On the water lapping of felines and the water running of lizards

A unifying physical perspective

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We consider two biological phenomena taking place at the air-water interface: the water lapping of felines and the water running of lizards. Although seemingly disparate motions, we show that they are intimately linked by their underlying hydrodynamics and belong to a broader class of processes called Froude mechanisms. We describe how both felines and lizards exploit inertia to defeat gravity, and discuss water lapping and water running in the broader context of water exit and water entry, respectively.

The majority of terrestrial creatures limit their exposure to aquatic environments. Yet, a number of species have developed sophisticated means to interact with water surfaces, for example for locomotion[1-3] or liquid ingestion.[4] The legs of a water strider are contoured with fluted nanogrooves and coated with hydrophobic wax, enabling the strider to skate across ponds with its weight supported by surface tension.[5] A phalarope's beak is partially wetting, allowing the bird to transport prey-filled, millimetric droplets into its mouth by repeatedly opening and closing its beak.[4] For both water strider legs and phalarope beaks, biological function emerges from a competition between capillary and gravity forces. For larger organisms or faster processes operating at the air-water interface, inertial forces typically replace capillary forces in counteracting gravity. These are called Froude processes (**Fig. 1A**) and represent the focus of this article. We compare two biological Froude processes—the water lapping of felines and the water running of lizards—and show that both involve the same fundamental mechanism that results from a balance between gravitational and inertial forces.

Water Lapping and Water Running

We recently reported that the domestic cat (*Felis catus*) laps by a subtle mechanism based on inertial entrainment of liquid from an air-liquid surface.[6] The cat lowers its tongue so that the tip of the top surface touches the liquid surface, without piercing it. It then rapidly pulls the tongue back up, thereby creating a liquid column (**Fig. 1A**), the top of which it captures in its mouth before gravity draws it down. We found that lapping frequency is tuned to maximize the volume ingested per lap and measurements of lapping frequency in wild cats suggest that the mechanism is conserved among felines. Here we draw a comparison between the lapping of felines and the water-running ability of certain species of lizards. The basilisk lizard (*Basiliscus basiliscus*) is well known for its ability to run across a water surface (**Fig. 1A**). Each step is made of a power stroke followed by a recovery stroke.[7-9] On the power stroke, the lizard strikes the water surface and sweeps its foot downwards, creating an air cavity above the foot. This generates the lift necessary for weight support and the thrust used for locomotion. On the recovery stroke, the lizard pulls its foot out from within the cavity, prior to its collapse, minimizing the drag on the foot and hence the energy required for locomotion.
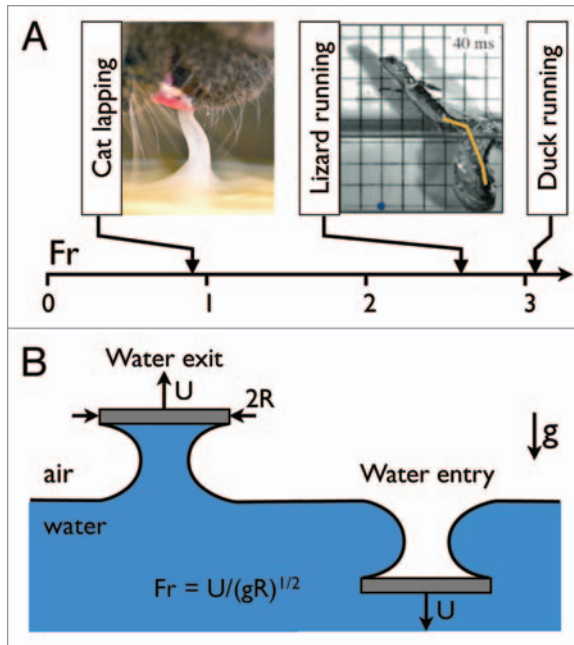
Figure 1. (A) Lapping in felines relies on the formation of a liquid column and water walking in the basilisk lizard on the generation of an air cavity. The dynamics of both processes are governed by the Froude number, Fr. These are just two examples of biological Froude processes, where organisms manipulate the air-water interface for diverse biological functions, including lapping (cat[6]) and running (lizard,[8] duck[18]). For an introduction to moving at the air-water interface, see an example in chapter 14 of reference 19. (B) Schematic of water entry and water exit. Water lapping and water running are examples of water-exit and water-entry processes, respectively. (Lizard image reproduced with permission from the Journal of Experimental Biology, ref. 8).

