



SYMPOSIUM

Mosquitoes Actively Remove Drops Deposited by Fog and Dew

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Synopsis We report mosquito behaviors for removing accumulated drops of water which would otherwise increase the energy expended during takeoff and free flight. These techniques take advantage of the insect’s small size and great structural strength. To dry their wings before takeoff, mosquitoes employ a flutter stroke, at double the wingbeat frequency of normal flight, generating nearly 2500 gravities of acceleration. Mosquitoes may also remove drops by the respective accelerations associated with takeoff and collision with the ground. We correlate the accelerations and size of drops ejected using a simple model involving the drop’s inertial force and surface tension. We note mosquitoes may use similar techniques to remove synthetic drops, making our observations applicable for understanding the resistance of insects to insecticides.

Introduction

Traditional studies of insect flight consider locomotion through a medium free of particles (Wang 2005). However, in nature, a flying insect contends with rain, fog, dewfall, and airborne particulates such as pollen and dust. These obstacles create challenges for the insect, both during flight and at rest. In this study, we consider the mosquito as our model organism. Understanding how mosquitoes dry themselves may help to understand their resistance to insecticides (Hoffmann et al. 2009). It may also inspire the development of robust MAVs, which might one day also fly under wet conditions (Richter and Lipson 2011).

Although mosquitoes are naturally water-repellent (Pal 1950), little research has been devoted to their ability to remove accumulated water. A review of the hydrophobicity of flying and other insects is given by Bush et al. (2008). Flying insects repel water by virtue of a combination of favorable surface properties and hairy texture (Quéré 2008). When a droplet is placed on a hairy surface, the droplet can exhibit one of two wetting states, Cassie–Baxter or Wenzel. In the Cassie–Baxter wetting state, the droplet sits atop the pillars, with air underneath (Yu et al. 2012). Some body parts, such as a mosquito’s eyes,

are anti-fogging, and will never collect droplets (Gao et al. 2007).

Small drops, such as a fog or condensate, can deposit between the insect’s hairs, wetting the insect and transforming it into a Wenzel state (Dorrer and Rühle 2007). The accumulation of such drops entirely fills the gaps between hairs, as seen in Fig. 1. Although drops easily roll off dry mosquitoes, condensed water can increase hysteresis, thereby decreasing mobility of the drop (Wier and McCarthy 2006). To avoid Wenzel states, insects should remove drops as quickly as possible. Dry particles on the body, such as pollen, are removed by a series of grooming rituals (Lipps 1974). However, little is known regarding the physical principles that dictate such grooming, in particular for wet particles.

In this study, we elucidate the behaviors used by mosquitoes to remove accumulated moisture. Our experimental methods for handling and imaging insects are provided in the “Methods” section. In the “Results” section, we present our experiments on mosquitoes removing drops, as well as theory rationalizing the accelerations required. In the “concluding remarks” section, we discuss our results and avenues for future work.

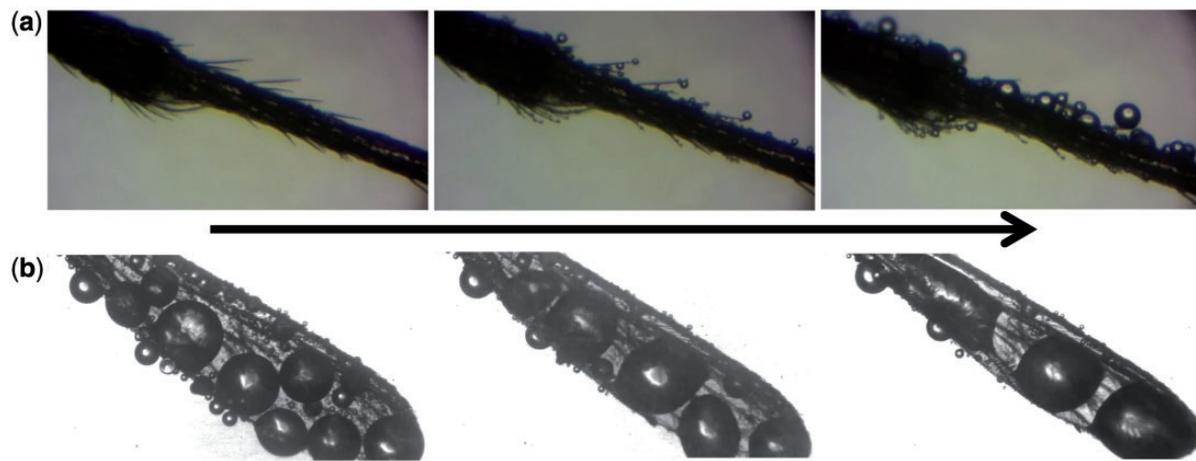


Fig. 1 Fog deposition on a mosquito. (a) Video sequence of drops depositing on a mosquito's leg. (b) Photographs of drops forming on a mosquito's wing, and folding the wing in the direction indicated. Characteristic size of smallest drops is $15\ \mu\text{m}$.

