Is viscous adhesion strong enough to allow prey capture by chameleons?

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Predators can be sorted in two main categories: ambush and active foragers [1–4]. Most iguanian lizards are ambush predators [4, 5]. They remain motionless waiting for active preys to come within the reach of a strike or approach them very slowly. Among them, chameleons have developed the ultimate specialized feeding systems based on the ballistic projection of the tongue combined with a very efficient adhesion able to sustain the large accelerations involved. The projection mechanisms were intensively studied [6, 9] but the mechanism responsible for the strong adhesion between the prey and the tongue remains controversial. Three different mechanisms are proposed in the literature: i) wet or Stefan adhesion where the adhesion strength relies on viscous flow in the thin film of fluid between the tongue and the prey surface [10, 11]; ii) interlocking where the roughness of both prey and tongue surfaces self-adjust to make physical crosslinks as in the hook-and-loop design of Velcro [12]; iii) suction mechanism similar to the one at play in rubber suction pads [13]. In recent papers, this last mechanism seems to be favored [14, 15]. Here we show from experimental measurements that chameleons have developed a specific mucus of very high viscosity at the tongue tip. Theoretical modeling of the adhesion mechanism have shown that viscous flows alone allows a chameleon to capture preys of at least 30% of its mass.

For chameleons, the capture kinematics put the largest constraints on the adhesion which must sustain very large accelerations. In order to determine if the wet adhesion alone is sufficient to explain the observed maximal mass of a prey caught by lingual prehension, the rheology of this mucus should be known. However, it is difficult to perform reliable measurements of the mucus viscosity which therefore remains largely unknown. This specific fluid is produced in very small amounts by small glands in the tongue pad [4] and cannot be collected for later analysis. This fluid contains proteins and/or glycoproteins dissolved in water. The evaporation of water makes irreversible changes in the fluid structure and subsequent addition of water to restore the initial composition does not ensure the recovering of the pristine mucus rheology.

For these reasons, the viscosity of the mucus was measured as close as possible to the production site without delays. The drag exerted by viscous forces on small rigid beads rolling on a fluid thin film is used to measure indirectly the viscosity [10]. The mucus is collected by scrubbing a microscope slide on the tongue pad which is then placed on a support tilted with an angle \( \theta \). The bead motion is then recorded immediately with a camera. A typical evolution of the bead position as a function of time is shown in Fig. 1A. After a transient stage, the bead moves at constant velocity, \( v_c \), which is determined by the slope, the fluid and the bead properties as follows

\[
v_c = D \frac{\gamma}{\eta} (\sin \theta)^\alpha \left( \frac{\rho g R^2}{\gamma} \right) \beta \left( \frac{R}{h_0} \right)^{0.5}.
\]

The quantities \( \gamma, \eta \) and \( h_0 \) are the surface tension, viscosity and thickness of the fluid. \( \rho \) and \( R \) are the density and radius of the bead, \( D = 0.0014 \) is a numerical constant and \( \alpha = 1.6 \pm 0.06, \beta = 1.35 \pm 0.05 \) [16]. No evidence of a viscoelastic behavior has been observed, the mucus behaves as a purely viscous fluid. As shown in Fig. 1B, the measurements of bead velocity are extremely reliable. For all studied specimens, we obtain a viscosity in the range \( \eta = 0.4 \pm 0.1 \) Pa s which is much larger than the viscosity of saliva \((10^{-3} \text{ Pa s})\) [17]. The relatively large error is related to the uncertainty about thickness of the fluid layer, \( h_0 = 25 \pm 10 \) \( \mu \)m, that was measured by weighing. This unexpectedly large value of the viscosity, approaching that of some honeys, suggests that the prey stick to the chameleon tongue through viscous adhesion. To our knowledge, such viscosity was never reported for a biological fluid found in a buccal cavity.

