Current Biology

Geckos Race Across the Water's Surface Using Multiple Mechanisms

Graphical Abstract

Multiple Mechanisms used by Geckos to Race Across the Water's Surface

1) Semi-planing

2) Surface tension

3) Slap and stroke impulses in air cavities

4) Body and tail undulation
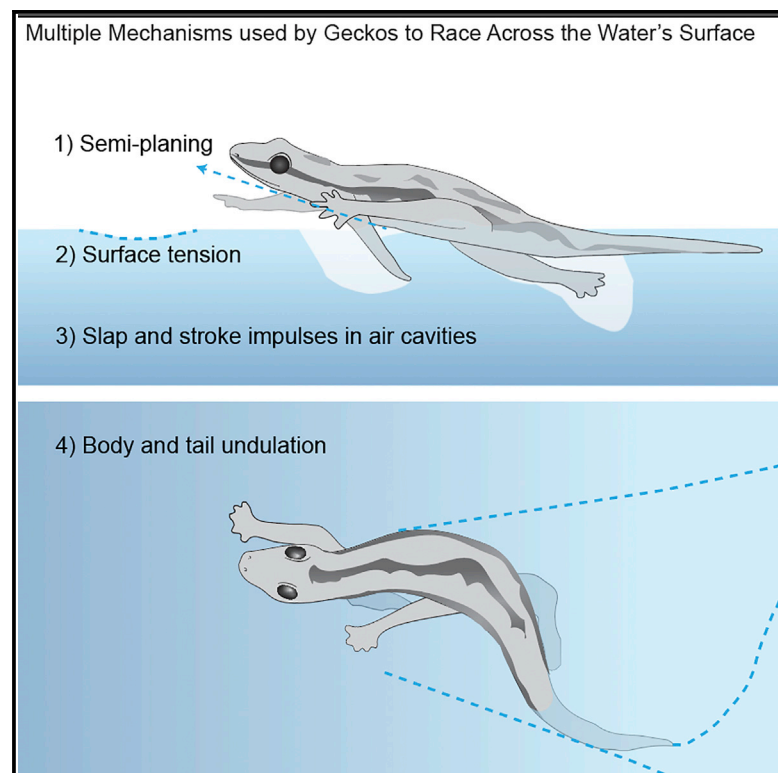
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In Brief

Nirody, Jinn, et al. describe quadrupedal locomotion at the air-water interface. Geckos race along the water's surface at speeds exceeding conventional surface swimming limits. The authors show that interfacial locomotion in intermediate-sized animals utilizes a combination of strategies: surface slapping, undulatory motion, and surface tension.

Highlights

- Geckos can race quadrupedally along the water's surface at close to land-running speeds

- Intermediate-sized geckos use multiple strategies for interfacial locomotion

- Mechanisms include surface slapping, body and tail undulation, and surface tension

- Superhydrophobic skin likely reduces drag during semi-planing

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Geckos Race Across the Water's Surface Using Multiple Mechanisms

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SUMMARY

Acrobatic geckos can sprint at high speeds over challenging terrain [1], scamper up the smoothest surfaces [2], rapidly swing underneath leaves [3], and right themselves in midair by swinging only their tails [4, 5]. From our field observations, we can add racing on the water's surface to the gecko's list of agile feats. Locomotion at the air-water interface evolved in over a thousand species, including insects, fish, reptiles, and mammals [6]. To support their weight, some larger-legged vertebrates use forces generated by vigorous slapping of the fluid's surface followed by a stroke of their appendage [7–12], whereas smaller animals, like arthropods, rely on surface tension to walk on water [6, 13]. Intermediate-sized geckos (*Hemidactylus platyurus*) fall squarely between these two regimes. Here, we report the unique ability of geckos to exceed the speed limits of conventional surface swimming. Several mechanisms likely contribute in this intermediate regime. In contrast to bipedal basilisk lizards [7–10], geckos used a stereotypic trotting gait with all four limbs, creating air cavities during slapping to raise their head and anterior trunk above water. Adding surfactant to the water decreased velocity by half, confirming surface tension's role. The superhydrophobic skin could reduce drag during semi-planing. Geckos laterally undulated their bodies, including their submerged posterior trunk and tail, generating thrust for forward propulsion, much like water dragons [14] and alligators [15]. Geckos again remind us of the advantages of multifunctional morphologies providing the opportunity for multiple mechanisms for motion.

RESULTS AND DISCUSSION

Gecko Surface Locomotion in the Field

High-speed video collected in the rainforest at the wildlife reserve in the Central Catchment area of the Republic of Singapore revealed the ability of geckos to race on the water's surface at speeds comparable to running [1] and climbing [2] (Video S1). Animals leapt from perches to travel across the water's surface to reach a nearby tree, but challenging field conditions prevented a complete analysis. Initial video observations showed unusual, rapid movement across the water's surface, the use of a quadrupedal trotting gait, slapping motion by all four legs, and lateral undulation of the posterior trunk and tail. Field observations prompted us to explore the possible mechanisms by which geckos rapidly traverse the air-water interface.