Methods

Care and handling of mosquitoes

Male and female mosquitoes, *Anopheles freeborni*, were provided by the Centers for Disease Control (CDC) in Atlanta, GA, USA. Mosquitoes were adults upon delivery. They were fed a nectar solution prepared by the CDC. No attempt was made to separate the sexes in our experiments. Mosquitoes were transferred to various containers with a John Hock brand aspirator. They were singularly held in place by a continuous vacuum pen (Virtual Industries Tweezer Vac), which can pick up and release mosquitoes without removing appendages or rupturing their exoskeleton.

Fog experiments

A Phantom V210 high-speed camera was the primary tool for observing mosquito flight (3000–10,000 fps). A Nikon AF Nikkor 50 mm 1:1.8D lens was used to capture the entire flight arena, whereas a Navitar 1-60135 was used for macro filming. Flight arenas are lit by four low-temperature LEDs (IDT Honeycomb LED-1). Measurement and tracking within videos were done with Tracker, an open source physics program.

Fog was produced with an Air O Swiss 7145 consumer humidifier with continuous adjustability in fog density, up to a maximum aggregate-output fluid density of $2\ \text{kg}/\text{m}^3$. A hose attached to the humidifier directed the stream of mist onto the subject. A droplet-sizing instrument (DC-III; KLD Labs Inc., New York, NY, USA) was used to characterize the spectra of droplets generated by the humidifiers. We used a wind tunnel (see Dickerson A, Shankles P, Berry B, Hu D, submitted for publication) to wet

mosquitoes in a flight arena. The wind tunnel allows a continuous supply of fog particles while keeping the viewing area clean.

Results

Insects must cope with a wide range of particles in their environments, including millimetric raindrops, micrometric droplets of fog, and nanometric water vapor. Figure 1a shows the progression of fog accumulation between the hairs of an insect's leg. Over time, the drops increase in size. The accumulated drops across the mosquito's body can be many times its mass (Dickerson A, Shankles P, Berry B, Hu D, submitted for publication), which are clearly detrimental to locomotion. In this section, we report three behaviors used by mosquitoes to remove drops.

Take-off

In other work (Dickerson A, Shankles P, Berry B, Hu D, submitted for publication), we have shown that a flying mosquito is grounded rapidly when encountering dense fog. We observe that water-laden mosquitoes remain at rest for minutes after the fog has settled, a behavior that is likely to conserve energy. After this waiting time, the mosquito attempts takeoff, whose vigor is strongly dependent on the direction of take-off. We discuss two types of take-off, those from the floor and those from a wall, in both of which the insect takes off normal to the surface.

Normal, dry mosquitoes take off from the floor with an acceleration of $1.6 \pm 1.1\ g$. If they are wet, they do not attempt take-off. In some cases, they cannot because they are entrapped by accumulated moisture. For example, a leg of diameter

$D_{\text{leg}} = 100 \mu\text{m}$ would require an applied force of $F_{\text{leg}} = \pi\sigma D_{\text{leg}} = 2.3$ dynes to pull free from a liquid film where σ is the surface tension. If all six legs are entrapped, upward of six times the mosquito's weight would be required to escape the film. We observe mosquitoes flapping in these scenarios, yet still remaining grounded.

Wet mosquitoes resting on a wall or a ceiling are much more likely to take off than those resting on the floor. Wet mosquitoes generate accelerations of $0.47 \pm 0.26 g$ ($N=4$), only one-sixth the take-off acceleration of dry mosquitoes ($3.1 \pm 1.9 g$, $N=5$). The lower acceleration of wet mosquitoes is explained by their higher mass, roughly a factor of six (6.22 ± 0.22 , $N=3$). Take-off from a wall is more vigorous, and so more effective at removing drops, than from the floor. Moreover, take-off from a wall involves forces applied perpendicular to gravity, and so necessarily involves higher accelerations than take-off from the floor. Indeed, take-offs from walls are higher than those from the floor by 1.5 g , which is close to the expected value of 1 g .

