

## How Cats Lap: Water Uptake by *Felis catus*

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**Animals have developed a range of drinking strategies depending on physiological and environmental constraints. Vertebrates with incomplete cheeks use their tongue to drink; the most common example is the lapping of cats and dogs. We show that the domestic cat (*Felis catus*) laps by a subtle mechanism based on water adhesion to the dorsal side of the tongue. A combined experimental and theoretical analysis reveals that *Felis catus* exploits fluid inertia to defeat gravity and pull liquid into the mouth. This competition between inertia and gravity sets the lapping frequency and yields a prediction for the dependence of frequency on animal mass. Measurements of lapping frequency across the family Felidae support this prediction, which suggests that the lapping mechanism is conserved among felines.**

Terrestrial animals have evolved diverse means to acquire water, including absorption through the skin (1) or extraction of moisture from food (2), but most rely on drinking (3–12). Drinking presents a challenge to land vertebrates, because freshwater occurs mainly as horizontal liquid surfaces, such as puddles, ponds, lakes, or streams, and animals must displace water upward against gravity to drink it. Crucial in the drinking process is the role of the tongue, which in vertebrates is used in two distinctly different ways. Vertebrates with complete cheeks, such as pigs, sheep, and horses, use suction to draw liquid upward and use their tongue to transport it intraorally (13, 14). In contrast, vertebrates with incomplete cheeks, including most carnivores, are unable (after weaning) to seal their mouth cavity to generate suction and must rely on their tongue to move water into the mouth (13). When the tongue sweeps the bottom of a shallow puddle, the process is called licking (4). When the puddle is deeper than the tongue excursion into the liquid, it is called lapping (15). Here we report on the lapping mechanism of the domestic cat (*Felis catus*).

Almost everyone has observed a domestic cat lap milk or water. Yet, casual observation hardly captures the elegance

and complexity of this act, as the tongue's motion is too fast to be resolved by the naked eye. We used high-speed imaging to capture the motion of both the tongue and liquid during lapping [Fig. 1 and movie S1 (16)]. With the cat's face oriented downward, the tongue extends from the jaw (Fig. 1A) and its tip curls sharply caudally (Fig. 1B). At the lowest position of the tongue's tip, its dorsal side rests on the liquid surface, without piercing it (Fig. 1B). When the cat lifts the tongue, liquid adhering to the dorsal side of the tip is drawn upward, forming a column (Fig. 1C). This liquid column is further extended by the tongue's upward motion (Fig. 1D), thinning in the process (Fig. 1E), and is finally partially captured upon jaw closure (Fig. 1, E and F). Inside the mouth, cavities between the palate's rugae and the tongue act as a nonreturn device and trap liquid until it is ingested every 3 to 17 cycles (15).

This sequence of events reveals two important aspects of how *Felis catus* laps. First, lapping does not rely on “scooping” water into the mouth as in dogs (*Canis lupus familiaris*). Although the dog's tongue also curls caudally in a cuplike shape, it penetrates the liquid surface and scoops up the water that fills its ventral side. In contrast, the cat's tongue does not dip into the liquid (Fig. 1B) and the cavity on its ventral side remains empty (Fig. 1, B and C), as also recognized in a 1940 Oscar-winning short film (17). Second, only the tip of the tongue is used for lapping. The tip is free of filiform papillae (18) (Fig. 1G), the semirigid hairlike structures that give a cat's tongue its characteristic roughness. Thus, papillae appear to have no function in lapping.

The movies allowed us to quantify the lapping kinematics. The position of the tip of the tongue was tracked over one lapping event (Fig. 2A) and averaged over 11 cycles (Fig. 2B). The tongue's vertical position during upward motion is well described by an error-function profile,  $Z(t) = \frac{1}{2}H\{1 + \text{erf}(U_{\text{MAX}}t\sqrt{\pi}/H)\}$ , where  $H = 3.0$  cm (Fig. 2B, red) is the total vertical displacement,  $U_{\text{MAX}}$  is the maximum speed, and  $t$  is the time measured with respect to  $Z(t=0) = H/2$ , the

half-height. As a result, the vertical velocity has an approximately Gaussian profile (Fig. 2B, blue): The tongue accelerates as it leaves the water surface, attains a remarkable maximum speed of  $U_{\text{MAX}} = 78 \pm 2 \text{ cm s}^{-1}$ , then decelerates as it enters the mouth. Recordings of 10 adult individuals (16) yielded a lapping frequency  $f = 3.5 \pm 0.4 \text{ s}^{-1}$  and an ingested volume per lap  $V = 0.14 \pm 0.04 \text{ ml}$ .

To help understand the mechanism of lapping, we performed physical experiments in which a glass disk of radius  $R$  (representing the tongue's tip), initially placed on a water surface, was pulled vertically upward (Fig. 3). The time series of the disk position was set by a computer-controlled stage and programmed to have the observed error-function profile (Fig. 2B), where we could control the lapping height  $H$  and speed  $U_{\text{MAX}}$ . The hydrophilic nature of glass (static contact angle =  $14^\circ$ ) mimicked the wetness of the tongue. High-speed imaging revealed the formation and extension of a water column, as in lapping (Fig. 3, A to G and movies S2 and S3) (16). The column's ascent was eventually interrupted by pinch-off, leaving a pendantlike drop on the lower surface of the disk (Fig. 3, F to H).

