

1 **Hydrodynamics of frontal striking in aquatic snakes: drag, added mass, and the possible**
2 **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 in a
16 group of aquatic predators using a fluid mechanics approach.

17 **Abstract**

18 Transient locomotion under water is highly constrained by drag and added mass, yet
19 some aquatic snakes catch their prey using a fast forward acceleration, with the mouth opened.
20 These aquatic snakes show a convergence of their head shape in comparison with closely related
21 species that do not forage under water. As both drag and added mass are related to some extent
22 to the shape of the moving object, we explored how shape impacts the hydrodynamic forces
23 applied to the head of a snake during a prey capture event. We compared two 3D-printed heads
24 representing typical shapes of aquatically-foraging and non-aquatically-foraging snakes, and
25 frontal strike kinematics based on *in vivo* observations. By using direct force measurements, we
26 calculated the drag and added mass coefficient of the two models. Our results show that both
27 drag and added mass are reduced in aquatic snakes. The drag coefficient of the aquatic model is
28 0.24, which is almost two times smaller than the non-aquatic model. The added mass coefficient
29 of the aquatic model is 0.15 versus 0.24 for the non-aquatic model, showing that the convergence
30 of head shape in aquatically foraging snakes is associated with a hydrodynamic advantage
31 during frontal striking. The vorticity field measurements with particle image velocimetry show
32 that a less intense recirculation bubble behind the jaw of the aquatic model, compared to the
33 non-aquatic model, might be the basis of this advantage.

34 **Key words:** snakes, fluid mechanics, forces, morphology, transient motion

35 **Introduction**

36 Aquatic animals have to overcome the strong viscous and inertial constraints associated
37 with underwater motion ¹. Physically, these constraints are related to the kinematics of
38 movement and the morphology of an animal (i.e. the shape of the object that is facing the flow).
39 For most aquatic vertebrates, viscous effects are confined to a thin boundary layer surrounding
40 the body, which couples the motion of the animal with that of the surrounding fluid and gives
41 rise to the skin friction that penalizes aquatic locomotion. In addition, fluid inertia causes the
42 boundary layer to separate from the animal's body, creating the recirculation zones associated
43 to pressure drag ². The specifics of the flow separation determine the relative importance of
44 pressure to skin friction drag ^{3,4}. Pressure drag and skin friction constitute together the steady
45 drag, which depends on the velocity of the animal. During transient maneuvers, such as
46 predatory strikes or predator escapes, an additional constraint is involved: the acceleration
47 reaction^{2,5}. This force that opposes the motion is related to the acceleration the animal imposes
48 on the surrounding fluid while accelerating its own body mass. The mass of fluid that is
49 accelerated along with the mass of the animal is called the added mass and it depends on the
50 acceleration ^{5,6}. Both drag and added mass depend, to some extent, on the size and shape of the
51 body ⁵. As transient maneuvers are involved in survival-related behavior (foraging and predator
52 avoidance), one can expect that the morphology of aquatic animals has evolved to reduce both
53 drag and added mass.

54 However, the morphology of an animal is also constrained by evolutionary history, functional
55 trade-offs, and developmental programs, thus restricting the range of possible morphological
56 adaptations. Environmental and biological constraints act simultaneously on an organism and
57 may all impact their evolution, sometimes leading to convergent phenotypes ⁷⁻¹⁰. These shape
58 convergences occur when constraints are strong, and solutions limited. These designs are
59 particularly interesting from an engineering point of view as the shape results from a long-term
60 selection often over millions of years and thus can provide insights to create new, more efficient
61 designs. There is a continuum between streamlined objects and bluff bodies, but in most cases,
62 hydrodynamic studies focus on rather simple geometries (e.g. sphere, cylinder, plates...; see ²).
63 We here propose to assess how more subtle shape changes may affect both drag and added mass
64 and the possible functional implications of such changes.