Hard landing

A dry mosquito will repeatedly attempt flight when held by any part of its body. Upon release, the mosquito will assume stable flight within 1 s (Dickerson A, Shankles P, Berry B, Hu D, submitted for publication). Surprisingly, a wet mosquito falls motionless when released from any height ($N=20$). It makes no attempt to flap during the fall, but resumes motion after collision with the floor. Figure 2a shows a photographic sequence of a wet, motionless mosquito impacting the ground. Before collision, the mosquito carries ~ 40 visible drops on its legs, wings, and body. After impact, the number of adhered drops falls by $\sim 75\%$, with roughly 10 drops remaining.

Figure 2b shows the time-course of the vertical position of the mosquito's head (open symbols), and a drop with radius of $280 \mu\text{m}$ near the head (closed symbols). Prior to collision, the mosquito is falling at a terminal velocity of $U = 0.44 \text{ m/s}$, which is significantly higher than the falling speed $U = 0.135 \text{ m/s}$ of an anesthetized, dry, and much lighter mosquito (Dickerson A, Shankles P, Berry B, Hu D, submitted for publication). During its 3.8-ms collision with the floor, the mosquito's head undergoes an acceleration $a = U/\tau = 115 \text{ m/s}^2$, or about 10 g , which is well within its limits of survival (Dickerson et al. 2012b, Dickerson A, Shankles P, Berry B, Hu D, submitted for publication), which is greater than 300 g . In fact, after collisions, the

insect stands up, shakes off a few additional drops by beating its wings (Fig. 2c) and flies away. The smallest drops are likely to remain attached through both impact and shaking, but nevertheless these behaviors are excellent methods for removing collected moisture.

Flutter stroke

The most unusual method of removing drops is a modified wingbeat. Shown in Fig. 3a, this maneuver can be compared with driving a beam, fixed at one end, at its natural frequency, such that the amplitude of deflection at its free end is much greater than that at its fixed end. This flutter stroke causes a mosquito's wings to flex dramatically, removing a number of small droplets.

Black lines in Fig. 3a trace the wing at various moments over the duration of the flap. The time-course of the displacement of the wingtip, with respect to its resting state, is plotted in Fig. 3b, with an interpolating spline through the data. We denote three consecutive regions in Fig. 3b as the flutter-stroke, transition, and normal-stroke phases.

The flutter-stroke phase is short, lasting 4 ms. In this phase, the wingtips beat at a high-frequency of 875 Hz, but at low amplitude of 0.8 mm, which is roughly 10% of the normal stroke. The flutter stroke produces accelerations of $a_{\text{max}} = A(2\pi f)^2 = 2470 g$, nearly 66% higher a normal stroke, which generates only 1500 g in acceleration. Clearly the flutter stroke, with its low amplitude, is poor for generating locomotion. Instead, it is explicitly intended for removing drops. In the transitional region, the wing's amplitude grows while the wingbeat slows to its normal frequency, 285 Hz.

Theory

Balancing the drop's adhesive force, scaling as $R\sigma$, with the drop's inertia, $R^3\rho a$, provides the critical radius R_c of expulsion as a function of the imposed acceleration:

$$R_c \sim \left(\frac{\sigma}{\rho a}\right)^{1/2}, \quad (1)$$

where σ is the surface tension of water, ρ is the density of water, R is the drop's size, and a is the acceleration of the drop. Large drops need little force to be removed: for instance, drops with a radius of 4.7 mm and larger may be removed by gravity alone. Since such drops are larger than a mosquito, they are rarely observed. For a mosquito, smaller drops are more dangerous as they can wet the mosquito's