Estimation of the forces involved suggests that the fluid dynamics of lapping are governed by inertia and gravity, whereas viscous and capillary forces are negligible (16). Inertial entrainment draws liquid upward into a column, while gravity acts to collapse it. Ultimately, gravity prevails and the column pinches off. Dimensional analysis reveals that two dimensionless parameters control lapping: the Froude number,  $\text{Fr} = U_{\text{MAX}}/(gR)^{1/2}$ , measuring the relative importance of inertia and gravity ( $g$  is the gravitational acceleration), and the aspect ratio,  $H/R$ . Experiments were therefore conducted over a range of  $\text{Fr}$  and  $H/R$  values (16), for a fixed lapping height,  $H = 3 \text{ cm}$ , determined from observations (Fig. 2B). The latter is possibly dictated by biological constraints, such as the need to keep whiskers dry to maintain their sensory performance (19) or to maximize peripheral vision while drinking.

To test the proposition that the column dynamics are set by a competition between inertia and gravity, we compared the height of the disk ( $Z$ ) at pinch-off,  $Z_p$ , with that predicted from our scaling analysis. We find (16) that  $Z_p/H \sim \text{Fr}^*$  for  $\text{Fr}^* < 1$  and  $Z_p/H \sim 1$  otherwise. Here  $\text{Fr}^* = (R/H)\text{Fr}^{2/3}$  is the ratio of the time scale for the gravitational collapse of the column,  $t_p = (R/U_{\text{MAX}})\text{Fr}^{2/3}$ , and the time scale for the upward motion of the disk,  $H/U_{\text{MAX}}$ . Experiments confirmed the existence of two regimes (Fig. 4A). For small disks ( $R = 2.5$  and  $5 \text{ mm}$ ),  $Z_p/H$  increased linearly with  $\text{Fr}^*$ , whereas large disks ( $R = 10$  and  $12.7 \text{ mm}$ ) reached the final height before pinch-off ( $Z_p/H = 1$ ). Theory also successfully predicts that pinch-off occurs close to the disk (Fig. 3).

Consequently, the balance between inertia and gravity dictates the lapping frequency,  $f$ , by controlling the time of

pinch-off. To maximize ingested volume, which is assumed to be proportional to the column's volume  $V$ , the lapping time,  $1/f$ , should match the pinch-off time,  $t_p$ , because faster lapping fails to maximize inertial entrainment, whereas slower lapping results in belated mouth closure that misses most of the column. This predicts  $f \sim (gH)^{1/2}/R$  or, because  $f \sim U_{\text{MAX}}/H$ , that  $\text{Fr}^*$  is of order one. For domestic cats, we find that  $\text{Fr}^*$  is indeed of order unity (0.4), using the experimentally measured values  $U_{\text{MAX}} = 78 \text{ cm s}^{-1}$  and  $H = 3 \text{ cm}$  (Fig. 2B) and a tongue size of  $R \approx 5 \text{ mm}$  (Fig. 1G).

The growth dynamics of the column's volume (Fig. 4B) (16) provide further evidence that the lapping frequency is set by the interplay between inertia and gravity. When the disk is close to the bath ( $Z \ll H$ ), the column is cylindrical and  $V$  increases as  $V/R^3 = \pi Z/R$  (Fig. 4B inset). Gravity-driven drainage then reduces the rate of volume increase, and  $V$  is at a maximum when gravity and inertia balance (Fig. 4B). A scaling argument predicts a maximum volume when the disk height reaches  $Z_{\text{MaxVol}}/H \sim \text{Fr}^*$  (16), in excellent agreement with observations (Fig. 4A). This also supports our assumption that  $V$  is maximum close to the time of pinch-off. In fact,  $V$  always peaks shortly before pinch-off (10 to 70 ms) (Fig. 4B), which suggests that mouth closure should also occur just before pinch-off to maximize captured volume. Observations of domestic cats showed that mouth closure indeed typically preceded pinch-off (movie S1) (16).

The balance of inertia and gravity yields a prediction for the lapping frequency of other felines. Assuming isometry within the Felidae family (i.e., that lapping height  $H$  scales linearly with tongue width  $R$  and animal mass  $M$  scales as  $R^3$ ), the finding that  $\text{Fr}^*$  is of order one translates to the prediction  $f \sim R^{-1/2} \sim M^{-1/6}$ . Isometry or marginally positive allometry among the Felidae has been demonstrated for skull (20, 21) and limb bones (22). Although variability by function can lead to departures from isometry in interspecific scalings (23), reported variations within the Felidae (23, 24) only minimally affect the predicted scaling  $f \sim M^{-1/6}$ . We tested this  $-1/6$  power-law dependence by measuring the lapping frequency for eight species of felines, from videos acquired at the Zoo New England or available on YouTube (16). The lapping frequency was observed to decrease with animal mass as  $f = 4.6 M^{-0.181 \pm 0.024}$  ( $f$  in  $\text{s}^{-1}$ ,  $M$  in kg) (Fig. 4C), close to the predicted  $M^{-1/6}$ . This close agreement suggests that the domestic cat's inertia- and gravity-controlled lapping mechanism is conserved among felines.

