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# Hydrodynamics of the frontal strike in aquatic snakes: drag, added mass and the possible consequences for prey capture success.

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- 14 *Running title:* Hydrodynamics of snake prey capture
- 15 *Summary statement:* The present work explores the functional implications of head shape
- 16 in a group of aquatic predators using a fluid mechanics approach.

#### 17 Abstract

18 Natural selection favors organisms that are the most successful in fitness-related behaviors such as foraging. Secondary adaptations pose the problem of re-adapting an 19 20 already 'optimized' phenotype to new constraints. When animals forage underwater, they 21 face strong physical constraints, particularly when capturing prey. Successful prey capture 22 requires a predator to be fast and to generate a high acceleration. This involves two main constraints due to the surrounding fluid: drag and added mass. Both constraints are related 23 to the shape of the animal. We experimentally explore the relationship between shape and 24 performance in the context of an aquatic snake strike. As a model, we use two different 3D-25 printed snake heads representing typical shapes of aquatically-foraging and non-aquatically-26 27 foraging snakes, and frontal strike kinematics based on *in vivo* observations. By using direct force measurements, we compare the drag and added mass faced by the aquatic and non-28 29 aquatic snake models during a strike. Our results show that both drag and added mass are 30 optimized in aquatic snakes. Using flow field measurements with particle image velocimetry, we examine the fluid dynamical mechanisms that could be behind the reduction 31 32 of hydrodynamic constraints observed for the aquatic snake head shape, which makes it well 33 suited to capture prey under water.

34 Key words: snakes, fluid mechanics, forces, morphology, prey capture

#### 35 Introduction

36 Aquatic animals have to overcome the strong viscous and inertial constraints associated with underwater movement<sup>1</sup>. Physically, these constraints are related to the 37 kinematics of movement and the morphology of an animal (i.e. the shape of the object that 38 39 is facing the flow). For most aquatic vertebrates, viscous effects are confined to a thin 40 boundary layer surrounding the body, which couples the motion of the animal with that of the surrounding fluid and gives rise to the skin friction that penalizes aquatic locomotion. In 41 addition, fluid inertia causes the boundary layer to separate from the animal's body, creating 42 the recirculation zones associated to pressure drag  $^2$ . The specifics of the flow separation 43 determine the relative importance of pressure to skin friction drag<sup>3,4</sup>. In addition to drag, 44 which depends on the velocity of the animal, the hydrodynamics are also dependent on 45 acceleration of the added mass <sup>5,6</sup>. This corresponds to the mass of fluid that is accelerated 46 together with the animal and which exerts a reaction force. Both drag and added mass depend 47 on the size and shape of the body <sup>5</sup>, and it can thus be expected that the morphology of 48 aquatic animals has evolved to reduce drag and added mass. However, organisms have a 49 50 morphology that is also constrained by evolutionary history, functional trade-offs, and developmental programs thus restricting the range of possible morphological adaptations. 51 Environmental and biological constraints act simultaneously on an organism and may all 52 impact their evolution, sometimes leading to convergent phenotypes <sup>7-10</sup>. Morphological 53 convergence is common across the animal kingdom, yet its impact on function has only 54 rarely been tested <sup>11–15</sup>. We here use the case of convergence in head shape in aquatic snakes 55 <sup>16</sup> to provide an experimental test of the suggested functional advantages of observed 56 similarities in the head shape of aquatic snakes. 57