The viscosity is however not sufficient to determine the adhesion strength. The strain/shear rate of the fluid film should also be known. Therefore, the kinematics of the prey prehension must be measured yielding the velocity, the acceleration and the duration of the different phases of the capture. Chameleons are filmed in lateral view using a high speed camera \((10^3 - 10^4 \text{ fps})\) while capturing crickets. From video analysis, the distance between the nose and the tip of the tongue is measured and plotted as a function of time in Fig. 2A. The velocity and acceleration were then computed from a nonlinear fit of the measured distances (Fig. 2B, C). The global kinematics of the capture process involving protrusion, protraction and retraction is described in Refs. [6, 13, 18]. We focus on the contact and retraction phases of the capture where the fluid strain is maximal. As shown in Fig. 2B, the contact is established within 10 ms and immediately followed by the rapid retraction of the tongue. During the retraction,

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the adhesive contact between prey and tongue tip should resist the very large acceleration measured \(a \approx 300 \text{ m/s}^2\). After the acceleration phase, holding for \(10 - 15\) ms, a constant velocity around 2 m/s is observed up to the final capture of the prey with the jaws. All the values for acceleration and velocity obtained here agree with previously published data about kinematics [9, 13, 15].

During a successful capture the prey remains tightly bounded to the tongue pad in spite of very large accelerations. This implies that: (i) the adhesion force always overcome the inertial force of the prey: \(F_{\text{adh}} > F_{\text{inert}} = ma_p\), where \(m\) is the prey mass and \(a_p\) its acceleration, (ii) the prey acceleration, \(a_p\), and the tongue acceleration, \(a\), are very close. A noticeable difference between both accelerations would obviously generate a rapid detachment of the prey from the tongue pad. For chameleons, the retraction of the tongue should be achieved through the continuous contraction of the hyoglossus muscle [18, 19]. The retraction force calculated from the kinematics data (Fig. 2) is equal to \(F_T \sim 0.6\) N assuming a mass of the tongue \(m_T \sim 2\) g [20]. This result is very close to the values reported in direct force measurements (\(~ 0.7\) N) for specimens of Chameleo oustaleti and Chameleo calyptatus [21]. The acceleration induced by the retraction force is given by the relation \(a = F_T/m_T\) (\(m_T\) being the mass of the tongue). Since both \(F_T\), related to the volume of muscles, and \(m_T\) should possess similar dependencies in chameleon snout-vent length, \(L_{\text{SVL}}\), we expect similar accelerations for different chameleons. Indeed, previous studies with various chameleons report similar accelerations during the tongue retraction (between \(200 - 400 \text{ m/s}^2\) [9, 13, 15]). In the following, we thus consider an acceleration of \(a = 300 \pm 100 \text{ m/s}^2\) to model the capture mechanism.

The inertial force of the prey is only significant during the acceleration phase of the retraction process, see Fig. 2. An adhesion model at constant acceleration is therefore enough to estimate the maximal mass of a prey captured by wet adhesion. This requires an extension of the classical adhesion model at constant velocity [10, 11, 22]. This new model describes the retraction at constant acceleration \(a\) of a compliant probe (the tongue) bounded to a fixed plate by a film of viscous fluid with an initial thickness \(h_0\) and a viscosity \(\eta\). The probe compliance is described through the parameter \(K = E S_T/L_T\), where \(E, S_T, L_T\) are the elastic modulus, the cross section and the length of the probe, respectively. Upon applying a constant acceleration to the probe, the adhesion force increases and presents a maximum just before a break-up of the fluid film. Considering a balance of elastic force in the deformed probe and the Stefan viscous force related to the Poiseuille flow within the fluid layer [10, 11], the equation giving the evolution of the thickness of the film of fluid \(h(t)\) as a function of time reads [22]

\[
F_{\text{adh}} = \frac{3}{2\pi} \frac{\eta \Omega^2 h^2}{h^2} = K \left( \frac{a t^2}{2} + R(t) \right),
\]

\[
\bar{F} = C \frac{h}{h_0} = 1 + T^2 - H(T), \quad H(0) = 1,
\]

where \(\Omega\) is the constant fluid volume. Equation (3) results from the normalization: \(H = h/h_0, T^2 = at^2/2h_0\), and \(\bar{F} = F_{\text{adh}}/Kh_0\). The compliance index is the only parameter of this model:

\[
C = \frac{3}{2\sqrt{2\pi}} \frac{\eta \Omega^2 a^{1/2}}{K h_0^{11/2}} = \frac{3}{2\sqrt{2\pi}} \frac{\eta \Sigma^2 a^{1/2}}{K h_0^{7/2}},
\]

where \(\Omega = \Sigma h_0\) and \(\Sigma\) is the initial contact area. The values of the parameters assumed to be constant are: \(a = 300 \pm 100 \text{ m/s}^2\), \(\eta = 0.4 \pm 0.1\) Pa s and \(h_0 = 25 \pm 10 \mu\text{m}\). In contrast, the morphological parameters, \(K\) and \(\Sigma\), depends on the body size, \(L_{\text{SVL}}\), of the specimen. From the morphological data found in literature for various chameleons (see Supplementary Information), we get \(K = (350 \pm 180) L_{\text{SVL}}\) and \(\Sigma = (5 \pm 2) \times 10^{-3} L_{\text{SVL}}^3\). We therefore find that \(C \approx 10^9 L_{\text{SVL}}^3 \gg 1\) (length being measured in meter).