The lapping of *Felis catus* is part of a wider class of problems in biology involving gravity and inertia, sometimes referred to as Froude mechanisms. For example, the water-running ability of the Basilisk lizard depends on the gravity-driven collapse of the air cavity it creates upon slapping the water surface with its feet. The depth to which the lizard's leg penetrates the surface depends on the Froude number, which

in turn prescribes the minimum lapping frequency (25). The Froude number is also relevant to swimming, for example setting the maximum practical swimming speed in ducks (26), and to terrestrial legged locomotion. In this respect, it is interesting to note that the transition from trot to gallop obeys nearly the same scaling of frequency with mass as lapping,  $f = 4.5 M^{-0.14}$  ( $f$  in  $s^{-1}$ ,  $M$  in kg) (27).

The subtle use of the tongue in the drinking process of *Felis catus* is remarkable, given the tongue's lack of skeletal support (28). Complex movement in the absence of rigid components is a common feature of muscular hydrostats, which in addition to tongues include elephant trunks and octopus arms (28, 29). The functional diversity and high compliance of these structures continue to inspire the design of soft robots (29) and a fundamental understanding of their functionality can lead to new design concepts and is essential to inform biomechanical models (29, 30).

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## Supporting Online Material

[www.sciencemag.org/cgi/content/full/science.1195421/DC1](http://www.sciencemag.org/cgi/content/full/science.1195421/DC1)

Materials and Methods

Movies S1 to S3

References

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**Fig. 1.** The lapping process. (A to F) Snapshots showing the movement of the tongue of *Felis catus* and the dynamics of the liquid column during a lapping cycle. Lapping occurs by

fluid adhesion to the dorsal part of the tongue's tip and by lifting a liquid column through the tongue's upward motion, before jaw closure. Time elapsed from the first frame is given in the top left corner of each frame. **(G)** Photograph of the dorsal side of the tongue of *Felis catus*, acquired under anesthesia (16). Only the smooth tip is used in lapping.

**Fig. 2.** The lapping kinematics. **(A)** Vertical position of the tip of the tongue of *Felis catus* over 11 lapping cycles. **(B)** Vertical position (red circles) and velocity (blue squares) of the tongue's tip during a typical lapping cycle, obtained by averaging 11 cycles. The dashed line (red) represents a fitted error-function profile for vertical position. The dotted line (blue) is its temporal derivative and represents upward speed, which yielded  $U_{MAX} = 78 \pm 2 \text{ cm s}^{-1}$ .

**Fig. 3.** Physical model of lapping. A disk of radius  $R$  is driven vertically upward, such that the elevation of the disk,  $Z(t)$ , from the liquid interface (dashed line,  $Z = 0$ ), has an error-function profile (16). Lowercase  $z$  denotes the distance of a generic liquid layer from the disk. The sequence illustrates the formation **(A to E)** and pinch-off **(F)** of the liquid column. After pinch-off, part of the column collapses into the bath **(G)**, which leaves a pendantlike drop attached to the disk **(H)**. The final height of the disk is  $Z = H$ . Time is measured relative to the moment the disk reaches height  $Z = H/2 = 1.5 \text{ cm}$ . This sequence corresponds to  $R = 12.7 \text{ mm}$ ,  $H = 3 \text{ cm}$ ,  $U_{MAX} = 50 \text{ cm s}^{-1}$  ( $Fr = 1.42$ ;  $Fr^* = 0.60$ ).

**Fig. 4.** Liquid column dynamics in the physical model and observed lapping frequency of felines. **(A)** Position of the disk at pinch-off,  $Z_p$ , versus  $Fr^*$ , for four disk radii  $R$  (solid squares), and position of the disk when the column achieves maximum volume,  $Z_{MaxVol}$ , versus  $Fr^*$ , for  $R = 5 \text{ mm}$  (open squares). **(B)** Time course of the liquid column volume,  $V$ , for different speeds  $U_{MAX}$ . Black open squares indicate the pinch-off time relative to the moment when the disk started moving (16). The maximum column volumes (0.12 to 0.26 ml) are of the same order as the volume per lap ingested by *Felis catus* ( $0.14 \pm 0.04 \text{ ml}$ ). The inset shows the volume as a function of relative disk height (solid circles) and the prediction from a scaling argument for low heights (black line,  $Z/H \ll 1$ ). At greater heights, drainage reduces the volume and then pinch-off occurs. **(C)** Lapping frequency as a function of animal mass for eight species of felines. Solid symbols represent data acquired at the Zoo New England, open symbols represent data from YouTube videos (16). The line of best fit (dashed red) has slope  $-0.181 \pm 0.024$ . The solid black line has slope  $-1/6$ .







