by an Asian *Nepenthes* pitcher plant to capture insect prey. We show that the pitcher lid functions as a rain-driven torsion spring that combines material properties adapted for momentum transfer with a unique friction-reducing surface coating. Unlike other pitcher traps, this capture mechanism employs rapid movement. It also differs from the metabolically costly mechanisms of active carnivorous plants such as Venus flytraps because the movement is externally driven. It therefore represents a new kind of rapid plant movement that challenges the conventional distinction between active and passive carnivorous plant traps.

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Introduction

The rapid trap closure of the Venus flytrap prompted Charles Darwin to call it the 'most wonderful plant in the world' (1). Arguably the most studied example, it is only one of many cases of plants employing rapid movement to trap insects. Often overlooked, the ability to move is as integral to plant life as it is to animals. From the reorientation of leaves and growth axes in response to external stimuli such as light, wind and gravity (2) to the opening and closing of stomata (3), many plant movements are driven by changes of osmotic pressure. As a result, these movements are limited by the speed of diffusion (4) and often too slow to be observed without the help of time-lapse recordings. In contrast, the rapid movements used to disperse seed (5), spores (6) or pollen (7) as well as the movement-based trapping mechanisms of carnivorous Venus flytraps (8) and

bladderworts (9) rely on the rapid release of stored elastic energy. While these movements can achieve extraordinary speeds (10), they often rely on single-shot mechanisms or, where repeatable, require considerable time and energy to regain the pre-release state.

Carnivorous plant traps are conventionally divided into 'active' (= moving) and 'passive' (= immobile) traps. Examples of active traps are the snap traps of *Dionaea muscipula* (Venus flytrap) and *Aldrovanda vesiculosa*, the suction traps of bladderworts (genus *Utricularia*) and the moving flypaper tentacles of *Drosera* sundews (11). A common feature of these traps is their reliance on rapid movements that are triggered by the prey and activated through electrophysiological signaling processes (12-17). In contrast, passive traps do not move and rely entirely on physical obstructions, slippery surfaces and sticky secretions to capture prey (11). The pitchers of Asian *Nepenthes* plants (Figure 1) are classic examples of passive carnivorous traps.

Around 120 *Nepenthes* species are distributed across the perhumid tropical regions of Southeast Asia (18). Like other carnivorous plants, they are found in habitats where nutrients are scarce, but light and water are abundant. The ability to derive nitrogen and phosphorus from trapped insects enables pitcher plants to thrive where most other plants fail. Prey is attracted to pitchers by visual and olfactory cues (19-22) and lured to the slippery trapping surfaces by the secretion of sugary nectar (23-25). The ubiquitous trapping surface is the upper pitcher rim, called peristome. It offers safe access to nectar when dry but turns into a deadly slide for insects when wet (26, 27). Once trapped, prey is prevented from escaping by the often viscoelastic pitcher fluid (28, 29) or by anti-adhesive wax crystal surfaces on the inner pitcher wall (30-32). Fluid viscoelasticity and wax crystal surfaces are only present in a subset of *Nepenthes* species and are often mutually exclusive (33, 34).

The pitcher lid is generally regarded as a protective structure against rain flooding the pitcher. In *N. gracilis*, the lid has an additional adaptive function as a trapping device. In this species only, the lower lid surface is covered with a crystalline epicuticular wax layer which superficially resembles the inner wall coating (35). However, the lid wax crystals are structurally different from those on the inner wall. Bauer *et al.* (35) showed that *N. gracilis* allocates a higher proportion of its nectar production to the lower lid surface than the sympatric *N. rafflesiana*, a conventional peristome-trapping species. Insects can walk upside down under the *N. gracilis* lid and harvest nectar but they regularly get knocked off by the impact of rain drops and end up as prey in the pitcher. The experimental application of an anti-slip coating to the lower lid surface significantly reduced the prey capture success of *N. gracilis* pitchers in the field (35). The same treatment applied to wax crystal-free *N. rafflesiana* lids had no effect on prey capture (29), suggesting that the wax crystals are crucial for the trap function of the *N. gracilis* lid.