58 Snakes are an ideal model to study convergence as they have invaded the aquatic 59 medium multiple times independently throughout their evolutionary history. However, they do not show any of the usual adaptations to aquatic prey capture (e.g. they cannot perform 60 suction feeding due to their reduced hyoid <sup>14</sup>). Snakes have to deal with the hydrodynamic 61 constraints when capturing a prey, and as these constraints are related with the shape <sup>1,13,17</sup>, 62 the head of aquatically foraging snakes should have evolved in a way to minimize the 63 constraints. Convergence in head shape in aquatic snakes has been demonstrated previously 64  $^{14-16,18,19}$ . In a previous work  $^{16}$ , we compared the head shape of 62 species of snakes that 65 capture prey under water (from sea snakes over homalopsids to North American 66 watersnakes) versus 21 phylogenetically closely related species that do not forage under 67

water. We used 3D geometric morphometrics on surface scans of these species and ran 68 phylogenetic analyses demonstrating a morphological convergence in head shape of 69 aquatically foraging snakes. Moreover, we characterized the shapes that are specific of both 70 group of snakes (i.e. the aquatic and the non-aquatic foragers). We hypothesized that the 71 convergent shape would provide a hydrodynamic advantage to aquatic foragers in 72 73 comparison with their close relatives that do not capture aquatic prey. Several previous studies similarly have suggested convergence to give rise to a functional advantage <sup>13,14,16,20</sup>, 74 yet this has never been tested experimentally. Thus, we here propose an experiment to test 75 76 this idea. In other words, we investigate whether the head shape associated with aquatically 77 foraging snakes has a hydrodynamic advantage over the shape associated with the non-78 aquatic foragers. The hydrodynamic constraints involved during a strike are the pressure drag - skin friction being negligible in the regimes of interest here  $^{11}$  - and the added mass. 79 80 Both of these constraints are related to a certain extent to the shape of the object that is moving through a fluid <sup>5,6</sup>. Thus, if our hypothesis is correct, the shape corresponding to the 81 82 aquatic forager should show less drag and added mass than the non-aquatic model.

83 Another constraint related to the capture of prey under water is the mechanosensitivity of aquatic prey like fish. The lateral line system of fish is composed of 84 mechanoreceptors that can detect very small pressure variations with an estimated threshold 85 of 0.1 to 1 mPa at 1 mm<sup>21,22</sup>. This system triggers a reflex escape response in the prey once 86 a pressure threshold has been reached. Previous studies have suggested that a snake moving 87 88 underwater generates a bow wave that might be able to trigger the reflex response of the prey <sup>11,14</sup>. We tested this hypothesis and predicted that aquatic snakes should be stealthier than 89 non-aquatic snakes during the strike such that the detection of the predator by the prey would 90 be delayed. 91

We use direct force measurements on two 3D printed models of snake heads derived 92 from our previous work based on the comparison of 83 species of snakes <sup>16</sup> (i.e. more than 93 400 snake specimens). As these models results from a 3D geometric morphometric analysis, 94 95 the models are scaled to the same size, allowing us to specifically test for the impact of shape on hydrodynamic constraints. Our experimental setup mimics a 'sit-and-wait' frontal strike 96 under water, meaning that the model remains motionless before the strike and is then 97 suddenly accelerated to reach an almost constant speed for a short time. We compared 98 models with the mouth open, as aquatic snakes keep their mouth opened during frontal 99 strikes (Fabre et al., 2016; van Netten, 2006; Vincent et al., 2009, Herrel and Segall pers 100

101 obs.). The force applied to the head during the strike was recorded to characterize the added 102 mass and drag, which determine the hydrodynamic efficiency of a strike. In addition, another 103 sensor was placed at the end of the strike track to assess the distance at which a prey is likely 104 to detect the presence of the snake during capture. Particle Image Velocimetry (PIV) was 105 used to visualize the flow field around the head during a strike. We also characterized the 106 evolution of the vortex intensity during a strike for each shape, as it is closely related to the 107 hydrodynamic forces generated by a moving object <sup>23–25</sup>.

