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## **Journal** Biology Letters, 12(9)

**ISSN** 1744-9561

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### **Publication Date** 2016-09-01

**DOI**

10.1098/rsbl.2016.0279

Peer reviewed

# **BIOLOGY LETTERS**

## rsbl.royalsocietypublishing.org





Cite this article: Ortega-Jiménez VM,

Arriaga-Ramirez S, Dudley R. 2016 Meniscus ascent by thrips (Thysanoptera). Biol. Lett. 12: 20160279. http://dx.doi.org/10.1098/rsbl.2016.0279

Received: 6 April 2016 Accepted: 18 August 2016

#### Subject Areas:

biomechanics, behaviour

#### Keywords:

locomotion, water surface, terrestrial insects, viscosity

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Electronic supplementary material is available online at [https://dx.doi.org/10.6084/m9.](https://dx.doi.org/10.6084/m9.figshare.c.3461742) [figshare.c.3461742](https://dx.doi.org/10.6084/m9.figshare.c.3461742).



## **Biomechanics**

# Meniscus ascent by thrips (Thysanoptera)

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Meniscus climbing using a fixed body posture has been well documented for various aquatic and neustonic insects, but is not known from small flying insects that inadvertently become trapped on water surfaces. Here, we show that thrips (order Thysanoptera) can ascend a meniscus by arching their non-wetting bodies to translate head-first and upward along a water surface; if initially oriented backwards, they can turn by  $180^\circ$  to ascend head-first, and climb upward on a surrounding boundary. Using variableconcentration sucrose solutions, we show that translational and climbing speeds during meniscus ascent vary inversely with fluid viscosity. Becoming trapped in water is a frequent event for flying insects, and given that most of them are very small, dedicated behaviours to escape water may be commonplace among pterygotes.

## 1. Introduction

Some millimetre-size insects that live on water can ascend the meniscus at boundaries while maintaining a rigid posture to deform the water surface, and to elicit capillary forces to overcome gravity and particularly drag forces at such small Reynolds numbers (i.e. the ratio of inertial to viscous forces). This method has been described for a number of small aquatic and semiaquatic animals [[1](#page-4-0)–[3\]](#page-4-0) and has been modelled theoretically as a condition for which local surface energy exceeds gravitational potential energy [\[4\]](#page-4-0), but it is unknown how viscosity can affect locomotor performance. Larger terrestrial non-volant insects such as ant workers can also ascend a meniscus using this technique [[1](#page-4-0)]. Many flying insects, however, become trapped on water surfaces, particularly during rain, and in turn are the target of vertebrate and invertebrate predators [\[5](#page-4-0)–[7\]](#page-4-0). For such small taxa (i.e. the average adult insect body size is only about 5 mm [[8](#page-4-0)]), escape from water surfaces may be a regular surviving strategy, but the associated mechanisms of meniscus ascent have not been studied.

Here, we analyse meniscus climbing by western flower thrips (Frankliniella occidentalis), a widespread and common pest in agriculture [\(figure 1](#page-2-0)a). Thrips often occur in very large swarms and, because of their small size, are highly susceptible to wind shear and drafts [[9](#page-4-0),[10\]](#page-4-0), along with deposition onto water surfaces, particularly during storms. We characterize body orientation and kinematics during meniscus ascent in this species, and also test effects of variable fluid viscosity on ascent kinematics.

## 2. Material and methods

Adult western flower thrips were collected from flowers of Abelia grandiflora (Caprifoliaceae) on the University of California (UC) Berkeley campus. A clear plexiglas box (10  $\times$  5  $\times$  5 cm) with an open top was filled to a depth of approximately 15 mm with tap water, and a glass slide was inserted vertically into the water column near the centre of the box to produce a meniscus. In order to assess the effects of viscosity on ascent performance, experimental trials were conducted using sucrose solutions at  $20^{\circ}Bx$ ,  $33^{\circ}Bx$ ,  $43^{\circ}Bx$  and  $50^{\circ}Bx$ , in addition to control