Froude Mechanisms

To understand the physics of motion on water, one typically relies on dimensionless numbers that quantify the relative magnitude of different forces. For example, the Bond number (Bo) measures the relative importance of gravitational to capillary forces, whereas the Reynolds number (Re) quantifies the ratio of inertial and viscous forces. A common feature of water running and water lapping is that they occur at Bo>>1 and Re>>1, meaning that viscous and capillary forces are negligible.[1,6,7] The dynamics of the liquid are thus in both cases governed by a competition between inertial and gravitational forces. Their relative importance is measured by the Froude number, $Fr = U/(gR)^{1/2}$, where R is the characteristic length of the organ interacting with water (the tongue or the foot), U its characteristic speed and g the gravitational acceleration.

In our study on lapping,[6] we found that the dynamics of the liquid column created by the cat's tongue upward motion is governed by the Froude number. For example,

the time at which the column pinches off is proportional to $(R/U)Fr^{2/3}$. As a consequence, we discovered that the lapping frequency for which the column's volume is maximal is $f \sim (gH/R^2)^{1/2}$, where H is the vertical excursion of the tongue. When we measured the lapping frequency of a range of felines, we found that it complied with this prediction, suggesting that many felines use the same Froude mechanism to drink.

The Froude number also controls the dynamics of the air cavity created by the basilisk lizard. The lifetime of the cavity, from formation to pinch-off, is proportional to $(R/U)Fr$. This dependence prescribes the minimum running frequency, $f \sim (g/R)^{1/2}$, that allows the lizard to pull its foot out of the water before the cavity collapses. Glasheen and McMahon found that the majority of lizards in their study satisfied this condition.[7]

Water Exit and Water Entry

The essential physics of water running and water lapping can be understood

as water-entry and water-exit processes, respectively (**Fig. 1B**), both of which are governed by the Froude number (provided their scale or speed is sufficiently large). In water entry, an object (e.g., a foot) penetrates the water surface and entrains air in its wake.[9-14] The resulting air cavity elongates as the object sinks. Hydrostatic pressure (from the weight of the surrounding water) causes the cavity to contract and eventually to split in two; air from the upper cavity escapes from the surface, whereas the lower cavity remains attached to the sinking object. In water exit, an object (e.g., a tongue) moves upward from the surface of water and entrains water in its wake.[14-17] This resulting water column elongates as the object rises. Hydrostatic pressure (from the water in the column) causes the column to thin and eventually break in two: water in the lower portion falls under gravity, whereas the upper portion remains attached to the rising object. Water entry and water exit are nearly specular; their similarity is not just one of appearances, but extends to the forces that govern the cavity and column dynamics. In both cases, the inertial forces imparted by the object's motion create a deformation of the air-water interface (downward for water entry, upward for water exit) and gravity acts to return the interface to its horizontal equilibrium configuration.

Concluding Remarks

A number of animals exploit the physics of water entry or water exit to handle or navigate water surfaces. Small animals like water striders or shorebirds rely on capillary forces for weight support and water uptake, whereas large animals like felines or lizards use inertial forces to perform the same functions. An understanding of the underlying fluid mechanics allows one to estimate the fundamental forces at play, whose importance can be quantified by means of simple dimensionless numbers such as the Froude number, and reveals physical principles unifying seemingly disparate biological processes.

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