108 Material & Methods

#### 109 *3D models*

We compared two models that we termed "aquatic" and "non-aquatic" (Fig. 1). These 110 111 shapes result from a 3D geometric morphometric study showing that the head shape of aquatic snake species has converged, possibly in response to the hydrodynamic constraints 112 involved during prev capture under water <sup>16</sup>. We compared the hydrodynamic forces that are 113 exerted on each of the head shapes during a simulated capture event. The geometric 114 morphometric analysis allows to extract shapes independent of variation of size such that the 115 shapes are directly comparable to one another. In a next step we opened the mouth of the 116 117 models as snake use to attack their prey with the mouth open. We used Blender<sup>TM</sup> to rotate the jaw and the top of the head to reach an angle of  $70^{\circ}$  based on previously published data 118 on frontal strikes in snakes <sup>14,26,27</sup>. The two models were then 3D printed using a Stratasys 119 Fortus 250 MC 3D printer with ABS P430 as a material (Fig. 2a.). 120



121

## Figure 1: 3D models of the head shape of non-aquatic (left) versus aquatic snakes (right) in front, side and top view.

124 *Experimental setup* 

Snakes capture their prey using high acceleration forward motions that we mimicked using springs (Fig. 2a). We generated a range of speeds and accelerations by applying a different compression on the spring. We used a force sensor FUTEK LSB210+/-2 Lb to

record the force exerted on the models which were positioned horizontally inside a water 128 129 tank. This sensor was attached to the model using an aluminum rod and recorded the axial forces applied to the head during a strike. The other side of the sensor was attached to a 130 bracket (sensor 1, Fig. 2a) that was itself hooked on the movable part of an air-bearing rail 131 that allows the system to remain frictionless. This movable part was compressed against the 132 spring and suddenly released. The length of the path was 20cm. Approximately 60 trials (i.e. 133 spring compressions) were done for each model. To obtain the kinematics of each strike, we 134 135 recorded the position of the movable part using a position sensor (optoNCDT1420, Micro-136 Epsilon) (Fig. 2a).

In addition, we wanted to assess what a prey would sense in terms of pressure, so we placed another, more sensitive, force sensor (FUTEK LSB210 100 g) at the end of the path to which we attached a round plastic piece of diameter 7 cm that allowed us to record the pressure changes (sensor 2, Fig. 2a). This sensor provided information about the distance at which a prey could potentially detect the presence of a snake during a strike. The force and position sensors were synchronized, and data were recorded at 1 kHz.



Figure 2: a. Experimental setup used to simulate a frontal attack of a snake towards a
prey. b. Example of the output of the force sensor 1 (red line), force sensor 2 (green dashed
line) and velocity (blue line) during one trial (i.e. one strike). The plateau and peak force
used to calculate the hydrodynamic forces are indicated.

#### 148 Drag coefficient and added mass

149 The first part of the strike is the acceleration phase during which the velocity 150 increases. This phase corresponds to the decompression of the spring. It is correlated with a dramatic increase in the force that is applied to the snake head model (red line, sensor 1, Fig. 151 152 2). Once the springs are completely decompressed, the system is no longer accelerating, and the velocity decreases slowly. In parallel, the force applied to the model decreases until it 153 reaches a plateau-like phase (Fig. 2b). Then, the system hits the stop at the end of the track 154 and moves backward generating a large drop in both velocity and force signaling the end of 155 156 the trial.

During the plateau phase (Fig. 2b), the only force that is applied to the model and thus, the only force that is recorded by the sensor is the drag force. Thus, we used the average force recorded during this phase ( $F_d$ ) to calculate the drag coefficient ( $C_d$ ) of both of our models by using the standard definition <sup>2</sup>:

161 
$$C_d = \frac{2F_d}{\rho U^2 S} \qquad (1)$$

where  $F_d$  is the drag force,  $\rho$  is the density of water, U the velocity of the object and S its projected frontal surface area, which was measured at 12.89 cm<sup>2</sup> for the aquatic model and 14.72 cm<sup>2</sup> for the non-aquatic model. The term  $2F_d/\rho S$  was plotted against  $U^2$  and the linear regression coefficient corresponds to the drag coefficient of the models (Fig. 3). The Reynolds number range of our experiments is  $1.10^4$ - $7.10^4$ .