<span id="page-2-0"></span>

Figure 1. (a) Western flower thrips. (b) Meniscus descent (smaller image) and ascent (larger image) by a thrip on tap water (i.e.  $0^{\circ}$ Bx) indicating a turn and subsequent successful climb. The water surface is offset vertically between descent and ascent for visual clarity. (c) Horizontal (x) and vertical (z) positions of individual thrips during ascent on aqueous solutions of varied sucrose concentration ( $n = 5$  at each Brix value). Open circles indicate digitized locations of the insect's centroid; lines correspond to smoothed trajectories (see text for details). Vertical positions for each Brix value are offset for visual clarity.

trials using tap water (i.e. at  $0^{\circ}Bx$ ). The Brix scale indicates the ratio  $(\times 100)$  of sucrose mass to solution mass. Viscosity and density of each sucrose solution were calculated following [[11](#page-4-0)] and [\[12\]](#page-4-0), respectively. Surface tension  $(\sigma)$  of sucrose solutions was calculated in dynes per centimetre as  $73 + [0.089 \times (\% \text{ sucrose})]$ , according to Hirschmüller [[13](#page-4-0)]. Water temperature was  $23^{\circ}$ C in all trials (measured with a Taylor #1523 thermometer/ hygrometer to an accuracy of 1°C). The contact angle ( $\theta$ ) for each sucrose solution was determined from a photograph of a solution drop on a horizontal glass slide and measured using IMAGEJ [\[14\]](#page-4-0) (electronic supplementary material, figure S1; [table 1\)](#page-3-0). Body masses of 15 individual thrips not used in experiments were measured individually using a Sartorius CP2P microbalance with an accuracy of  $1 \mu$ g. Each sampled insect was attached to a small piece of tape; the net difference in tape masses with and without attached insect was assumed to equal the body mass. Mean individual body mass (95% confidence intervals) was then calculated to be  $30 \mu g$  (26–35  $\mu g$ ).

In each experimental trial, we used a steel wire (0.2 mm diameter, 10 cm long) to manually detach individual thrips from a collected flower. The insect was dropped onto the water surface at a distance of 1–2 cm from the vertically oriented glass slide, such that the body was parallel to the plane of the slide. In this configuration, insects typically oriented and moved towards the glass slide in approximately 15 s or less, and then ascended the meniscus. For each experimental solution and for the control solution, the climbing performance of five individuals was recorded using a

high-speed video camera (AOS Technologies, with a resolution of  $800 \times 600$  pixels operated at 120 frames s<sup>-1</sup>) positioned parallel to the plane of the glass slide. Automatic tracking of individuals in each video sequence was carried out using Matlab code for the background subtraction technique [[15\]](#page-4-0), whereby the background is estimated as the median pixel intensities of all frames of the sequence, and the foreground for each frame is then determined by subtraction of this average background. Contrast was increased for all images and edge-detection filters were applied to resolve the moving insect and to determine its centroid position for each frame. Comparison of a trajectory ( $n = 241$  frames) using this automatic detection method with direct digitization of frames showed no significant differences in either estimated x-values ( $t_{480} = 0.24$ ,  $p = 0.8$ ) or y-values ( $t_{480} = 1.01$ ,  $p = 0.3$ ). Cartesian coordinates obtained for each trajectory were smoothed using a square-error quintic spline [\[16\]](#page-4-0). The first and second temporal derivatives of these positional data were used to estimate average and maximum values of speed and acceleration. Reynolds (Re), Weber (We) and Bond (Bo) numbers were calculated based on the average speed [\[17\]](#page-4-0). Body lengths for each individual were obtained via digitization from a single video frame at the beginning of a meniscus ascent when the insects were perpendicularly oriented to the glass slide (figure 1b). Data are presented as the mean value (95% CI).