Between Two Regimes of Interfacial Locomotion

Locomotion at this interface is widespread in mammals, birds, reptiles, and invertebrates [11–24]. But interfacial locomotion poses unique challenges—at small scales, animals can be trapped by surface-tension forces; at large scales, wave drag sharply increases the cost of movement relative to subsurface swimming [12, 25]. To escape these challenges, animals both large and small have evolved a form of interfacial legged locomotion, known as water walking or water running, that maintains the body above the surface where drag is greatly reduced. Small invertebrates stand on the interface with specialized feet that harness surface tension [19–21]. These forces scale poorly [26], forcing larger animals to use different mechanisms. The relatively few known water-running vertebrates, including the basilisk lizard [7–10], harness hydrodynamic forces arising from
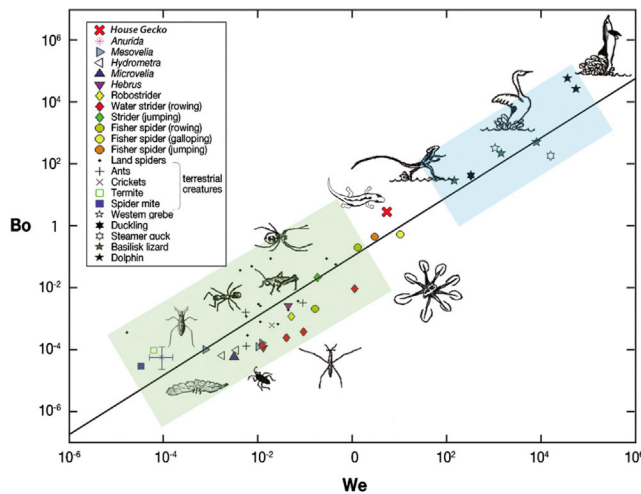
Figure 1. Bond and Weber Numbers for Water-Walking/Water-Running Animals

The Bond number, $Bo = \rho g h_{leg} r_{eff}/\sigma$, where ρ is the density difference between water and air, g is the gravitational acceleration, r_{eff} is the radius of the foot, and h_{leg} is the maximum depth of the foot, and σ is the surface tension; and the Weber number, $We = \rho U_{leg}^2 r_{eff}/\sigma$, where ρ is the density difference between water and air, U_{leg} is the leg velocity, and σ is the surface tension. These dimensionless quantities concern the relative importance of gravitational and inertial forces versus surface forces, respectively. Note that the best-fit line through all points is $Bo \sim We$. Animals for whom surface tension is important ($Bo << 1$) are highlighted in green; those who are too large to be concerned with surface tension effects ($Bo >> 1$) are highlighted in blue. Fisher spiders are a unique case in which their Bo falls below 1, but at high speeds, their legs break the water surface. House geckos (shown as a red X) fall squarely between these two regimes with a Bond number of approximately 8.7 ± 0.5 and a Weber number of approximately 47.4 ± 31.7. Figure adapted from [6].

"slapping" the water's surface with their limbs and "stroking" below it [7–11, 22].

A natural division exists between the two major water-walking/water-running strategies: the use of surface tension and surface slapping and stroking ([6]; Figure 1). Small water-walkers have dimensionless ratios of gravitational force to surface tension or Bond numbers <1 (see STAR Methods). Likewise, to maintain the menisci to drive their legs, small water walkers require that the ratio of a fluid's inertia relative to its surface tension or Weber number also be <1. Large vertebrates with accordingly large Bond number (Bo) and Weber number (We) cannot use surface-tension mechanisms for water running and rely on creating sufficient opposing forces from slapping and stroking through water.

We discovered that estimates of Bo and We dimensionless ratios for our intermediate-sized geckos ($Bo = 8.7 ± 0.5$, $We = 47.4 ± 31.7$) fell between these two regimes (Figure 1). To test the hypothesis that geckos might use a combination of the above strategies, we estimated forces arising from slapping and stroking using a hydrodynamic model and estimated surface tension's contribution by experimentally disrupting its strength with a surfactant.

Kinematics of Gecko Interfacial Locomotion

We quantified interfacial locomotion in eight individuals over 63 trials (see STAR Methods). Unlike basilisk lizards, geckos did

not maintain their bodies completely above the surface, though the geckos' legs slapped and stroked the water's surface, generating air cavities observed in basilisk locomotion. The anterior half of the body was lifted out of the water (average head height 13.4 ± 2.2 mm, Figure 2 and Table 1), while the posterior half of the body remained in contact with the water (Video S2). Animals' tails remained submerged and parallel to the water's surface. Geckos on the water's surface exhibited a quadrupedal trotting gait similar to running gaits used on land [1], where each forelimb moves in phase with the contralateral hind limb and ipsilateral limbs move out of phase. This behavior is not observed in conventional reptilian swimming [14–16]. Crocodile geckos are the only other reptile reported to cycle all four limbs when moving at high speeds in water [23]. Though geckos remained partially submerged, they attained high speeds: on average, 60.7 ± 5.4 cm-s^{-1} (approximately 10.5 body lengths-s^{-1}), similar to measured running [1] and climbing [2] speeds in the same species. The maximum speed recorded during a trial was 97.5 cm-s^{-1}.