167 During the acceleration phase, both drag and inertial forces are at play, meaning that 168 the peak force ( $F_{peak}$ , Fig. 2b) recorded by the force sensor is composed of these two forces. 169 To calculate the added mass generated by both models, we used the following calculation 170 steps for each trial, we first calculated the inertial force by subtracting the instantaneous drag 171 force from the peak force measured by the sensor:

172 
$$F_i = F_{peak} - F_{d(t1)}$$
 (2)

where  $F_i$  is the inertial force applied to the model and  $F_{d(t)}$  is the instantaneous drag force when the acceleration reaches its maximum:

175 
$$F_{d(t1)} = \frac{1}{2} \rho U_{(t1)}^2 C_d S \quad (3)$$

176 Here  $\rho$  is the density of water, U<sub>(t1)</sub> the velocity at the instant the acceleration is maximal 177 and *S* the projected frontal surface area of each model. Now, the added mass *M* can be 178 computed as:

$$M = \frac{F_i - ma}{a}$$
(4)

180 where m is the mass of the object, and a the acceleration.

181 Finally, the added mass coefficient  $(C_a)^2$ :

182 
$$C_a = \frac{M}{\rho V}$$
(5)

183 where *V* is the volume of the model:  $7.33.10^{-5}$  m<sup>3</sup> for the aquatic model and  $5.78.10^{-5}$  m<sup>3</sup> for 184 the non-aquatic model.

185 The added mass coefficient was obtained by plotting the added mass term  $(F_i - ma)/\rho V$ , 186 against the acceleration (a). The linear regression coefficient corresponds to the added mass 187 coefficient of the models (Fig. 4).

188 *Detection distance* 

To compare the effect of the head shape on the detection by a possible prey we used the output of the second force sensor (sensor 2, Fig. 2a). This sensor can detect pressure variations of approximately 0.3 Pa which is around the hearing and the startle threshold of some fish (i.e. between 0.01Pa and 0.56Pa)  $^{28,29}$ . To estimate the position at which the prey could detect the predator, we defined the detection distance *d* as the position at which the force detected by sensor 2 deviates from the unperturbed value by more than one standard deviation of the sensor output before the strike (green dashed line, Fig 2b, Fig. 5).

196 Particle Image Velocimetry

We used 2D Particle Image Velocimetry (PIV) with a high-speed camera, DantecDynamics SpeedSense M, to obtain a time-resolved recording of the strike from the bottom

of the tank (Fig. 2a.). Water was seeded with polyamid particles of 20 µm in diameter and a 199 200 Quantronix® Darwin-Duo laser was used to produce the light sheet. Image acquisition was 201 performed at 733Hz. We choose to record three different planes on each head to obtain a 202 complete picture of the fluid flow around the head during the attack (see Supplementary Fig. 203 S1). We applied the same compression to the springs (i.e. maximal compression) to get an 204 equivalent comparison for the different shapes. Acquisition was performed using the Dantec DynamicStudio 2015a software. The PIV vector computation was performed using LaVision 205 7.2 with a 16 x 16 pixel<sup>2</sup> interrogation window and 50% overlap. Additional post-processing 206 and analysis was done in Matlab using the PIVMat toolbox <sup>30</sup>. A more quantitative analysis 207 was performed by computing the overall primary circulation  $\Gamma = \int \omega^+ dA$  in each PIV plane 208  $(\omega^+$  being the positive vorticity in Fig. 6b.). The evolution of the dimensionless circulation 209 210  $\Gamma/UL$  as a function of time, where L is the characteristic length scale of the acceleration regime of the strike maneuver (which is constant for all experiments) and U is the velocity 211 212 of the strike is plotted in Fig. 6b.

213

#### Statistical analyses

To test for differences between the drag coefficients of the two shapes, we ran a Pearson correlation on the force component of the drag coefficient  $(2F_d/\rho S)$  with the square velocity ( $U^2$ ). An ANCOVA with mass as a co-variate was performed to test for statistical differences in the drag coefficient between the two models. To compare the detection distance, we ran an ANCOVA with the distance as the response variable, the model as a factor, and the velocity as covariate. All the variables were Log<sub>10</sub>-transformed and the statistical analyses were performed using R<sup>31</sup>. The significance level was set at 5%.