The present study unveils an additional and unique adaptation of the *N. gracilis* lid that goes beyond anti-adhesive wax crystals. Starting from the observation that the *N. gracilis* lid is more rigid than that of *N. rafflesiana*, we hypothesized that the material properties of the *N. gracilis* lid are adapted to facilitate prey capture by making use of the mechanical impacts of rain drops. To test this hypothesis, we used high-speed video analysis, non-contact vibration monitoring, and kinematic modelling techniques to investigate whether the impact response of the *N. gracilis* lid is different from that of the peristome-trapping *N. rafflesiana*. We further propose that this impact response allows *N. gracilis* to use momentum from falling rain drops to 'flick' insects into the pitcher – making it the only pitcher plant with a dynamic trapping mechanism. Capture trials and friction force

measurements with live ants were conducted to disentangle the effects of surface structure and material properties on trap performance.

Results

The pitcher lid of *N. gracilis* resembles a stiff plate articulated with a basal torsional spring. High speed video recordings revealed that *N. gracilis* lids (n = 12) responded to drop impacts with harmonic oscillations. The initial amplitude of these oscillations at the lid tip was 3.83 ± 3.09 mm peak to peak (mean ± s.d. used throughout). The oscillations were highly stereotyped even if the impact location was varied randomly. Three points along each lid (proximal, medial and distal) moved in phase, establishing that the lid did not bend but pivoted around a flexible hinge point in the pitcher neck (Figure 2A). In contrast, the larger and more compliant *N. rafflesiana* lids (n = 10) responded to the drop impact by bending, resulting in hardly any motion of the proximal half and more pronounced movement distally (initial tip amplitude = 2.23 ± 0.43 mm). While the *N. rafflesiana* lids bent easily, their average rotational stiffness was 2.5 times higher than that of the *N. gracilis* lids (Table 1). However, the *N. gracilis* lids are not only smaller (Figure 2A, C) but also much lighter, resulting in a significantly faster oscillation in response to similar impacts (81.92 ± 32.73 Hz vs. 21.16 ± 3.06 Hz; Welch's t test, t = 6.40, d.f. = 11, P < 0.001; Figure 2B).

Trapping risk is a function of ant position under the lid. The stiff plate pivoting behavior implies that acceleration and inertial forces acting on insects on the lower lid surface should increase linearly with distance from the pivot point. The peak accelerations calculated for the *N. gracilis* lids were an order of magnitude higher than those of the *N. rafflesiana* lids (Figure 2C). Capture trials with ants on six different *N. gracilis* lids showed that the likelihood to be dislodged by a drop impact was dependent on the position of the ant under the lid (Figure 2D). Although there is some morphological variation between the individual lids, ants never fell from the proximal 20% of the lid. The fall frequency increased significantly from the proximal to the distal end of the lid (Page test for trend, n = 6, L = 14475.0, P < 0.001; Figure 2E). Ants at the very edge of the lid, however, were able to hold on to the edge, making them resistant to falling. We repeatedly observed ants successfully holding on to the edge of a vibrating lid with just one foot while others, positioned away from the edge, were dislodged by the same impact. On all observed lids, ants showed a strong preference to position themselves under the thicker, wedge-shaped proximal end of the lid centerline. Ants were rarely dislodged from this position (Figure 2D).

Rain drops exclusively activate the pivoting mode of the *N. gracilis* lid. High resolution vibration measurements resolved the impact response of a *N. gracilis* lid in more detail (Figure 3A). A series of scan points along the length of the lid (Figure 3B) was shown to oscillate in phase, with the amplitude increasing with distance from the lid base (Figure 3C), confirming the results from the video analysis. Drop impacts caused a rapid initial downstroke with a sharp change of direction at the lowest point (Figure 3C, D). After the initial transient response (Figure 3D, top), the lid settled into a regular damped oscillation with a gradual slight decrease of frequency over time due to air resistance (Figure 3D, bottom).

Sound-driven oscillations exhibited a resonant frequency of 69 Hz where deflection shapes corroborate the previously described pivoting motion (Figure 3E, and Supplementary video S1). Additional resonant modes were identified at higher frequencies. Prominent deflection shapes

included side-to-side rolling at 148 Hz, level up-and-down movement at 278 Hz, and additional higher order bending modes at 514 Hz and 925 Hz (Supplementary videos S2-S5). Actuating the same lid with simulated rain drops mainly activated the first mode of resonance, pivoting at 69 Hz (Figure 3E, and Supplementary video S6).