65 Capturing elusive prey under water usually involves fast, accelerated motions of the
66 predator (or part of it) towards the prey¹¹ which inevitably involves both drag and acceleration
67 reaction. Among aquatic tetrapod predators, both snakes^{12–17} and turtles use a fast forward
68 motion of the head. The latter have, however, developed suction feeding to overcome the strong
69 physical constraints^{18–20}. Snakes cannot perform suction because of the reduction of their hyoid
70 apparatus^{15,21}, yet convergence in head shape in aquatic snakes has been demonstrated several
71 times^{15,22–25}. As hydrodynamics and shape are intricately related, it is possible that the physical
72 constraints have driven the convergent evolution of the head of snakes toward a more efficient
73 shape (i.e. reducing drag and added mass)^{1,26,27}. In a previous study²⁵, we compared the head
74 shape of 62 species of snakes that capture prey under water (from sea snakes over homalopsids
75 to North American watersnakes) versus 21 phylogenetically closely related species that do not
76 forage under water. Using 3D geometric morphometrics in a phylogenetic framework, we
77 demonstrated morphological convergence in the shape of the head of aquatically foraging
78 snakes and we characterized the shapes that are specific to both groups of snakes (i.e. the aquatic
79 and the non-aquatic foragers). We hypothesized that the head shape of aquatically foraging
80 snakes provides them with a hydrodynamic advantage during the strike and is more efficient.
81 The hydrodynamic constraints involved during a strike are the pressure drag – skin friction being
82 negligible in the regimes of interest here²⁸ – and the added mass. Both of these constraints are
83 related to a certain extent to the shape of the object that is moving through a fluid^{5,6}. Thus, if
84 our hypothesis is correct, the shape corresponding to the aquatic snake should induce less drag
85 and a reduced added mass compared to the non-aquatic snake.

86 Another constraint related to the capture of prey under water is the mechano-sensitivity
87 of aquatic prey like fish. The lateral line system of fish is composed of mechanoreceptors that
88 can detect very small pressure variations with an estimated threshold of 0.1 to 1 mPa at 1 mm
89^{29,30}. This system triggers a reflex escape response in the prey once a pressure threshold has been
90 reached. Previous studies have suggested that a snake moving underwater generates a bow wave
91 that might be able to trigger the reflex response of the prey^{15,28}. We predicted that aquatic snakes
92 should be stealthier than non-aquatic snakes during the strike, such that the detection of the
93 predator by the prey would be delayed.

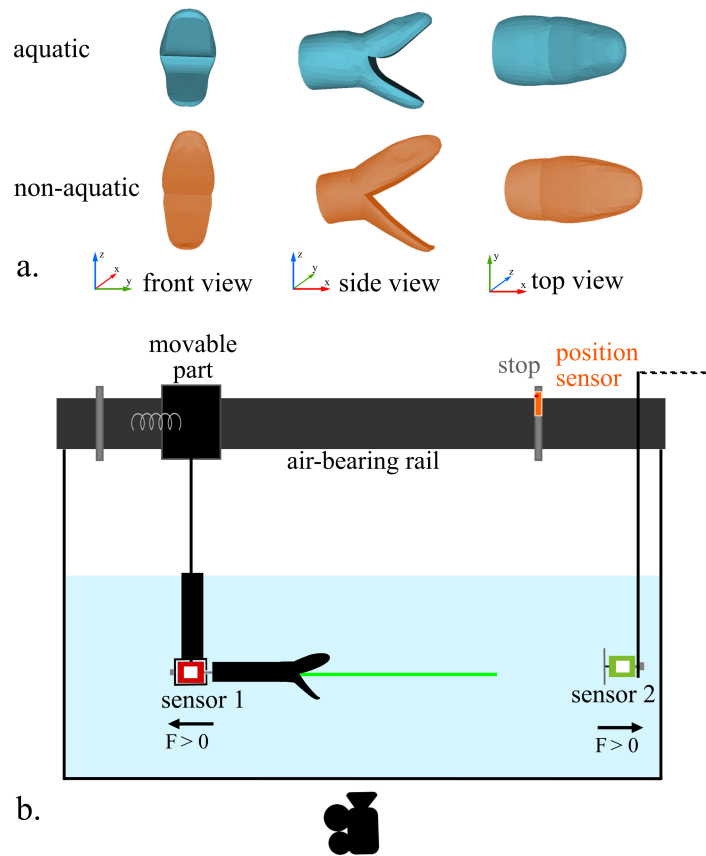
94 We used direct force measurements using two 3D printed models of snake heads derived
95 from our previous work based on the comparison of 83 species of snakes²⁵ (i.e. more than 400
96 snake specimens). As these models result from a 3D geometric morphometric analysis, the
97 models are scaled to the same size, allowing us to specifically test for the impact of shape on
98 hydrodynamic constraints. Our experimental setup mimics a ‘sit-and-wait’ frontal strike under
99 water, meaning that the model remains motionless before the strike and is then suddenly
100 accelerated. The frontal strike is the strategy used by snakes to catch non-aquatic prey, and even
101 though another aquatic prey capture strategy exists (lateral strike¹⁷), many aquatic snake species
102 use fast forward strikes¹²⁻¹⁶. We decided to focus on this strategy as it has been associated with
103 some piscivorous specialists and as it is allegedly the most hydrodynamically constrained²⁷.
104 We measured the force applied to the head during the strike to calculate the added mass and
105 drag, which determine the hydrodynamic efficiency of a shape. In addition, another sensor was
106 placed at the end of the strike track at the level of the model to assess the distance at which a
107 prey is likely to detect the presence of the snake during capture. Particle Image Velocimetry
108 (PIV) was used to visualize the flow field around the head during a strike. We also characterized
109 the evolution of the vortex intensity during a strike for each shape, as it is closely related to the
110 hydrodynamic forces generated by a moving object³¹⁻³³.