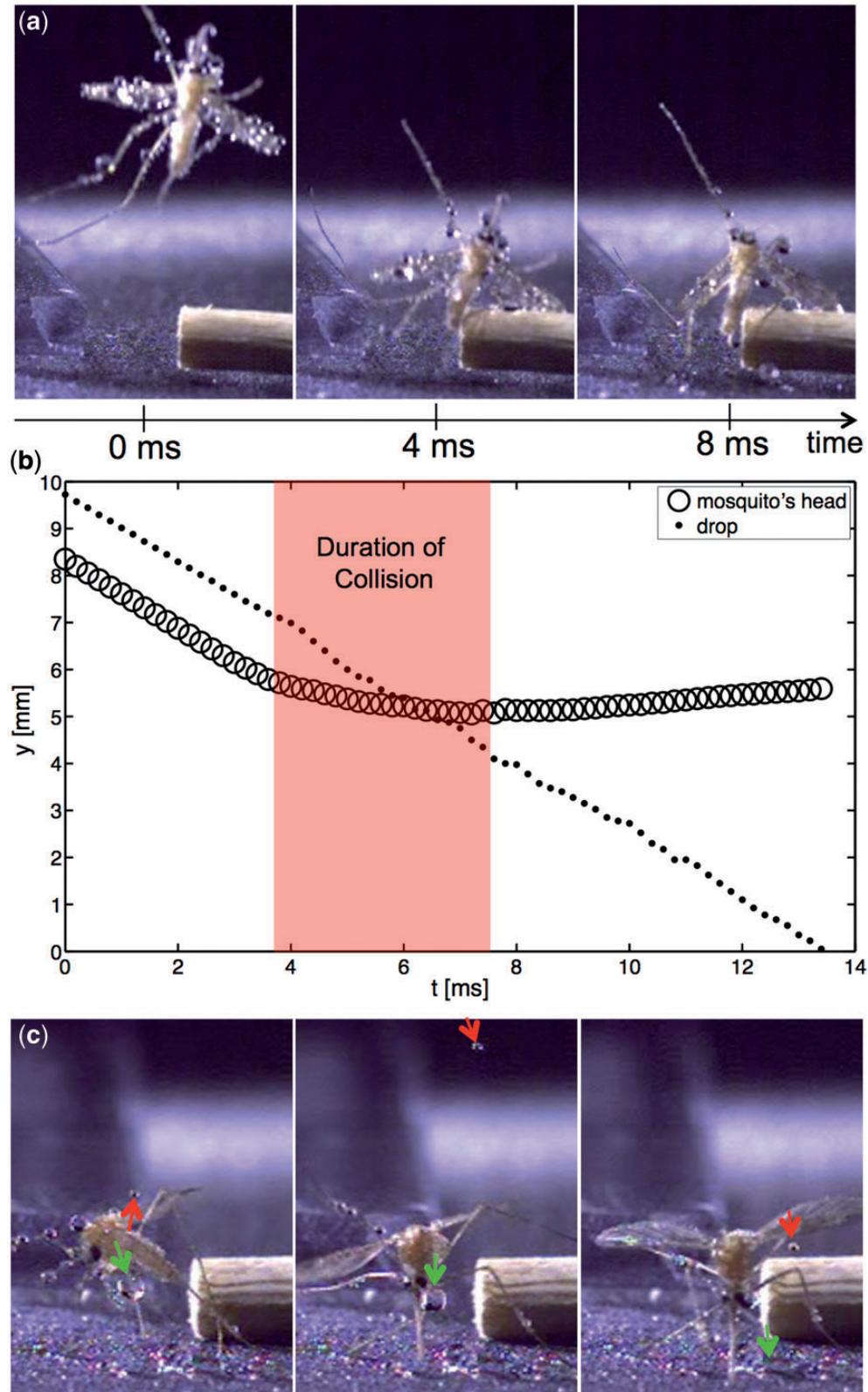


Fig. 2 (a) Photographic sequence of a live mosquito, falling motionless and covered with dew droplets. Drops are dislodged upon impact. (b) Time-course of the vertical position of a mosquito's head (open symbols) and a drop of water 0.8 mm in diameter (closed symbols), originally attached to the mosquito. (c) Photographic sequence of a mosquito standing and shaking after a hard fall. Arrows denote the direction of travel of the drops.