### 3. Results

Thrips dropped onto the water surface engaged in coordinated leg motions to start moving slowly towards the meniscus and the glass slide. If sufficiently close to the glass slide, however, they would immediately arch their bodies to initiate climbing. Thrips typically adopted an U-shaped body posture and translated head-first while climbing the meniscus (figure 1b), completing the ascent on tap water in 0.9 s (0.5–1.4 s); by contrast, this duration averaged 3.4 s (2.1–4.8 s) at the highest sucrose concentration tested [\(table 1\)](#page-3-0). In general, speeds and accelerations during ascent were reduced as aqueous sucrose concentration was increased (figures 1c and [2](#page-3-0); [table 1;](#page-3-0) electronic supplementary material, video S1). One-way ANOVAs showed significant differences between treatments in average speed ( $F_{4,20} = 14.1$ ,  $p < 0.01$ ), peak speed ( $F_{4,20} = 24.9$ ,  $p <$ 0.01), average acceleration ( $F_{4,20}$  = 10.5,  $p \ll 0.01$ ), and peak acceleration ( $F_{4,20} = 11.6$ ,  $p \ll 0.01$ ) during ascent. Post hoc tests with pairwise comparison of average and peak speeds and accelerations indicate significant differences between the control and all treatments, except for the lowest sucrose concentration (Tukey HSD,  $p < 0.05$  for all pairwise contrasts, except for 20°Bx, for which  $p > 0.05$ ).

When individual thrips initially translated backwards toward the meniscus, they were unable to scale the glass slide, and instead straightened the body and moved downslope (figure 1b; electronic supplementary material, video S2). They then rapidly rotated the body by up to  $180^\circ$ about vertical (figure 1b; mean duration of 207 ms (136– 278 ms);  $n = 11$  individuals) and ascended the meniscus head-first, although some individuals had to repeat this manoeuvre several times to obtain a head-first orientation.

### 4. Discussion

Meniscus-climbing insects use two distinct mechanisms to deform the water's surface, and to generate capillary work that exceeds gravitational potential energy [\[4\]](#page-4-0). Water-walking insects with long legs (e.g. various Mesovelia spp., Microvelia



<span id="page-3-0"></span>Table 1. Morphological and kinematic data for thrips ascending the meniscus (average value with 95% C);  $n = 5$ ; body length  $h_p$  average speed  $U_{\text{mean}}$  peak speed  $U_{\text{mean}}$  average acceleration  $a_{\text{mean}}$ , peak acceleratio

Morphological and kinematic data for thrips ascending the meniscus (average value with 95% CI;  $n = 5$ ; body length  $l_{\rm{b}}$ , average speed Upean, peak average acceleration a<sub>mean</sub>, peak acceleration a<sub>mean</sub>, aqueous



Figure 2. Climbing speeds  $(a)$  and accelerations  $(b)$  of thrips in meniscus ascent versus sucrose concentration. Peak and average values are represented by triangles (black) and circles (grey), respectively (sample size of five individuals at each concentration; error bars indicate 95% CI).

spp. and Hydrometra spp.) use hydrophilic claws on their foreand hindlegs to pull up on the water surface, and to thereby affect ascent with a rigid and linearly aligned body. By contrast, short-legged aquatic bugs (such as the beetle larva Pyrrhalta sp. and the collembolan Anurida maritima) adopt an arched U-shaped posture with the body and ascend using hydrophilic forces which alter the water's surface. Any bent hydrophobic structure can ascend a meniscus if it has sufficiently low mass or high curvature [\[18](#page-4-0)]. For example, even the hydrophobic petals and filaments of glossy abelia flowers placed on water can passively ascend the meniscus (V.M.O.-J. 2015, personal observation). The body of thrips visibly repels water, in contrast to the aforementioned beetle larva which uses partial wetting and body bending to ascend [\[4\]](#page-4-0).