#### 221 **Results**

#### 222 Drag and added mass

The drag coefficient of the non-aquatic shape is higher than the coefficient of the aquatic model, respectively 0.64 and 0.26 (Pearson's correlation: nonaq: df = 67, P < 0.001, R<sup>2</sup> = 0.996; aq: df=64, P < 0.001, R<sup>2</sup> = 0.995; ANCOVA:  $F_{2,132} = 671.1$ , P < 0.001) (Fig. 3).



226

Figure 3: Drag term  $2F_d/\rho S$  depending on the velocity term of the strike (U<sup>2</sup>) for the two head models tested. Linear regression lines are drawn. The slopes correspond to the drag coefficient of each shape and the R<sup>2</sup> are the regression coefficients. Squares: non-aquatic model, circles: aquatic model.

The mean added mass obtained is 12.67 g for the aquatic model versus 14.95 g for the non-aquatic model. The added mass coefficients obtained from the linear regression on Fig. 4 are 0.151 for the aquatic model and 0.235 for the non-aquatic model.



234

Figure 4: Normalized inertial force term  $(F_i - ma)/\rho V$  depending on the acceleration of the strike (a in m.s<sup>-2</sup>) for the two head models tested. Linear regression lines are drawn.

### The slopes correspond to the added mass coefficient of each shape and the $R^2$ are the regression coefficients. Squares: non-aquatic model, circles: aquatic model.

#### 239 *Detection distance*

The force signal was too noisy to get any accurate measures of the detection distance at low velocities (i.e. U > 0.5 m.s<sup>-1</sup>). There is moreover no statistical difference between the distances at which the prey could detect the presence of the snake depending on their head shape. However, this distance depends on the maximal velocity of the strike, the faster the strike, the earlier the detection of the predator (ANCOVA:  $F_{2,84} = 5.05$ ; P = 0.008; model: P= 0.65; Umax: P = 0.008) (Fig. 5).

246



Figure 5: a. Zoom on the prey sensor output highlighting the method used to determine the detection distance, using the 1sd (standard deviation) threshold (not at scale here). b. Distance (cm) at which the prey could potentially detect the snake depending on the maximal velocity of the strike (m.s<sup>-1</sup>). For each graph: squares: non-aquatic model, circles: aquatic model.

253 Flow characterization

The frontal strike maneuver involves strong flow separations due to the high shear produced by the impulsive acceleration. The flow features can be characterized by examining the vortex structures formed at the corner of the mouth and on both tips of the jaw and of the skull. We created videos of the vortex formation during a strike, obtained from PIV in three planes around the snake heads (see Materials and Methods section), to compare both models (see Supplementary videos S2-4). The PIV measurements show the

formation of vortices during the strike maneuver. In Fig. 6a, we compare the vorticity field 260 261 at the end of the acceleration phase (at t  $\approx 0.8$  s) in the three measurement planes; bottom view, jaw view, and skull view (Supplementary Fig. S1) for the aquatic and non-aquatic 262 263 heads. Looking at the bottom view, the advantage of the aquatic model seems to be related to a smaller primary vortex. The picture is not as straightforward considering the jaw and 264 skull view, where opposite observations on the primary vorticity production can be observed 265 qualitatively: on the jaw view the primary vorticity patch appears more detached from the 266 jaw in the non-aquatic case, whereas in the skull view the same is true for the aquatic case. 267 268 Fig. 6b shows the quantitative analysis of the primary circulation. First, we can see that in the bottom view the aquatic model induces a slightly (~10%) lower overall circulation over 269 270 the whole acceleration phase. Second, for the jaw view it can be remarked that a much lower 271 overall circulation is produced by the vorticity detached from the tip of the jaw in the aquatic 272 case (around 40% of the non-aquatic value at the end of the acceleration phase). The picture 273 in the skull view is the opposite with the aquatic shape generating more overall circulation 274 but the difference between the two models is less important than for the jaw view. We note 275 also for the skull view that the computed value for the circulation is more variable.