A combination of high accelerations and friction-reducing wax crystals enable *N. gracilis* to trap prey with the lid. Simulated rain drops dislodged 14 out of 37 ants (27.5%) from the underside of a *N. gracilis* lid. In contrast, not a single ant (n = 20) fell from the lid of a *N. rafflesiana* pitcher or from a *N. gracilis* lid attached to the underside of a *N. rafflesiana* lid (n = 39 ants, counting only ants on the *N. gracilis* part of the lid). This confirms that the rapid vibration of the *N. gracilis* lid is crucial for its trapping function. Removal of the wax crystals from the lower lid surface of the *N. gracilis* pitcher reduced the trapping rate drastically to 4% (two out of 46 ants; Fisher's exact test, P = 0.002), revealing that the wax crystals are also essential for the trapping function of the *N. gracilis* lid. Ants consistently generated much lower friction forces on the wax crystal surfaces of three different *N. gracilis* lids (1.56 ± 0.61 mN) than on a clean glass surface (9.02 ± 2.29 mN; Wilcoxon signed-rank test, n = 11, Z = 2.93, P = 0.003; Figure 4A, B). In contrast, friction forces on the wax crystal-free undersides of two *N. rafflesiana* lids (4.38 ± 1.39 mN) were similar to those in control trials on glass (4.73 ± 1.43 mN; Wilcoxon signed-rank test, n = 10, Z = 0.56, P = 0.58; Figure 4B). The friction forces on glass provided a control to allow comparisons between the measurements on *N. gracilis* and *N. rafflesiana*, which were conducted on separate days. This is necessary because absolute friction forces vary depending on shear rate, temperature, and the motivation of the individual (36). From the body mass of the ants (2.15 ± 1.0 mg, n = 48) and the lid acceleration (Figure 2C) we calculated that the peak inertial force acting on a *Crematogaster* ant was 0.57 ± 0.27 mN at the tip of an oscillating *N. gracilis* lid, and 0.03 ± 0.01 mN at the tip of the *N. rafflesiana* lid.

Discussion

We show that *N. gracilis* uses a rapid, rain-powered oscillation of the pitcher lid to capture prey. Although morphologically similar at first sight, the kinematic impact response of the *N. gracilis* lid (Supplementary video S7) was found to be fundamentally different to that of the *N. rafflesiana* lid (Supplementary video S8). Adaptations of lid geometry and material properties combined with a friction-reducing wax crystal surface render the *N. gracilis* lid a highly effective insect trapping device. To our knowledge, this is the only case of an externally driven functional plant movement reported to date.

The torsional spring behavior of the stiff *N. gracilis* lid results in a pivoting motion. This type of motion entails a linear increase of acceleration along the length of the lid. In contrast, the bending response of the *N. rafflesiana* lid (Supplementary video S8) results in a whipping motion and leads to a concentration of the acceleration at the very tip of the lid. This does not only limit the surface area where high accelerations are experienced, but also places it at the edge of the lid where insects can get a much better grip by hooking around with their claws. Conversely, the combination of a high bending stiffness along the lid, associated with lower mass and damping coefficient allows the *N. gracilis* lid to reach higher accelerations spread over a larger surface area. The resulting inertial forces acting on the prey were, in case of the *Crematogaster* ants, approximately one third of the measured peak friction forces on the wax crystal covered lower lid surface. Adhesion forces of smooth insect pads are typically about seven times lower than friction forces on the same surface

(37). We would therefore predict the trapping threshold for *Crematogaster* to be located about halfway along the length of the *N. gracilis* lid, and closer to the base for ants that have fewer than six feet in contact at the moment of impact. Our observations of trapping locations (Figure 2D, E) confirm this prediction. The absence of trapping events from the *N. rafflesiana* lid (with or without attached wax crystal surface) and from the wax crystal-free *N. gracilis* lid is also predicted by both measured frictional and calculated inertial forces.

The impact-driven oscillations of the *N. gracilis* lid are remarkably fast. During the initial downstroke, the tip of the lid reached peak velocities of nearly 1.5 ms^{-1} and maximum accelerations of almost 300 ms^{-2}, similar to the take-off speed and acceleration of some jumping insects (38). Peak lid velocity is also an order of magnitude faster than the snap traps of the Venus flytrap (8), and the catapulting tentacles of the sundew *Drosera glanduligera* (15). The only known carnivorous plant movement that exceeds the *N. gracilis* movement in speed is the rapid opening of the *Utricularia* suction traps (9, 17). In contrast to these active mechanisms, the *N. gracilis* lid movement requires neither mechanical pre-loading nor physiological activation. The fastest reported plant movements – up to 170 ms^{-1} in extreme cases – are catapult-based mechanisms for seed dispersal (5, 39, 40), spore release (6) and pollen transfer (7, 41). These super-fast motions invariably rely on irreversible, single-shot mechanisms. In contrast, the rapid lid movement of *N. gracilis* can be repeated instantly and indefinitely as long as the external driver, rain drop fall, persists. The finding that rain drops only elicit the trapping-relevant pivoting mode of resonance is testament to the remarkable fine-tuning of the lid properties to this unique mechanism. By filtering out other movement responses, the *N. gracilis* lid maximizes the downward impact transmission.