111 **Material & Methods**

112 *3D models*

113 We assessed the impact of shape on hydrodynamics by comparing two models of head
114 shape of snakes that we termed “aquatic” and “non-aquatic” (Fig. 1a.). These shapes result from
115 a 3D geometric morphometric study showing that the head shape of aquatic snake species has
116 converged²⁵. We measured the hydrodynamic forces that are exerted on each of the head shapes
117 during a mimicked capture event. The shapes are the result from a geometric morphometrics
118 analysis, meaning they went through a process (i.e. Generalized Procrustes Analysis) that scales
119 the models to the same size (i.e. centroid size of 1.0) and removes differences in position by
120 translating and rotating the models (see³⁴). Thus, the only difference between the models is
121 their shape. As snakes catch their prey with the mouth opened, we divided the two models in a
122 homologous way by cutting the head in three parts (the top of the head, the jaw, and the rear of
123 the head) following the same landmarks on each model. Then, we used Blender™ to rotate the

124 jaw and the top of the head to reach an angle of 70° based on previously published data on
 125 frontal strikes in snakes ¹⁴⁻¹⁶ (Supplementary Material 1). The two models were then 3D printed
 126 using a Stratasys Fortus 250 MC 3D printer with ABS P430 as a material, no surface treatment
 127 was applied to the models after printing (Fig. 1a.).



128

129 **Figure 1: a. 3D models of the head shape of aquatic (first line) and non-aquatic snakes**
 130 **(second line) in front, side and top view (see also Supplementary Material 1). b. Experimental**
 131 **setup used to mimic the frontal attack of a snake towards a prey (see also Supplementary**
 132 **Material 2). The snake model is directly linked to the force sensor 1 which is itself vertically**
 133 **attached to the mobile part of the air-bearing rail. The force sensor 2 is placed at the end of**
 134 **the track. It is recording the pressure variation thanks to a round plate attached to the sensor**
 135 **(vertical grey line). The directions of the positive forces of each sensor is indicated ($F > 0$).**
 136 **The position sensor is placed at the end of the track, on the rail. The horizontal green line**
 137 **represents the laser sheet used for the PIV. The model is turned to obtain three different views**
 138 **of the flow pattern around the head (see Supplementary Material 3).**

139

Experimental setup

140 Snakes capture their prey by using an explosive strike toward it, meaning that they generate a
141 high acceleration once the prey is within reach³⁵. Many species of aquatically foraging snakes
142 use a fast forward strike. To mimic this behavior, we projected our models using two springs
143 (Fig. 1b.). Our system is composed of two parts: a rail and a mobile part (Fig. 1b.). The rail
144 insured a strict forward motion of the mobile part. The movable part is composed of the cart that
145 can move along the rail with negligible friction thanks to the air-injection system and two
146 springs, on the left and right part of the cart that allow to generate a transient motion in our
147 system. A copper tube of diameter 1.5 cm is attached to the cart and plunges into the water. We
148 designed a NACA profile to cover the part of the tube that is immersed into the water and we
149 add a space to screw the force sensor 1 (FUTEK LSB210+/-2 Lb; Fig. 1b.). The model is
150 horizontally attached to the force sensor using an aluminum rod of 5 mm diameter. Thus, the
151 model is pushed by the force sensor.