276

Figure 6: a. Snapshots of the vorticity field  $\omega_z$  around the snake head models at the end of the acceleration phase for the aquatic (first line) and non-aquatic (second line) models, in the three measurement planes: bottom, jaw and skull views are shown on the first to third columns, respectively. The color bar for the vorticity field is given in s<sup>-1</sup>. b. Evolution

# of the dimensionless integrated positive circulation during the acceleration phase depending on the time for both models in each of the three views considered.

#### 283 Discussion

Drag is well known for its importance during steady locomotion. However, it is also 284 involved in transient behaviors such as the capture maneuver studied here. Certainly, the 285 286 aquatic shape appears better adapted to capture aquatic prey using a frontal strike than the 287 non-aquatic shape in terms of drag. The aquatic model has a drag coefficient that is almost 3 times smaller than the non-aquatic model. As mentioned above, drag in this fast-impulsive 288 289 maneuver is mainly pressure drag, which is intimately linked to the flow separation in the 290 near wake of the snake head as it moves. The PIV measurements illustrate the vortices that 291 are formed very early during the strike (see Supplementary videos S2-4). Looking at the bottom view in Fig. 6, the drag advantage of the aquatic model could be related to a smaller 292 293 primary vortex, the non-aquatic case showing a more fluctuating and disordered flow field. 294 Moreover, the vorticity produced at the tip of the jaw shows a clear quantitative difference 295 and is consistently higher for the non-aquatic model. However, the skull view shows the 296 opposite pattern of vorticity; the non-aquatic shape produces fewer vortices with an integrated primary circulation that is less important than for the aquatic model. It should be 297 298 noted that the 2D nature of the PIV measurements presented here does not allow us to 299 provide a quantitative link between drag and the vorticity profile of the flow around the head. 300 Nonetheless, from the present results we can conjecture that a reduction of the recirculation 301 bubble behind the jaw may be one of the main physical mechanisms explaining the physical 302 advantage of the head shape observed in aquatically foraging snakes.

Transient maneuvers under water, such as the underwater prey capture in snakes, 303 304 implicate an acceleration phase that not only involves drag but also inertia. Inertial forces 305 under water are associated with the mass of the object but also with a mass of the fluid that 306 is accelerated. Thus, the relationship between inertia and shape is not straightforward. However, some studies suggested that an optimal body shape for transient propulsion, such 307 as a snake strike, would be an elongated, streamlined, and flexible body and non-muscle 308 mass reduction, which corresponds to a snake-like configuration  $^{1,17}$ . To our knowledge, no 309 study to date has focused on the shape of the head and its role. In this study, we highlight 310 311 that the hydrodynamic forces associated with a transient maneuver are important in 312 comparison with drag (e.g. the peak of force in comparison with the plateau on Fig. 2).

Moreover, we demonstrated that the aquatic shape allows to reduce the added mass and is associated with a smaller added mass coefficient. This suggests that drag is not the only driver of the evolution of head shape in aquatic snakes. Moreover, added mass and drag optimization do not require divergent morphological features in the case of aquatic snake strikes, unlike what suggested for the body shape of fish <sup>17</sup>.

318 Regarding the prey detection distance, our results show that this distance does not 319 depend on the snake head shape, but rather that it increases with strike velocity. However, we cannot conclude on the biological relevance of the absolute prey detection distance 320 measured in our experiment as our setup was built with as primary purpose to measure drag 321 322 and added mass. Snakes usually strike when the prey is close to their head (e.g. 0.5-0.8 cm for Erpeton tentaculatum<sup>32</sup>; 4.87 cm for T. couchii; 2.81 cm for T rufipunctatus<sup>33</sup>; less than 323 3 cm for *Hydrophis schistosus* <sup>34</sup>). The detection distance measured here is around 6 to 10 324 cm, so we could consider that the prey can possibly detect the snake almost instantaneously 325 326 upon the strike initiation, the reaction time of a fish being around 7 ms  $^{32}$ . Capture success is thus more likely determined by the hydrodynamic profile of the snake head than being 327 328 dependent on the reaction of the prey.