Peak ascent speeds reached by thrips were only 20% of those reached by the beetle larva [[4](#page-4-0)], in part because of no obvious water pulling-up by thrips. How do thrips climb the meniscus? Both hydrophobic and amphiphilic inanimate strips with a non-uniform mass distribution can ascend a meniscus [\[18](#page-4-0),[19\]](#page-4-0), and a comparable asymmetric mass distribution may derive from arching of the longitudinal body axis by thrips. In the low-Re and Stokesian flow regimes studied here (table 1), drag force is linearly proportional to fluid viscosity [\[20](#page-4-0)], which increases exponentially with sucrose concentration [\[11](#page-4-0)]. As a consequence, we see an exponential decline in meniscus-climbing performance of thrips (i.e. in speeds and accelerations during ascent) with increasing sucrose concentration of the fluid (figure 2). Effects of sugar concentration on surface tension are, by contrast, much smaller than the effects on viscosity. For example, as sucrose concentration of pure water increases from zero to 50 8Bx, surface tension increases only by 9% [[21\]](#page-4-0), compared

<span id="page-4-0"></span>to a concomitant increase of approximately 14 times in viscosity ([table 1](#page-3-0)). We attribute most of the kinematic effects seen here to changes in the latter quantity.

The dimensionless Bond and Weber numbers quantify the relative contributions of gravitational and inertial forces, respectively, with respect to capillary forces acting due to surface tension. For thrips in meniscus ascent, both dimensionless numbers were much less than one [\(table 1](#page-3-0)), indicating that capillary forces were dominant. By contrast, values of these numbers for the aforementioned beetle larva are much higher (1.3 and 0.4, respectively), indicating that gravity is more influential for this much heavier insect. Waterstriders and springtails in meniscus ascent [17] are characterized by values of Bo and We similar to those of thrips (i.e. less than 1), which are derived from the small leg radius of the former taxon and the small body size of the latter. The Ohnesorge number (Oh) is given as  $\dot{W}^{0.5}/Re$  [20], indicating the influence of viscous forces relative to the combined effects of inertia and surface tension. For thrips in meniscus ascent, values of *Oh* are less than one for unaltered tap water, but at high sucrose content (e.g. more than  $43^{\circ}Bx$ ) exceed it one order of magnitude in comparison, indicating dominance of viscous forces, consistent with degradation of ascent performance at higher Brix values [\(table 1](#page-3-0)). A  $log$ -log fit of speed versus 1/viscosity  $(\nu^{-1})$  also supports this claim (electronic supplementary material, figure S2,  $R^2$  = 0.7328,  $F_{1,23} = 63.1$ ,  $p < 0.001$ ). Accordingly, at extreme high viscosities we can predict near zero speeds. For example, thrips trapped on honey ( $v_{\text{honey}}$  approx. 10<sup>4</sup> mPa s) can hardly move in any direction (V.M.O.-J. 2016, personal observation).

Ecologically, thrips can be seasonally abundant and are important pollinators; they also damage plant tissues during feeding and spread pathogens among their plant hosts [22]. Thrips seem to be very susceptible to rain impact and displacement; more than 70% of individuals can be washed out from their host plants to the flooded ground during a downpour [22,23]. Escape from water surfaces is probably a regular occurrence for these and for other small holometabolous insects, particularly in mesic environments. The meniscus-climbing strategies shown by thrips suggest that transient locomotor behaviours on this spatial scale may be commonplace for insects trapped in natural aqueous solutions.

Ethics. This research adheres to the ASAB/ABS Guidelines for the Use of Animals in behavioural research. No permission was required to collect thrips at the UC-Berkeley campus. The present study did not involve regulated, endangered or protected species.

Data accessibility. Raw data are deposited at: [http://dx.doi.org/10.5061/](http://dx.doi.org/10.5061/dryad.kf132) [dryad.kf132](http://dx.doi.org/10.5061/dryad.kf132) [24].

Authors' contributions. V.M.O.-J. conceived the project and collected the data; V.M.O.-J., S.A.-R. and R.D. designed the experiments and wrote the manuscript, V.M.O.-J. and S.A.-R. analysed data. All authors approve the final version of the manuscript and agree to be held accountable for the content therein.

Competing interests. We have no competing interest.

Funding. No funding was involved.

Acknowledgements. We thank members of the UC-Berkeley Animal Flight Laboratory and anonymous reviewers for their comments and suggestions on the manuscript.

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