Rain plays a key role as an activator for lid and peristome trapping alike (26, 35). In both cases, this leads to a stark bimodality where traps are either switched on or off. The frequent change between dry, safe and wet, dangerous times promotes the survival of worker ants scouting for new food sources, thereby boosting recruitment and ultimately capture rates (42). The erratic nature of rain in the tropical habitats of pitcher plants makes it highly unpredictable. This makes it difficult for insects to avoid rain altogether. Insect activity tends to temporarily decrease during heavy rain (43-46); however, this might not affect capture rates if pitcher visitors are already present at the onset of heavy rain. In addition, *N. gracilis* might benefit from the tendency of insects to seek shelter from rain on the underside of leaves. Even after the rain has stopped, accumulated water keeps dripping from the vegetation. These usually large drops might lead to further captures once the ants resume their foraging activity.

The lid trapping mechanism of *N. gracilis* is a striking example of how relatively small evolutionary changes to surface and material properties can add an adaptive function, trapping, to a structure that already serves a completely different purpose, protection from the elements. Hypothetically, similar mechanical adaptations in leaves could enable other plants to literally shake off herbivorous insects during rain. Slippery epicuticular wax crystals are found throughout the plant kingdom and their insect-repellent function has been extensively studied (47). Counterintuitively, highly effective insect-repellent plant surfaces do not necessarily convey increased herbivore resistance because they also exclude most predators and parasitoids, creating a predation-free niche for specialist herbivores that can overcome the anti-adhesive barrier (48, 49). Impact- or wetness-dependent insect-repellent mechanisms could provide a strategy to circumvent this trade-off. More research is

needed to investigate the surface structures and impact responses of leaves in order to potentially exploit passive-dynamic movements for the protection of crop plants.

The use of a rapidly moving plant part for prey capture makes *N. gracilis* unique amongst pitcher plants and challenges the conventional divide between active and passive carnivorous traps. Passive prey capture is generally considered motionless while active trapping implies the involvement of metabolically costly, physiological activation mechanisms (11). The externally driven, passive-dynamic movement of the *N. gracilis* lid represents a new kind of functional plant movement that is facilitated by specific structural adaptations of the plant but activated and powered exclusively by abiotic factors. The passive-dynamic *N. gracilis* trap indicates the existence of a continuum between active and passive trapping mechanisms in carnivorous plants.

Materials and methods

High speed video analysis. We used high speed video recordings to investigate the oscillation of *N. gracilis* (n = 12) and *N. rafflesiana* (n = 10) lids. Each pitcher was collected from a field site in Brunei Darussalam, transferred to a nearby field station and mounted on a lab stand to resemble the natural orientation on the plant. The impact of rain was simulated with an infusion drip system (Exadrop®, B. Braun, Melsungen, DE) releasing droplets from a height of 40cm centrally above the pitcher lid, with a drip frequency of 0.25-0.35 Hz. The experiments were conducted on an open porch and the setup was subject to natural air flow, causing the location of the drop impact on the lid to vary randomly. A Basler A602f high-speed video camera (Basler AG, Ahrensberg, DE) with a 60mm macro lens (Nikon, Tokyo, JP) was mounted at the same height as the lid, providing a 90° side view of the oscillation. A ruler was positioned in the frame to provide a scale. We recorded three oscillations per pitcher at frame rates ranging from 250 to 457 fps.

In each video, three points on the lid (proximal, medial and distal) were tracked manually using a custom-built Matlab code (The MathWorks Inc., Natick, MA, US; Data Supplement S9). Frequency was calculated directly from the number of oscillations per time, averaging across replicate recordings and tracking positions. Kinematic modelling techniques in the software Mathematica 5.0 (Wolfram Research, Champaign, IL, US) were used to calculate rotational stiffness, damping, velocity and acceleration from the point tracking results, approximating the lid movement as a rotation of a stiff rectangular beam about a fulcrum located at one end (Supplementary Figure S10). For each tracking position i and pitcher p, we calculated the angle of deflection $\theta_{i,p}$ defined as