To compare performance to surface swimming, where speed is limited by wave drag, we calculated the Froude number ($Fr = v/\sqrt{gl_w}$, where v is forward velocity and l_w is the length of the waterline, here estimated as snout-vent length). Surface swimmers rarely exceed $Fr = 0.4$, the critical Froude number at which the swimmer exceeds its hull speed [23] (approximately 41.5 cm/s for geckos) and begins to hydroplane. Geckos averaged $Fr = 0.8$, and 98% of observed trials were above $Fr = 0.4$. Geckos sprinting on the surface exceeded the absolute swimming speeds of many larger, aquatic specialists, including ducks [25], mink [18], muskrat [17], marine iguanas [16], and juvenile alligators [15], and were faster in relative speed than any recorded surface swimmer other than whirligig beetles [27, 28]. At high velocity, geckos are able to lift up to 72% of their snout-vent length out of the water, thereby reducing wave drag, likely in proportion with the body length above water (Figure S1) [29]. While geckos did not use water running exclusively, like basilisk lizards, their high-speed performance defies characterization as typical swimming.

Surface Slapping and Stroking Forces

Whereas surface swimmers can support their weight entirely with body buoyancy, water-running basilisk lizards [7–10] and grebes [11] generate vertical support with fluid impulses from the slap and stroke applied by their feet. Geckos moving on the water's surface used limb kinematics resembling those of the basilisks, with feet retracting through the air, slapping the surface, and stroking beneath to complete a locomotion cycle. We defined slap to be when the limb begins moving vertically downward from above water until it begins to move posteriorly and stroke as the period when the limb moves posteriorly through the water (Figure 2B). Air cavities, identified as a critical feature of basilisk water running, were formed by the limbs during the stroke [7, 8].

A major difference between our observations and those described in basilisks is that geckos, with their shorter legs and inability to adopt an erect posture, are confined to quadrupedal running, with the animals' hind end trailing beneath the surface of the water (Video S2). Fore- and hindlimbs exhibited similar patterns of movement to those of basilisks, and their
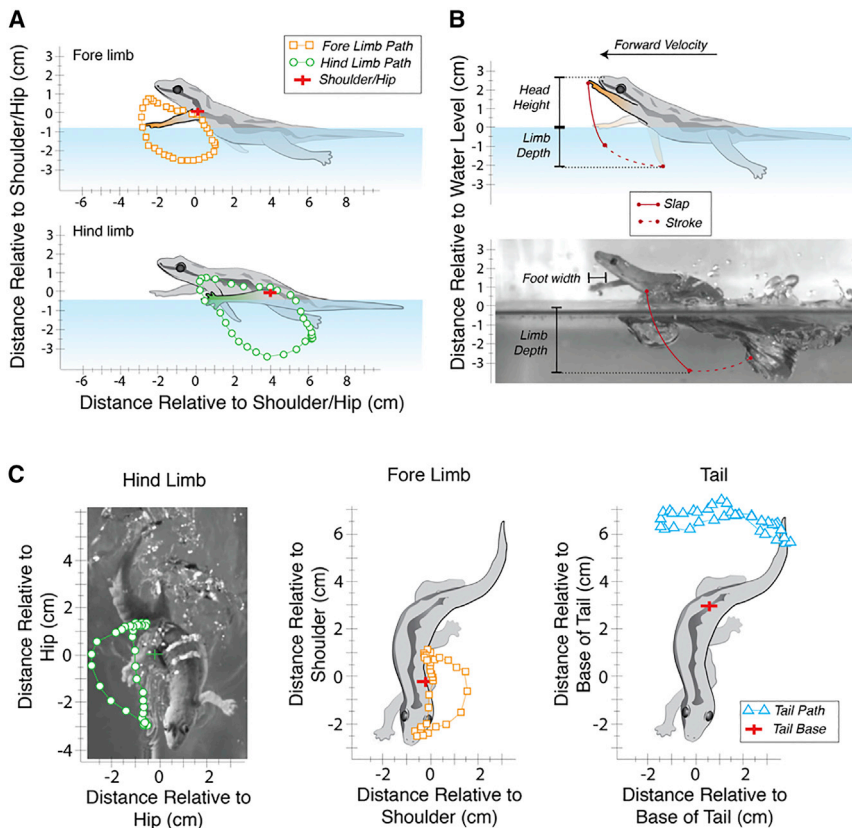
Figure 2. Kinematics of Water Running in the Gecko *Hemidactylus platyurus*

(A and B) Diagrams denoting the forelimb and hindlimb locomotor cycle of the gecko's interfacial gait (Video S2). Note that each limb goes through its own cycle; similar to running gaits on land, each forelimb moves in phase with the contralateral hindlimb. The red cross marks the shoulder and hip location relative to the trajectories. (B) Side view of interfacial locomotion shows the distances used to determine fore- and hindlimb height along with head height. Peak slap velocity was measured when the limb passed through the areas shown by the solid line. Peak stroke velocity was calculated during the phase shown by the dotted line.

(C) Dorsal view of interfacial locomotion (Video S3) shows that geckos utilize limb movements (left), as well as body and tail undulation (center and right). Wave properties for the body and tail for thrust were calculated using the position of the middle of the trunk and the tail tip points, respectively.

See also Figure S1 and Videos S2, S3, S4, and S5.

slap velocities (56.9 ± 27.5 cm-s^{-1} and 59.5 ± 33.9 cm-s^{-1} for fore- and hindlimbs, respectively) were not significantly different (Table 1). The hindlimb, however, did display a significantly greater stroke velocity (91.5 ± 29.4 cm-s^{-1}) than the forelimb (76.2 ± 33.1 cm-s^{-1}, $p < 0.01$). Body undulation resulted in longer hindlimb step lengths during the stroke phase (Figure 2A). Geckos' subsurface limb strokes traveled posteriorly at high speeds, providing the potential for substantial impulses toward forward propulsion (see Table 1).