![Figure 1](image)

**Figure 1.** a. Typical evolution of the position of a spherical bead rolling on an inclined plane covered by a viscous fluid as a function of time (yellow circle). Before the bead is in contact with the fluid layer of thickness \(h_0\), the motion is a simple free fall (green solid curve). Once the bead is in contact with the fluid, its velocity decreases to reach a constant value. The mass of the bead is \(m_b = 0.88\) g \((R = 3.00\) mm and \(\rho_b = 7795\) kg/m\(^3\)). b. Several plots of rolling bead position as a function of time for different specimens of Chameleo calyptatus. The mass of the bead is \(m_b = 0.175\) g \((R = 1.75\) mm and \(\rho_b = 7795\) kg/m\(^3\)).
One of the major argument against the Stefan adhesion mechanism is related to the ability of chameleons to capture with their tongue large preys such as lizards and birds [13, 20]. The body mass and the SVL of chameleons are related by the allometric relation $M = 21.9 L_{SVL}^3$ (in MKS units, see Supplemental Information) [20]. Combined with Eq. (7) and measured viscosity, we find that the maximal prey mass is a significant fraction of the chameleon mass, $m^* > 0.3M$. The wet adhesion alone is therefore sufficient to allow the capture of very large preys. The adhesive mechanism appears then to be outsized with respect to the usual preys found in stomachal contents (see Figure 4). This outstanding adhesion strength allows however chameleons to capture birds, lizards or mammals when they are close enough for a shot.

Considering that adhesion compensates inertial forces, the maximum prey mass is then directly related to the maximum adhesion strength Eq. (5) as follow

$$m^* = \rho V^* = F_{\text{max}}/a = \left[ \frac{9}{8\sqrt{2\pi}} \right]^{2/3} \left[ \frac{K\eta^2\Sigma^4a h_0^{-4}}{4\pi aK h_0^4} \right]^{1/3},$$

where $\rho \approx 1050$ kg/m$^3$ is a typical prey density [23]. In the literature, two studies report in vivo analysis of the stomachal contents for a large number of chameleons to determine various parameters including the mean maximum prey size in relation to the chameleon SVL [24, 25]. The maximal prey volume is obtained as a function of the SVL in Ref. [25] whereas, the maximal prey width is measured as a function of the chameleon head length in Ref. [24]. To gather these data into a single graph, we calculate, from various scaling laws found in literature, the average prey size (given by $V^* = 1/3$) as a function of the SVL for both studies (see Supplemental Information). The results are presented in Fig. 4 together with the maximum prey size derived from the physical model (7) which, using the parameter values reported above, reduces to $V^* = (0.34 \pm 0.2)L_{SVL}$. The maximum prey size estimated from the adhesion model is close but always larger than the experimental data. The global trend of the data follows a scaling similar to the theoretical prediction, see Fig. 4.

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For $T < T^*$, Fig. 3 shows that the film thickness remains essentially constant during the retraction phase, the elastic deformation of the compliant tongue accommodates the displacement.