$$\theta_{i,p} = \arctan\frac{d_{i,p}}{L_{i,p}} \tag{1}$$

where d is the vertical displacement from neutral and L is the distance from the center of rotation to the tracking point. To minimize the effect of measurement errors, we averaged across recordings prior to the calculation of $\theta_{i,p}$, and then across tracking positions to obtain an angle of deflection θ_p as a function of time for each individual pitcher. The resulting smoothed curve of angular deflection over time was fit to the equation

$$I\ddot{\theta}_p + \mu\dot{\theta}_p + k\theta_p = 0 \tag{2}$$

where I is the moment of inertia, μ is the damping coefficient and k is the stiffness of the lid. I was calculated from the mass and length of the lid (mass × length$^{2/3}$) and μ and k were fit to match the resonant frequency and damping rate of the oscillation. Each model fit returned a function of angle over time. The maximum angular velocity ($\dot{\theta}_{max}$) and acceleration ($\ddot{\theta}_{max}$) were derived by

differentiating and locating the maxima of the resulting curves. Multiplication by lid length yielded the corresponding linear velocity and acceleration values. The Mathematica code used for the kinematic modelling can be requested from the authors.

Laser vibrometry. A *N. gracilis* plant was obtained from Kew Gardens (London, UK) and kept in a climate-controlled room between 30 °C/60 % rel. hum. (day) and 24 °C/80 % rel. hum. (night). A scanning laser Doppler vibrometer (PSV-400, Polytec GmbH, Waldbronn, DE) was used to measure lid oscillations of a live pitcher in the lab. The complete setup including the plant was placed on a vibration-free table (Model 784-443-12R; Technical Manufacturing Corp., Peabody, MA, USA). Resonant frequencies and mode shapes were identified by recording the response of the lid to repeated 0.1-2 kHz sound sweeps with a data acquisition rate of 5.12×10^4 Hz. The pitcher (fluid removed) was mounted so that the lid was orientated vertically, tip pointing down, at 90° to the optical axis of the laser source. Sound from a loudspeaker (Bass, 30 cm diameter, positioned outside the vibration isolation vibrometer table) was used to acoustically drive lid motion. Lid vibrations were monitored across a grid of ninety-eight measurement points. Mechanical responses were recorded in both frequency and time domains using Polytec PSV v.8.2 software.

We recorded the simulated rain drop impact response of the same pitcher using a similar setup as described above for the video analysis. Because the pitcher was now mounted upright, we used a front-coated mirror to deflect the laser beam onto the lid surface from underneath (Figure 3A). Due to spatial constraints it was not possible to position the mirror so that the proximal 20% of the lid could be scanned. The remaining lid area was scanned across a grid of sixty-two measurement points. The focus distance for each scan point was determined prior to the scan. During the scan, individual measurements were triggered using a photoelectric sensor positioned in the drop fall path. The sensor was orientated so that the trigger beam was perpendicular to the midrib and crossed the midway point along the length of the lid.

Ant capture trials. Running experiments with *Crematogaster* sp. ants on lids of *N. gracilis* and *N. rafflesiana* were performed in a field station in Brunei Darussalam. Carton nests with partial ant colonies were collected from the same field site as the pitchers and were kept in open plastic containers with a slippery PTFE wall coating (Fluon®, AGC Chemicals, Thornton Cleveleys, UK). The ants were fed with honey water and the nests were sprayed regularly with rain water. A freshly collected pitcher was mounted in natural, upright orientation and the ants were given access via a wooden skewer. We waited 5-10 min to allow the ants to start foraging before simulating rain with a drip system as described above. A Sony DCR-PC120E video camera was used to film the underside of the lid (Supplementary Figure S11). Videos were analyzed by counting the number of dislodged ants relative to the number of visitors, defined as an ant fully entering the underside of the lid with all six feet. We tested the performance of ants on the undersides of 1) a *N. gracilis* lid, 2) the same lid after removing the wax crystal layer by gently wiping the surface with a soft cloth until it appeared glossy, 3) a *N. rafflesiana* lid and 4) an unmanipulated *N. gracilis* lid that had been cut at the base and glued centrally under the lid of a *N. rafflesiana* pitcher. In the latter case, only ants that fully entered the wax crystal-bearing *N. gracilis* surface were counted as visitors.

A second series of capture trials was performed to investigate whether the probability of an ant to be dislodged depended on its location under the *N. gracilis* lid. In order to be able to film almost directly from underneath, we cut a lid complete with the pitcher neck and a small section of the rear

pitcher wall and mounted it in a horizontal orientation (Supplementary Figure S12). Two plastic container lids mounted at an angle, with a narrow gap in between to film through, formed a splash protection for the video camera. Ants were given access to forage on the lid nectar and rain was simulated as previously described. The videos were analyzed by comparing the last still image before and the first one after each droplet impact and mapping the thorax positions of dislodged and 'successful' ants on the underside of the lid. The experiment was repeated with six individual *N. gracilis* lids.