Using the hydrodynamic model from Glasheen and McMahon [8] (see STAR Methods), we estimated the impulses produced by limbs slapping and stroking over a step and compared them to the downward impulse of body weight. We defined a step as half the full gait cycle, where a pair of fore- and contralateral hindlimbs are moving through water together. For complete water running, the vertical impulses equal the weight impulse on average, but small basilisks can generate up to 225% of weight impulse in a single step [8]. By contrast, geckos generated only 41.8% ± 16.2% of their weight impulse over a step despite having twice as many limbs in contact. Hindlimbs generated more impulse than the forelimbs (Table 1). Surface slapping represented a smaller portion of vertical impulse in geckos than in basilisks (on average 16% of the vertical limb impulse compared to up to 50% in basilisks of a similar size). Geckos' average hindlimb slap velocity (59.6 ± 33.9 cm-s^{-1}) was lower than observed in juvenile basilisks of similar size (approximately 2 m s^{-1} [8]). Geckos also have smaller feet (radius of bounding circle 3.3 ± 0.2 mm, 4.4 ± 0.5 mm for geckos' fore- and hindfeet) than the smallest juvenile basilisks (effective radius 5 mm [8],). Further-

more, the air cavities produced by the geckos are longer and extended further caudally when compared to those produced by the basilisks, suggesting they may be more biased toward thrust than lift (Video S2). The reduced role of stroking and slapping impulses in vertical support agrees with the observation that geckos are performing a form of mixed-mode locomotion. Additional bodyweight support must come from surface tension, buoyancy, and/or hydrodynamic forces on the body.

Surface-Tension Forces

Given their intermediate Bond and Weber numbers, we postulated that surface-tension forces play an important role in gecko interfacial locomotion. Smaller lizards can rest on the surface of water without penetrating (with surface-tension forces supporting ~100% of body weight). The geckos used in this study penetrated the surface when placed gently in water and floated buoyantly with most of their body submerged. However, surface tension could still affect performance by adding partial weight support or by decreasing drag. We found that the skin of the geckos in our study is superhydrophobic (contact angle $\alpha = 138.4 ± 2.5°$; n = 20; Figure S3) independent of location, and therefore might decrease drag through mechanisms that rely on high surface tension at the skin-water interface [26, 30, 31].

To test importance of surface tension, we compared the performance of geckos in water with and without the addition of a surfactant that reduced surface tension by about 50%. Whereas basilisk water running is unhindered by a reduction in surface tension (appendix A of [8]), the geckos were significantly slowed by the presence of a surfactant. Forward speed of geckos in the soap-water mixture was reduced by 58% compared to controls (Table 1, $F_{(1,8)} = 61.73$, $p < 0.001$; Figure 3A). Froude numbers fell concomitantly, with average $Fr = 0.5$ and 36% of trials below hull speed (Figure 3B).

Table 1. Mean ± SD for Kinematic Variables and Impulses in Water and Soap-Water-Mixture Trials

Variable	Water Mean ± SD	Surfactant Mean ± SD	$F_{(1,7)}$	p Value
Head height (mm)	13.4 ± 2.2	6.6 ± 3.0	12.9	0.007[a]
Percent body submerged (%)	28.0 ± 13.4	49.8 ± 7.6	11.9	0.01
Forward velocity (cm-s^{-1})	60.6 ± 5.2	33.1 ± 5.7	61.7	5.0e−5[b]
Stance period (ms)	16.5 ± 4.1	27.9 ± 3.9	16.5	0.004[a]
Swing period (ms)	72.7 ± 8.7	81.1 ± 112.0	1.6	0.24
Stride period (ms)	89.6 ± 9.0	107.3 ± 10.8	7.3	0.03[c]
Forelimb height (mm)	13.6 ± 3.1	4.0 ± 1.6	25.3	0.001[a]
Forelimb slap speed (cm-s^{-1})	57.0 ± 27.5	34.1 ± 28.1	1.4	0.27
Forelimb stroke speed (cm-s^{-1})	76.2 ± 33.1	51.6 ± 10.3	1.5	0.26
Hindlimb height (mm)	14.4 ± 2.1	6.1 ± 3.8	20.5	0.002[a]
Hindlimb slap speed (cm-s^{-1})	59.6 ± 33.9	58.4 ± 45.4	0.002	0.96
Hindlimb stroke speed (cm-s^{-1})	91.6 ± 29.4	53.2 ± 18.4	4.2	0.07
Forelimb slap impulse (mN-s)	0.03 ± 0.01	0.02 ± 0.01	2.4	0.16
Forelimb stroke horizontal impulse (mN-s)	0.6 ± 0.9	0.2 ± 0.03	0.6	0.47
Forelimb stroke vertical impulse (mN-s)	0.03 ± 0.01	0.2 ± 0.02	2.0	0.20
Hindlimb slap impulse (mN-s)	0.06 ± 0.02	0.06 ± 0.06	0.1	0.79
Hindlimb stroke horizontal impulse (mN-s)	0.7 ± 0.4	0.5 ± 0.1	1.1	0.32
Hindlimb stroke vertical impulse (mN-s)	0.6 ± 0.3	0.5 ± 0.1	0.9	0.38
Total limb vertical impulse (mN-s)	1.0 ± 0.3	0.8 ± 0.2	1.0	0.34
Min impulse to counter gravity over step duration (mN-s)	2.5 ± 0.3	2.8 ± 0.3	1.7	0.26
Total limb impulse/min impulse (%)	41.8 ± 16.2	28.6 ± 7.6	1.9	0.15
Body undulation amplitude (mm)	16.0 ± 4.3	13.6 ± 4.9	6.9	0.01[c]
Body undulation frequency (rad s^{-1})	0.1 ± 0.02	0.2 ± 0.1	0.6	0.43
Tail undulation amplitude (mm)	41.7 ± 13.4	46.1 ± 13.4	0.8	0.40
Tail undulation frequency (rad s^{-1})	0.1 ± 0.02	0.1 ± 0.01	9.3	0.005[a]