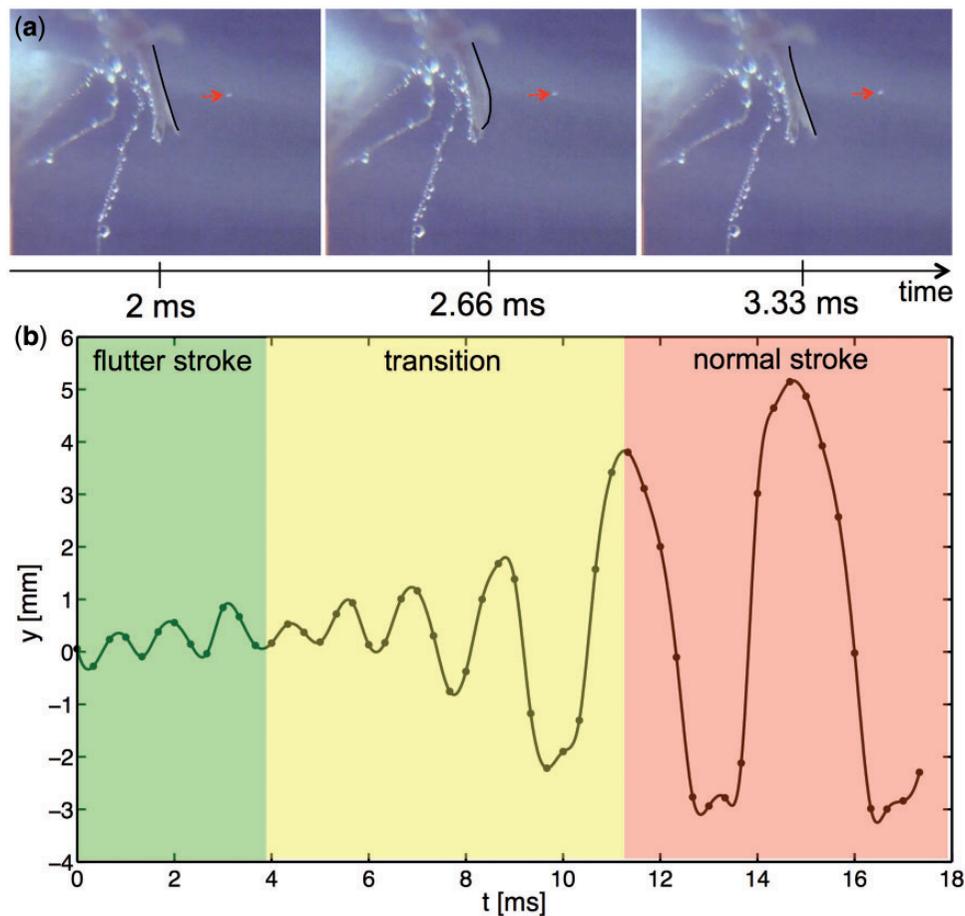


Fig. 3 (a) Photographic sequence of a mosquito employing a flutter stroke to remove drops. The drop denoted by the arrow has a radius of ~ 0.15 mm. (b) Time-course of the vertical position of the wingtip measured with respect to its initial state.

surface. Moreover, according to Equation (1), smaller drops require greater accelerations to remove.

We compare the effectiveness of the three drop-removal techniques in Table 1. Using the observed acceleration, we can compare the size of the released drop in Figs. 2b and 3a to that predicted using Equation (1). The smallest drops necessitate the development of the flutter stroke, which generates the highest acceleration (2500 g), followed by hard landings and take-off, which are roughly comparable (0.5–10 g). The last column of Table 1 shows the expected range of sizes for the removed drops, roughly consistent with those observed. Specifically, the hard landing can only remove drops of 1 mm, whereas the flutter stroke can remove drops nearly 20 times smaller, of size 50 μ m.

Concluding remarks

The ejection of drops by insects represents part of a universal behavior shared by all animals that wish to stay dry. Like insects, many aquatic mammals are covered with hair, which acts to repel water by an

oily coating on the fibers (Sokolov 1982). However, mammals can trap large amounts of water within their fur after swimming, which they need to remove (Dickerson et al. 2012a). By rapidly oscillating their bodies, producing up to 180° of displacement of the skin, mammals generate centrifugal forces sufficient to remove 70% of the water trapped in their fur within seconds. The animals' loose skin is crucial to their ability to generate large amplitudes of shaking and achieve such high forces.

While insects do not have the advantage of loose skin (Dickerson et al. 2012a) or feathers (Ortega-Jimenez and Dudley 2012), there is a rich set of strategies for removal of water across the gambit of insect species. Mosquitoes employ a number of active strategies such as the flutter stroke, and passive strategies, such as hard falls. Other strategies may be species specific, or subtler than those we observe. Future work should be conducted to compare and contrast the various grooming and drying techniques in insects. The techniques will vary by climate, the insects' geometry, and its style of locomotion.