Friction force measurements. Friction forces of *Crematogaster* sp. ants on the lower lid surfaces of three *N. gracilis* lids (n = 11 ants) and two *N. rafflesiana* lids (n = 10 ants) were measured against a control (a smooth, clean glass surface) using a one-dimensional bending beam force transducer with two semiconductor strain gauges (SS-060-033-500PU-S1, Micron Instruments, Simi Valley, CA, US) in half-bridge configuration, and a wire hook on the free end (Fig. 4A). Each ant was tethered to the hook on the bending beam using a human hair glued to the thorax and placed on the test surface, which was then slowly and steadily pulled away from the beam. Only trials where the ants remained stationary and used all six legs to hold on to the surface were considered valid. To account for behavioral variation, we performed six valid measurements for each ant and used means for the data analysis.

Pitchers were collected in the field immediately prior to the measurements. Test surfaces were prepared by cleaning new glass microscope slides with ethanol and allowing them to air-dry. They were then either used directly as control surfaces, or a freshly abscised lid (or lid section, in case of *N. rafflesiana*) was superglued flat onto the slide, underside facing up. Care was taken not to damage the wax crystals when mounting *N. gracilis* lids. In between trials, pitcher surfaces were kept on moist tissue paper in a closed petri dish. The plant surfaces were replaced as soon as the edges started to roll upwards, indicating the onset of drying.

Author contributions

U.B. conceived of the study, planned and conducted experiments, analyzed data and wrote the manuscript. M.P. performed the laser vibrometry measurements. D.R. contributed to the design of the laser vibrometry experiments and the writing of the manuscript. G.S. performed the kinematic modelling and helped writing the manuscript.

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Figure legends

Figure 1. Pitcher traps of *Nepenthes gracilis* (scale bars: 1cm).

Figure 2. Mechanical drop impact response of pitcher lids and effect on insect visitors. **A.** Impact-driven oscillation of a *N. gracilis* and a *N. rafflesiana* lid recorded in the field with a high-speed video camera. **B.** Oscillation frequency of *N. gracilis* ($n = 12$) and *N. rafflesiana* ($n = 10$) lids in response to a rain drop impact. **C.** Peak acceleration as a function of position along the length of the lid for both species, estimated from modelling both lids as stiff rectangular prisms rotating about a proximal fulcrum (cf. Supplementary Figure S7). **D.** Fate of visiting ants following a drop impact, depending on the position under six individual *N. gracilis* lids. Each circle represents an ant ($N = 44$ to 361 ants per lid, 993 ants in total). **E.** Capture rate as a function of relative distance from the lid base (in 5% increments) as determined from data in **D**. In **B**, **C** and **E**, circles represent means and error bars represent standard deviation. For statistics see text.

Figure 3. High-resolution vibration analysis of a *N. gracilis* lid. **A.** Experimental setup for measuring the drop impact response of the pitcher lid with a scanning laser Doppler vibrometer (LDV). A front coated mirror was used to deflect the laser beam onto the lower lid surface. **B.** Velocity 'heat map' of an impact response showing increasing velocity from lid base to tip. The colored squares highlight 8 sample scan points along the centerline of the lid. **C.** Time resolved lid oscillation constructed from sample points in **B** (c_1, c_2 = cycle 1, 2). **D.** Deflection shapes of the *N. gracilis* lid during the first two oscillation cycles following drop impact, showing a linear increase of velocity along the length of the lid. The first cycle is characterized by shorter period and higher velocities than subsequent cycles (cf. **C**). **E.** Frequency spectrum of lid vibration in response to a 0.1-2 kHz sound sweep (top) and a simulated rain drop impact (bottom). The black lines represent the average response spectrum calculated for all measurement points, and the grey spectra represent the standard deviation.

Figure 4. Ant friction forces on pitcher lid surfaces. **A.** Experimental setup. **B.** Peak friction forces generated by *Crematogaster* ants on the lower lid surfaces of *N. gracilis* ($n = 3$) and *N. rafflesiana* ($n = 2$) pitchers in comparison to control surfaces (glass). Bars denote medians, boxes represent the inner two quartiles and whiskers contain all values within 1.5 times interquartile range. For statistics see text.