Impulses are calculated over a single step (half stride). F statistics and p values are reported from repeated-measures ANOVA comparisons between experimental conditions.
See also Figures 2 and 3.
[a]significant at 0.05 level.
[b]significant at 0.01 level.
[c]significant at 0.001 level.

We observed no significant difference in front or hind leg slap or stroke impulses, but stroke periods were slightly longer ($p < 0.01$). Notably, geckos sank further into the water under reduced surface tension. Head height was lowered by over 49% relative to moving on pure water (13.4 ± 2.1 mm versus 6.6 ± 3.0 mm, $F_{(1,8)}$ = 12.9, p = 0.007; Video S3).

Semi-planing and Hydrodynamic Lift Forces
Unlike most surface-swimming vertebrates [17, 24], interfacial locomotion of rapidly moving geckos on pure water exceeded hull speed up to a factor of two or more. Above Froude numbers of 1.0, animals can skim on the water's surface by hydroplaning, generating hydrodynamic lift as the body is inclined with a positive trim angle [23, 30]. Between Froude numbers of 0.6 to 1.0, animals are supported by both hydrodynamic and hydrostatic (buoyant) forces, a strategy known as semi-planing. Because we found Froude numbers in the range of possible semi-planing, we speculate that geckos might be partially supported by hydrodynamic lift forces in addition to buoyant, surface-tension, and slap and stroke forces. We found a strong positive correlation between head height and velocity (beta = 0.01, T = 7.0, p value = 0.01, adjusted R^2 = 0.38; Figure 3A), supporting the role of semi-planing in gecko surface locomotion. The gecko's body or trim angle was 26.4 ± 9.4. House gecko morphology is suited to exploit hydrodynamic lift. They are dorsoventrally flattened with a length to width ratio of 3.7 ± 0.4, have a flat abdomen or venter, and a short vertical distance from the water line to the bottom of the abdomen (i.e., a shallow draft). Drag reduction from their superhydrophobic skin could also contribute. Dynamic lift is well studied for rigid hulls and bodies, but substantiating this hypothesis of hydroplaning with an undulating body requires further testing and analysis.

Undulatory Propulsive Forces
Dorsal views showed that geckos used the conventional technique of lateral undulation of their body and tail (Figure 2C and Video S4). The frequency and amplitude of undulation remained constant across pure and soapy water conditions (Table 1 and Video S5). The similarity of subsurface limb, body, and tail kinematics suggests that a change in thrust might not explain the reduction in speed observed under reduced surface tension. These observations suggest that an increase in total drag force
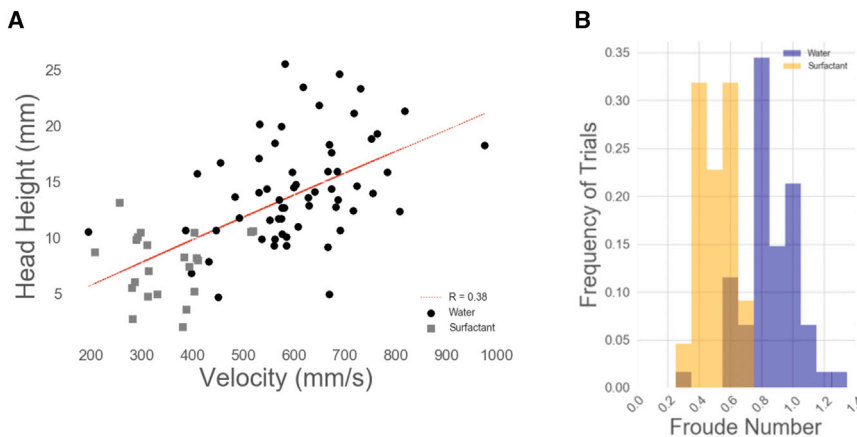
A

B

Figure 3. Effects of Surface Tension on Gecko's Ability to Perform Interfacial Locomotion

(A) As geckos increase their forward velocity, head height above the surface of the water increases. The velocity and head heights of trials in the water-surfactant mixture are lower than in control trials.
(B) Froude number of geckos in the control experiment were higher than those in the experimental water-surfactant group.
See also Videos S3 and S5.

is responsible for the observed reduction in speed, but how decreasing surface tension increases drag remains unclear. The tightly coupled and nonlinear interaction between body drag and body height, itself a function of overall hydrostatic and hydrodynamic lift, results in potentially high sensitivity to loss of vertical support or increases in skin drag.

Geckos' rapid locomotion on the water's surface clearly depends on a complex combination of physical mechanisms typically found at only large or small sizes. Here, we provide the first identification and initial quantification of these possible mechanisms with the hope that others will take the next step to test these hypotheses at this intriguing intermediate regime.