Table 1 Measured and predicted drop sizes for each behavior reported in this study

Mechanisms of deposition removal	Associated acceleration (g)	Observed drop radius (μm)	Predicted drop radius (μm)
Rapid takeoff	0.5–3	>500	1575–3850
Hard landing	10	280	860
Wing flutter	2500	150	55

Notes: Predicted drop sizes are based on the acceleration observed. Measured radii and accelerations of drops represent characteristic values from our experiments.

MAVs (Richter and Lipson 2011) may employ the techniques reported here to remove water. In particular, hard landing is the most easily implementable strategy. For a perched MAV, a fall at terminal velocity should be <1 m/s and easily survivable by on-board components.

For larger fliers, such as birds, crash-landing is not an option for removal of water due to their higher mass and consequently higher terminal velocity. Instead, birds have been known to shake water from their bodies (Ortega-Jimenez and Dudley 2012). Moreover, birds can generate large accelerations on take-off sufficient to remove drops. The European migratory quail (Earls 2000), *Coturnix coturnix*, uses its wings and hind limbs to produce accelerations of 8 g, enough to dispel medium-sized to large-sized drops.

In this study, we have shown that mosquitoes possess specialized behaviors to remove water. Clearly, mosquitoes are accustomed to dealing with water. Unlike the lotus plant, which is water-repellant by virtue of material properties alone, the mosquito actively removes water. We observe three behaviors, including a specialized flutter stroke, take-offs, and crash landings. Crash landings to remove water are applicable only for the smallest fliers, which are tolerant of high accelerations (Dickerson et al. 2014b). It would be useful to learn the sensory pathway by which mosquitoes and other insects know they are wet. Such an understanding would help determine whether such behaviors are also at play when insects are exposed to other types of fluid, such as insecticides.

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References

- Bush JWM, Hu DL, Prakash M. 2008. The integument of water-walking arthropods: form and function. *Adv Insect Physiol* 34:117–92.
- Dickerson A, Mills Z, Hu D. 2012a. Wet mammals shake at tuned frequencies to dry. *J R Soc Interface* 9:3208–18.
- Dickerson A, Shankles P, Hu D. 2014b. Raindrops push and splash flying insects. *Phys Fluids* 26:027104.
- Dickerson A, Shankles P, Madhavan N, Hu D. 2012b. Mosquitoes survive raindrop collisions by virtue of their low mass. *Proc Natl Acad Sci U S A* 109:9822–7.
- Dorrer C, R uhe J. 2007. Condensation and wetting transitions on microstructured ultrahydrophobic surfaces. *Langmuir* 23:3820–4.
- Earls KD. 2000. Kinematics and mechanics of ground take-off in the starling *Sturnis vulgaris* and the quail *Coturnix coturnix*. *J Exp Biol* 203:725–39.
- Gao X, Yan X, Yao X, Xu L, Zhang K, Zhang J, Yang B, Jiang L. 2007. The dry-style antifogging properties of mosquito compound eyes and artificial analogues prepared by soft lithography. *Adv Mater* 19:2213–7.
- Hoffmann WC, Walker TW, Fritz BK, Farooq M, Smith VL, Robinson CA, Lan Y. 2009. Spray characterization of ultra-low-volume sprayers typically used in vector control. *J Am Mosq Control Assoc* 25:332–7.
- Lipps KL. 1974. Comparative cleaning behavior in *Drosophila* [dissertation]. University of California, Davis: ProQuest Information and Learning.
- Ortega-Jimenez VM, Dudley R. 2012. Aerial shaking performance of wet Anna’s hummingbirds. *J R Soc Interface* 9:1093–9.
- Pal R. 1950. The wetting of insect cuticle. *Bull Entomol Res* 41:121–39.
- Qu er e D. 2008. Wetting and roughness. *Annu Rev Mater Res* 38:71–99.
- Richter C, Lipson H. 2011. Untethered hovering flapping flight of a 3D-printed mechanical insect. *Artificial Life* 17:73–86.
- Sokolov VE. 1982. Mammal skin. Oakland: University of California Press.
- Wang Z. 2005. Dissecting insect flight. *Annu Rev Fluid Mech* 37:183–210.
- Wier K, McCarthy T. 2006. Condensation on ultrahydrophobic surfaces and its effect on droplet mobility: ultrahydrophobic surfaces are not always water repellent. *Langmuir* 22:2433–6.