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FIG. 2. Kinematics profiles for one representative capture of a cricket by a Chamaeleo calyptratus specimen. a. Position of the tip of the chameleon tongue as a function of time. b. Velocity as a function of time computed from a nonlinear fit of $x(t)$. c. Acceleration as a function of time. The onset of tongue projection is characterized by a large acceleration ($\sim 300$ m/s$^2$) which decreases continuously until it vanishes when the velocity is maximal. It is followed by continuous deceleration which continues after the prey contact until the tongue elongation is maximal and the velocity is vanishing. The onset of retraction is also characterized by a large acceleration ($\sim 300$ m/s$^2$) which decreases (in modulus) until it vanishes and the velocity stays then essentially constant. The vertical dashed lines define three different stages of the prey capture process. d-i. Time sequence of a capture extracted from a movie shown in Supplementary Information where the three different stages are indicated.
The relations (6) and (7) clearly pave the way to the optimization of prey capture with an adhesive probe. To be efficient the capture system should maximize both the prey maximum mass, \( m^\ast \), and the detachment time, \( t^\ast \). For instance, increasing the acceleration decreases \( m^\ast \) and shortens \( t^\ast \). Decreasing \( K \), i.e., the elastic modulus of the tongue, increases \( t^\ast \) to the detriment of \( m^\ast \). Therefore, only two parameters influence positively the adhesive trap: the fluid viscosity and the contact area. The specific shape of the tip of the chameleon tongue which is large and form a kind of cup during the projection due to the action of specific muscles [13] allows a drastic increase of the tongue-prey contact area, \( \Sigma \). Indeed, a cup shape with highly deformable lips allow a large embedding of the prey within the tongue. Interestingly, P. (salamanders) use also a ballistic tongue for prey capture and have also developed a large and flexible tongue pad to engulf the prey and thus maximize the contact area [27]. A large mucus viscosity, as measured above, is also necessary. To illustrate the importance of viscosity, considering adhesive fluids similar to usual saliva (\( \eta \approx 10^{-3} \) Pa s) would reduce the maximal prey mass by a factor 50. In that case, the chameleons would only be able to capture very small preys, weighing much less than 1 g. To get a similar benefit, the lizards should capture much more preys which is not favorable for an ambush predator.

Within this framework, considering that large accelerations improve prey capture with adhesive tongue appears clearly as a misconception. Equations (6) and (7) show that both the critical prey mass and the detachment time can be maximized by a vanishing acceleration. Indeed, for most predators capturing preys with their tongue, drastically smaller accelerations are involved (e.g., for Pogona vitticeps, \( a \approx 4 \) m/s\(^2\) [29]). The extremely high accelerations observed for chameleons can thus be penalizing.

The advantage of such outstanding accelerations about 300 m/s\(^2\) must then be related to the tongue projection at distance larger than the body size which is a great evolutionary advantage for ambush predators. The ability of chameleons to throw their tongue requires a large initial acceleration generated by a muscular spring [6, 9]. This acceleration ensures a projection of the tongue as a ballistic projectile, leading to a quasi-straight trajectory making easier the shot towards the target and decreasing the time needed to reach the prey. With this system, the chameleon can visually explore its environment without moving [30] and catch preys at long distance in a rather large surrounding. However, the mechanisms of adhesion must be able to sustain these very large accelerations. As shown in this study, this was achieved through an increase of the adhesive fluid viscosity and of the contact area.

**METHODS SUMMARY**

**Rolling beads experiments.** The viscosity of the adhesive fluid was measured from a rolling bead method. Steel beads were used with known mass (0.175 – 0.88 g) and diameter (1.75 – 3 mm). The mucus fluid was collected by scratching a glass plate on the chameleon’s tongue, the thickness of the fluid being measured by weighing on a micro-balance. The sequence of rolling was recorded with a camera operating at 500 fps. The position of the bead was obtained by direct analysis of digitalized video with ImageJ. The velocity of the bead was then measured in the fluid viscosity, as measured above, is also necessary. To illustrate the importance of viscosity, considering adhesive fluids similar to usual saliva (\( \eta \approx 10^{-3} \) Pa s) would reduce the maximal prey mass by a factor 50. In that case, the chameleons would only be able to capture very small preys, weighing much less than 1 g. To get a similar benefit, the lizards should capture much more preys which is not favorable for an ambush predator.

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**Kinematics of capture.** Sequences of cricket capture by Chameleo calyptratus were recorded with a Photron high speed camera operating at 1000 fps. The nose-tongue pad distance data, \( x(t) \), were directly measured with ImageJ on digitalized video. The velocity and acceleration were calculated from a nonlinear fit of the \( x(t) \) data.
AUTHOR CONTRIBUTIONS

P.D. and V.B. designed the research. L.Z., D.L. and F.B. measured the viscosities with the rolling beads method. L.Z. and P.D. recorded and analyzed the videos of the prey capture kinematics. F.B. and P.D. modeled the adhesion physical mechanisms. P.D. and F.B. wrote the paper.

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Supplementary information for “Is viscous adhesion strong enough to allow prey capture by chameleons?”