Bioinspired Robots Locomoting at the Air-Water Interface

A bipedal water-running robot inspired by highly specialized basilisk lizards would require high power, many degrees of freedom, and active stabilization [32–38], so existing water-running machines are mostly quadrupedal. Interfacial locomotion by geckos suggests that by harnessing semi-planing, high speeds can be attained even when the body contacts the surface. Adding an undulating tail to these devices might not only improve stability [37], but also improve forward velocity. Super-hydrophobic materials could significantly reduce drag [39–41]. Proposed adaptations like these could stimulate the development of physical models to test these hypotheses in animals and enable robots to show the high performance both on land and in water that we see in geckos.

STAR★METHODS

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- QUANTIFICATION AND STATISTICAL ANALYSIS
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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental Models: Organisms/Strains		
Hemidactylus platyurus	California Zoological Supply	N/A
Software and Algorithms		
MATLAB code	This paper	https://github.com/jnirody/geckos
R code	This paper	https://github.com/jnirody/geckos
Python code	This paper	https://github.com/jnirody/geckos

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Jasmine A. Nirody (jnirody@rockefeller.edu).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Laboratory animals

Geckos (*Hemidactylus platyrus)* were obtained from a commercial vendor (California Zoological Supply). Primary kinematic measurements were taken from eight individuals (three females and five males; Table S1). We kept animals in an environmental room illuminated for 12 hours per day and maintained at $25 \pm 2°C$. Experimental procedures were approved by the Animal Care and Use Committee at the University of California, Berkeley.

Field observations

Using off-road vehicles, we brought two large Manfrotto tripods, ethernet and power cables, a portable power source, a laptop and two high-speed video cameras (AOS X-PRI) plus a heat sink for system cooling to the field location at the Wildlife Reserves in Central Catchment Area of the Republic of Singapore. We attempted to collect data from two views at two sites. Because of the complex terrain and water, the low probability of recording a gecko performing the behavior, we collected approximately 20 trials with two viewable recordings. We obtained field research permits from the government of Singapore and a specimen collection permit from the National Parks Board prior to the onset of field work.

METHOD DETAILS

Experimental apparatus

Our laboratory apparatus consisted of a 35-cm long, 34-cm wide water track (volume 9.5 L; Figure S2), enclosed on all sides by Plexiglas walls. A 10 cm opening was cut midway on the wall at the end of the water track. Animals entered the track via a 0.39 m Plexiglas runway. A touch to the geckos' tail was used to elicit an escape response prompting animals to run down the runway and across the water track. Water was kept at a temperature of 27°C.

Trials were deemed acceptable if the geckos maintained a straight course. Each trial was recorded from both dorsal and sagittal views using synchronized high-speed cameras with imaging software (HiSpec) at 500 frames s^{-1}. Both cameras were kept approximately 100 cm from the recording plane. Animals exited the apparatus through the wall opening exit ramp or by the climbing the wall.

Surfactant trials

To test the effect of surfactant, we added 2 mL of dish soap (Dawn, Procter & Gamble) to the water. A small plastic ruler was floated at the surface and the soap and water were gently mixed with a stirring rod until the ruler no longer could remain floating. Bubbles created by mixing were removed.

Contact angle trials

The animal was placed horizontally under a water injector syringe. A camera (Olympus EM 10 II) was placed laterally with its back or abdomen in the middle of the camera view. Before releasing a water droplet, the animal was cleaned with absorbent towels to eliminate possible moisture on its body surface. A small water droplet was dripped vertically to the back (or abdomen) of the gecko. After waiting about one minute for stabilization, we took photos of the droplet. The procedure was repeated for five times at five different

points at the back and abdomen of the animal in an isolated room with humidity of 42%–45% and temperature about 22°C. The photos were imported into ImageJ and measured with a contact angle plug-in.

QUANTIFICATION AND STATISTICAL ANALYSIS

Kinematic and statistical analysis

Limb kinematics were analyzed for trials where all four limbs exited the water. Limb kinematics were determined using side view videos, and undulation was determined using top view videos. If fewer than four limbs exited the water, then forward velocity and head height above the water surface were measured (water trials n = 61 with 8 individuals. 38 trials analyzed for their limb kinematics and 28 were analyzed for velocity and head height only; soap trials n = 22 with 5 individuals. Eight trials were analyzed for limb kinematics, 15 for velocity and head height only). For each trial, the last two strides were analyzed using ProAnalyst software (Xcitex, 2013) and we extracted relevant parameters using MATLAB (2014b, Mathworks). Means and standard deviations are reported for metrics across all trials within an experimental condition. F-statistics and p values are reported from repeated-measures ANOVA comparisons between experimental conditions. Data were analyzed using statistical software R and Python.

Bond and Weber Numbers

Locomotion on water surfaces can be characterized by Bond (Bo) and Weber (We) numbers [6]. Small water walkers which rely on surface tension to fully support their legs and body weight without breaking the water surface have Bond and Weber values < 1. Larger water runners with Bond and Weber values >> 1 use the forces produced by slapping the water with their limbs or rowing with their limbs to stay above the water. House geckos have Bond and Weber numbers that place them in an intermediate zone between small and large water walkers whereby they use a multi-modal form of locomotion to move rapidly on the surface of the water.

$$Bo = \frac{\rho g h_{leg}}{\sigma / r_{eff}}$$

where ρ is the density of water, g is the gravitational acceleration, h is the maximum depth of the leg below the water surface, σ is the surface tension, and r_{eff} is the effective radius of the gecko's foot (here, estimated as the average for front and hind feet).

$$We = \frac{\rho U_{leg}^2 r_{eff}}{\sigma}$$

where U_{leg} is leg velocity (averaged over both the slap and stroke periods).