In conclusion, we investigated the role of head shape on the hydrodynamic forces 329 330 generated by a predator using an experimental approach focusing on a transient maneuver. 331 We were able here to quantify the role and impact of head shape in the hydrodynamics of 332 prey capture in aquatic snakes. We highlighted a clear hydrodynamic advantage of the 333 aquatic head shape when capturing a prey being associated not only with a smaller drag 334 coefficient but also a smaller added mass coefficient. These results validate the hypothesis 335 that the morphological convergence of the head shape in aquatic snakes is an adaptation to 336 an aquatic lifestyle as it provides a clear hydrodynamic advantage. In this work, we focused 337 on the shape of the head of aquatically foraging snakes, as several studies have highlighted convergence therein, and as shape plays a crucial role in the hydrodynamic constraints as 338 well. Size could be an important feature regarding the hydrodynamic constraints. However, 339 340 we did not detect any allometry in our morphological study, meaning that the aquatically foraging snakes are not significantly different in size than their closely related non-aquatic 341 species. Thus, the present work focuses on the functional meaning of shape irrespective of 342 size. The other factors that could play a role in the hydrodynamics of the prey capture of 343 aquatic snakes could be the gape angle and macro and microscopic skin features which 344 remains to be investigated. 345

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421 Asknowledgments		

421 Acknowledgments

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#### 428 Author contributions

All authors helped revise and approved the manuscript and conceived the study. MS carried out the data collection, the statistical analyses, and wrote the manuscript. RGD helped to build the experimental setup and to interpret the data. RGD carried out the particle image velocimetry analysis. AH participated in the scientific interpretation of the data in a

433 biological context.

#### 434 Competing interests

- 435 We have no competing interests.
- 436 Data availability
- 437 See Supplementary Table S5
- 438 Figure legends

*Figure 1:* 3D models of the head shape of non-aquatic (left) versus aquatic snakes (right) in
front, side and top view.

441 *Figure 2: a.* Experimental setup used to simulate a frontal attack of a snake towards a prey.

*b*. Example of the output of the force sensor 1 (red line), force sensor 2 (green dashed line)

and velocity (blue line) during one trial (i.e. one strike). The plateau and peak force used tocalculate the hydrodynamic forces are indicated.

*Figure 3:* Drag term  $2F_d/\rho S$  depending on the velocity term of the strike (U<sup>2</sup>) for the two head models tested. Linear regression lines are drawn. The slopes correspond to the drag coefficient of each shape and the R<sup>2</sup> are the regression coefficients. Squares: non-aquatic model, circles: aquatic model.

*Figure 4:* Normalized inertial force term  $(F_i-ma)/\rho V$  depending on the acceleration of the strike (a in m.s<sup>-2</sup>) for the two head models tested. Linear regression lines are drawn. The slopes correspond to the added mass coefficient of each shape and the R<sup>2</sup> are the regression coefficients. Squares: non-aquatic model, circles: aquatic model.

*Figure 5: a.* Zoom on the prey sensor output highlighting the method used to determine the
detection distance, using the 1sd (standard deviation) threshold (not at scale here). *b.*Distance (cm) at which the prey could potentially detect the snake depending on the maximal
velocity of the strike (m.s<sup>-1</sup>). For each graph: squares: non-aquatic model, circles: aquatic
model.

**Figure 6:** *a*. Snapshots of the vorticity field  $\omega_z$  around the snake head models at the end of the acceleration phase for the aquatic (first line) and non-aquatic (second line) models, in the three measurement planes: bottom, jaw and skull views are shown on the first to third columns, respectively. The color bar for the vorticity field is given in s–1. *b*. Evolution of the dimensionless integrated positive circulation during the acceleration phase depending on the time for both models in each of the three views considered.