I. SCALING RELATIONSHIPS BETWEEN RELEVANT PARAMETERS AND SVL LENGTH

Compliance of the tongue – The model developed in the main text involves two morphological parameters which vary with the chameleon sizes defined as the snout-vent length (SVL). The compliance of the tongue is one of these parameters and is defined as \( K = ES_T / L_T \), where \( E \), \( S_T \), \( L_T \) are the elastic modulus, the cross section area and the length of the tongue respectively. To determine the evolution of \( K \) with \( L_{SVL} \), the evolution of \( S_T \) and \( L_T \) with \( L_{SVL} \) should therefore be known.

The length of the unstretched tongue, \( L_T \), is approximated by the length of the entoglossal process (the tongue’s skeletal support), \( L_{ent} \), and is reported as a function of the SVL in Fig. 5 for a large number of specimens among various species [1]. In good accuracy, \( L_T \) behaves linearly with \( L_{SVL} \), as follows

\[
L_T \simeq L_{ent} = (0.27 \pm 0.05) L_{SVL}. \tag{8}
\]

The cross section area of the tongue is obtained indirectly from the mass of the tongue by approximating the volume of the unstretched tongue by the one of a cylinder such that \( m_T \simeq \rho_m S_T L_T \). The evolution of the tongue mass as a function of \( L_{SVL} \) is shown in Fig. 6 for a large number of specimens among various species [1]. In good approximation, \( m_T \) behaves as the third power of \( L_{SVL} \) as follows

\[
m_T = (0.45 \pm 0.09) L_{SVL}^3 \tag{9}
\]

where all quantities are expressed in MKS units. These two relations 8 and 9, together with the typical density and elastic modulus of muscles (\( \rho_m \simeq 1060 \text{ kg/m}^3, E \simeq 50 \text{ kPa} \) [2], gives then the evolution of the compliance \( K \) as a function of the chameleon size:

\[
K = (350 \pm 180) L_{SVL}. \tag{10}
\]

Area of the tongue pad – The second morphological parameter needed in the model developed in the main text is the contact area between the prey and the tongue, \( \Sigma \). Since our intend is to quantify the maximal size of the prey which can be captured by wet adhesion, \((V^*)^{1/3}\), has been obtained as a function of the chameleon sizes. The corresponding prey mass, \( m^* = \rho V^* \), is then compared to the total mass of the chameleon, \( M \). For this purpose, the evolution of \( M \) with respect to \( L_{SVL} \) should be known. This relation is reported in Fig. 6 for a large number of specimens among various species [1]. As expected, \( M \) behaves as the third power of \( L_{SVL} \) as follows

\[
M = (21.9 \pm 4.0) L_{SVL}^3, \tag{12}
\]

in MKS units.

Head length – In order to compare the predictions of the model with available data, the measures performed in Ref. [5] needed to be manipulated. In particular, the head length, \( L_{head} \), must be related to the SVL. This evolution is shown in Fig. 8 for a significant number of specimens among several species [3]. In good approximation, \( L_{head} \) behaves linearly with \( L_{SVL} \) as follows

\[
L_{head} = (0.27 \pm 0.05) L_{SVL}. \tag{13}
\]
II. MAXIMUM PREY SIZE VS SVL LENGTH - DATA MANIPULATIONS

In order to test the adhesion model presented in the main text, we compare the estimation of the maximal prey size with two studies reporting in vivo data giving the maximal prey size as a function of the chameleon size [5,6]. They use the analysis of the stomachal contents for a large numbers of chameleons to determine various parameters including the mean maximal prey size. In Ref. [6], the authors measured the maximal prey volume as a function of the SVL. These data can therefore be used directly in Fig. 4 of the main text. However, in Ref. [5], the authors measured the maximal prey width as a function of the head length. The relation between the head length and the SVL has been obtained in Eq. (13). Therefore, the complete conversion of the data requires the estimation of the prey volume from the prey width in order to obtain the average prey size (given by $V^{1/3}$) as a function of SVL for both studies.

The prey volume is approximated by the one of a cylinder: $V = (\pi/4)W^2L$, where $W$ is the width and $L$ the length of the prey. The evolution of $L$ with respect to $W$ is reported in Fig. 9 for a large set of invertebrates and insects [7-10]. By using the following relation,

$$L = (2.8 \pm 1.5)W,$$

90% of the data are included (see grey area in Fig. 9). This last relation allows to express the volume as a function of the width only. Therefore, the conversion for the prey size is made with the relation

$$V^{1/3} = (1.3 \pm 0.2)W.$$

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