Impulse analysis

We used the hydrodynamic model presented by Glasheen and McMahon [7] to estimate the forces produced during locomotion along the water surface. During a single step the animal generates impulse during (i) slap, when the limb initially impacts the water, and (ii) stroke, during which the limb actively pushing through the water [7, 8]. Assuming that an individual's feet can be approximated by flat circular disks, we calculated the maximum impulse that the animal could generate during a slap (I_{slap}) as:

$$I_{slap} = \frac{4}{3} \rho r_{eff}^3 \mu_{slap}$$

where μ_{slap} is the average downward velocity of the foot during slap. During stance, the maximum impulse an animal can generate is given as the product of the average drag force and the time over which this force is applied:

$$I_{stroke} = \frac{C_D S h \left(\mu_{stroke}^2 + gh \right)}{2 \mu_{stroke}}$$

where C_D is the drag coefficient for the foot, S is the surface area of the gecko's foot (as estimated from the bounding circle), h is the maximum depth of the limb below the water surface during stroke, and μ_{stroke} is the average velocity of the gecko's foot during the stroke. The value of C_D was found to be relatively insensitive to size for basilisks, so we used the value reported in [8]. The vertical and horizontal components of μ_{stroke} were used to separate out the respective contributions of stroke to the vertical and horizontal impulses generated by the gecko. Because the geckos move on the water quadrupedally, we calculated the total impulse generated by a gecko during a step as the upward impulse generated during each phase by the two limbs of the gecko:

$$\text{Total I} = I_{front\ slap} + I_{front\ stroke}^{vertical} + I_{hind\ slap} + I_{hind\ stroke}^{vertical}.$$

DATA AND SOFTWARE AVAILABILITY

MATLAB, R, and Python codes used in analysis will be made available in a repository at https://github.com/jnirody/geckos.

Supplemental Information

Geckos Race Across the Water's Surface

Using Multiple Mechanisms

Jasmine A. Nirody, Judy Jinn, Thomas Libby, Timothy J. Lee, Ardian Jusufi, David L. Hu, and Robert J. Full
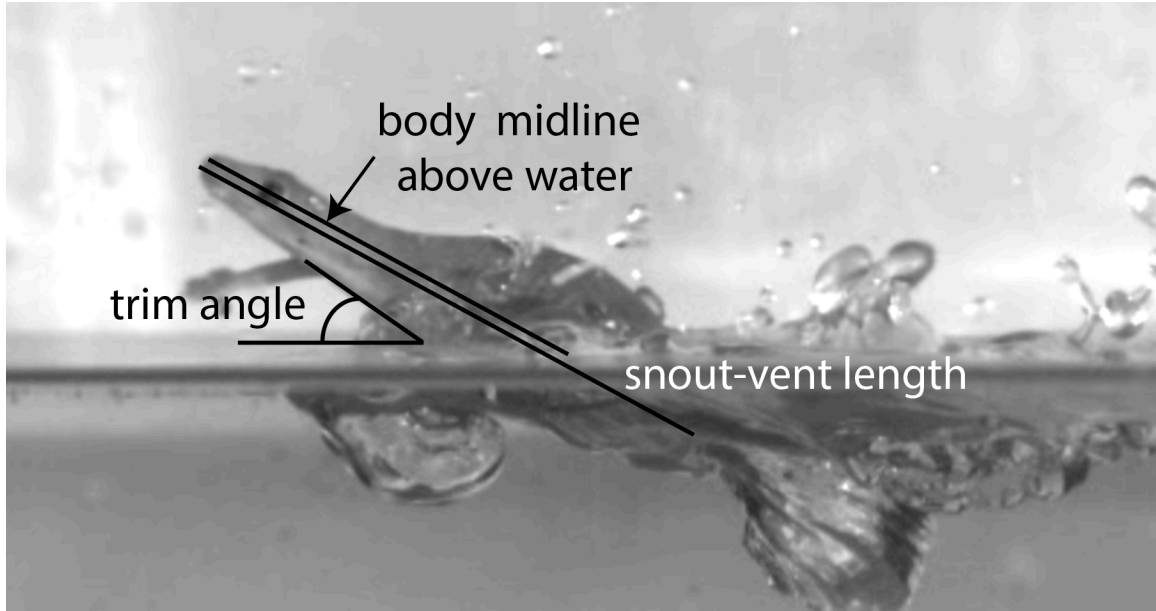
Figure S1. Calculation of trim angle from side-view trials. Related to Figure 2 and Videos S2-S5. The body of the gecko was approximated as a cylinder, and so the proportion of the gecko above the surface of the water was calculated as the ratio of the length of the body above the water over the snout-vent length of the gecko. Trim angle was measured as the angle formed between the gecko's ventral torso and the water's surface.
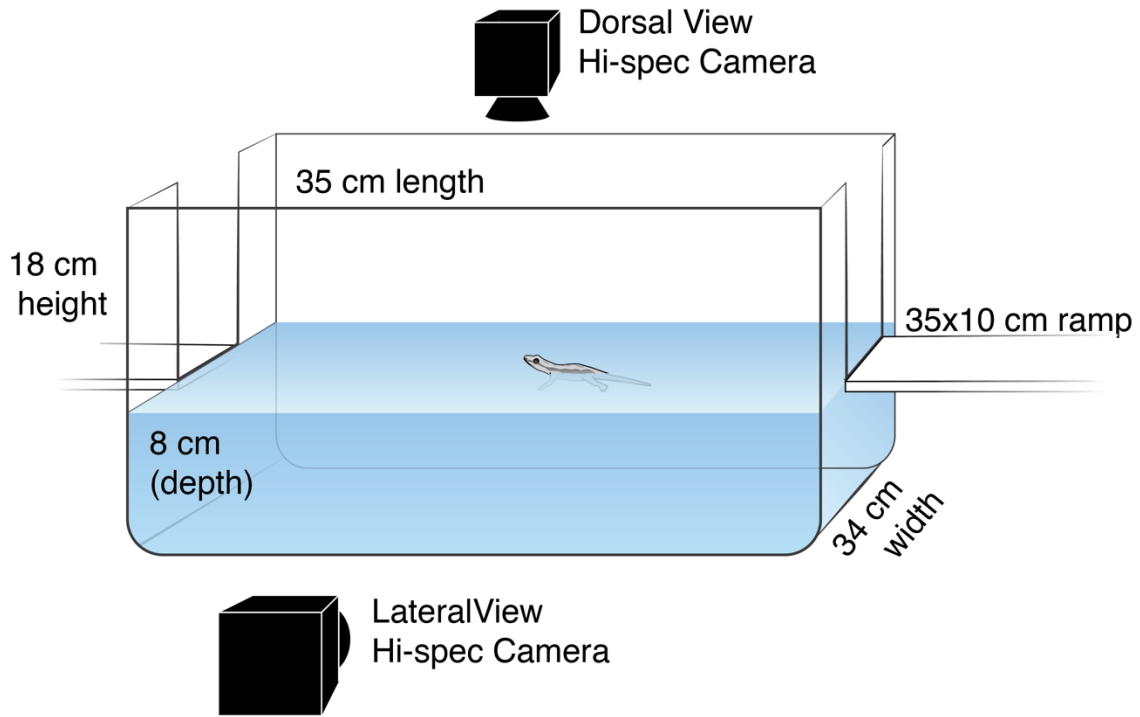
Figure S2. Experiment Tank. Related to STAR Methods. Two openings were cut into the sides of the tank for geckos to enter and exit the water track. A platform was placed at one end of the track and water was filled such that it was level with the platform. Geckos were encouraged to run across the water track by a light touch on their feet or tail. Two Hi-spec cameras filming at 500 fps recorded the trials.
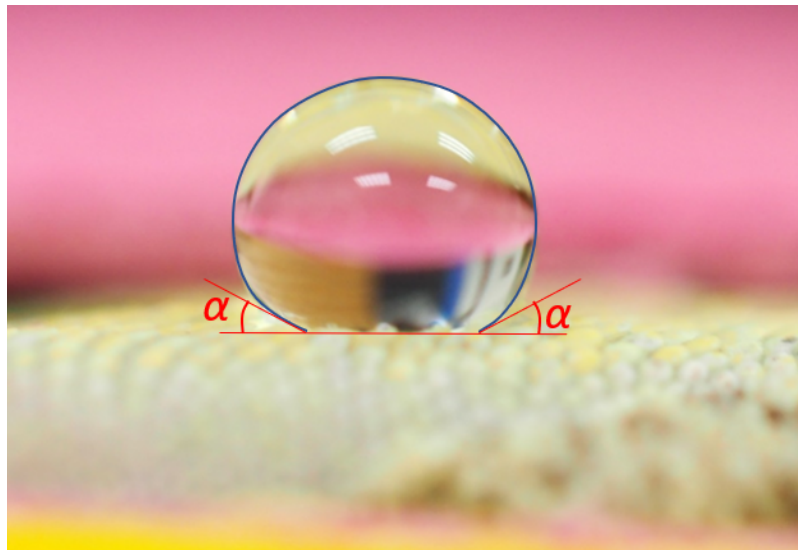

Figure S3. Contact angle (180°- α) of a droplet on the abdomen of the house gecko. Related to STAR Methods. Angle shows superhydrophobicity of the skin.

Variable	Description (units)	Value
S	Surface area of foot as estimated from bounding circle (cm^2)	0.3 ± 0.1 (front foot) 0.6 ± 0.1 (hind foot)
L_b	Snout to vent length (mm)	57.6 ± 1.8
L_t	Tail length (mm)	52.4 ± 8.7
r_{eff}	Effective foot radius (mm) for	3.8 ± 0.4 (average of front and hind foot)
m	Total body mass (g)	5.8 ± 0.7
C_D	Coefficient of drag [S1]	0.703
σ	Surface tension of 25C water (N/m)	0.0720
ρ	Water density ($kg\text{-}m^{-3}$)	999.97
U_{leg}	Speed of foot during stroke ($mm\text{-}s^{-1}$)	838.9 ± 296.9 (average of front and hind limb)

Table S1. Measurements and constants used in the main text (mean ± SD). Related to STAR Methods.

Supplemental References

S1. Glasheen, J.W. and McMahon, T.A. (1996). A hydrodynamic model of locomotion in the basilisk lizard. *Nature* 380, 340.