152 For each strike, the two springs on each side of the cart are compressed against a vertical
153 platform attached to the rail. The cart is held in the compressed position for a few seconds, so
154 we got a resting value for the sensors. Then, the cart is released thus generating a transient
155 motion of the cart and the model. The strike stopped when the cart hit the foam stop at the end
156 of the track. We used different compressions of the springs to generate a range of speeds and
157 accelerations. Approximately 60 strikes (i.e. spring compressions) were performed for each
158 model. To obtain the kinematics of each strike, we recorded the position of the movable part
159 using a position sensor (optoNCDT1420, Micro-Epsilon) (Fig. 1b.). The kinematics of the
160 strike, namely the velocity $U_{(t)}$ and the acceleration $a_{(t)}$ (Fig. 2), are computed from the output
161 of the position sensor using Eq (1) and Eq (2)

162
$$U_{(t)} = \frac{x_{(t+dt)} - x_{(t)}}{dt}; Eq (1),$$

163
$$a_{(t)} = \frac{U_{(t+dt)} - U_{(t)}}{dt}; Eq (2),$$

164 where $x_{(t)}$ is the filtered position of the model recorded by the sensor at instant t , $U_{(t)}$ is the
165 instantaneous velocity and $a_{(t)}$ is the instantaneous acceleration. $x_{(t)}$ and $U_{(t)}$ were filtered
166 using the moving average filter with a moving average of 50.

167 In addition, we wanted to assess what a prey would sense in terms of pressure, so we
168 placed another, more sensitive, force sensor (FUTEK LSB210 100 g) at the end of the path in
169 line with the moving model, to which we attached a round plastic piece of 7 cm in diameter that
170 allowed us to record the pressure changes (sensor 2, Fig. 1b., Fig. 2b.). Thus, we were able to
171 detect pressure variations of approximately 0.01 Pa which is in the range of the hearing and the
172 startle threshold of some fish (i.e. between 0.01 Pa and 0.56 Pa) ^{36,37}. The force and position
173 sensors were synchronized, and data were recorded at 1 kHz (Fig. 2).

174 *Drag coefficient and added mass*

175 Our primary goal was to characterize the hydrodynamic profile of our two head models
176 by using the output of the force sensor 1. The forces involved in our experiment are the steady
177 drag (F_d), the acceleration reaction (F_a) and the solid inertia of our model ⁶ (Fig. 3). The forces
178 recorded can be expressed as follow ²:

$$179 \quad F = F_d + F_a + ma; \text{ Eq (3),}$$

$$180 \quad F = \frac{1}{2}\rho U_{(t)}^2 C_d S + C_a \rho V a + ma; \text{ Eq (4),}$$

181 where ρ is the density of water, $U_{(t)}$ the velocity at the instant of interest and S the projected
182 frontal surface area of the model, C_d is the drag coefficient of the model, m is the mass of the
183 model, C_a is the added mass coefficient of the model, V is the volume of the model, a is the
184 acceleration.

185 First, we calculated the drag coefficient of each model by solving Eq (4) when $a = 0$
186 and $U = U_{max}$. When the system is not accelerated, the force measured by the sensor 1 is pure
187 steady drag; $F = F_d$. The force reaches a plateau, but the signal is oscillating so we took the
188 average value of this plateau as a measure of the steady drag force F_d (Fig. 2a.). Then, we
189 calculated the drag coefficient (C_d):

190
$$C_d = \frac{2F_d}{\rho U_{max}^2 S}; Eq (5)$$

191 The term $2F_d/\rho S$ was plotted against U^2 and the linear regression coefficient corresponds to the
 192 drag coefficient of the models (Fig. 4.). This representation allows to visualize the experimental
 193 data and to check the consistency of the measurement. The Reynolds number range of our
 194 experiments is $10^4 - 7.10^4$ which is consistent with previous observations¹.

195 To calculate the added mass coefficient of each model, C_a , we chose the instant t when
 196 $a = a_{max}$ as it also corresponds to the peak of the force measured by the sensor:

197
$$C_a = \frac{F_{(t)} - F_{d(t)} - ma_{(t)}}{\rho V a_{(t)}}; Eq (4),$$

198
$$C_a = \frac{F_{(t)} - \frac{1}{2}\rho U_{(t)}^2 C_d S - ma_{(t)}}{\rho V a_{(t)}}; Eq (5)$$

199 where $F_{d(t)}$ is the “instantaneous drag”. For simplification, we named the numerator of Eq (7):
 200 F_M , such as: $F_M = F_{(t)} - \frac{1}{2}\rho U_{(t)}^2 C_d S - ma_{(t)}$. To obtain the added mass coefficient, we
 201 plotted $F_M/\rho V$, against the acceleration a . The linear regression coefficient corresponds to the
 202 added mass coefficient of the models (Fig. 4.). See table 1 for the features of each 3D printed
 203 model.

204

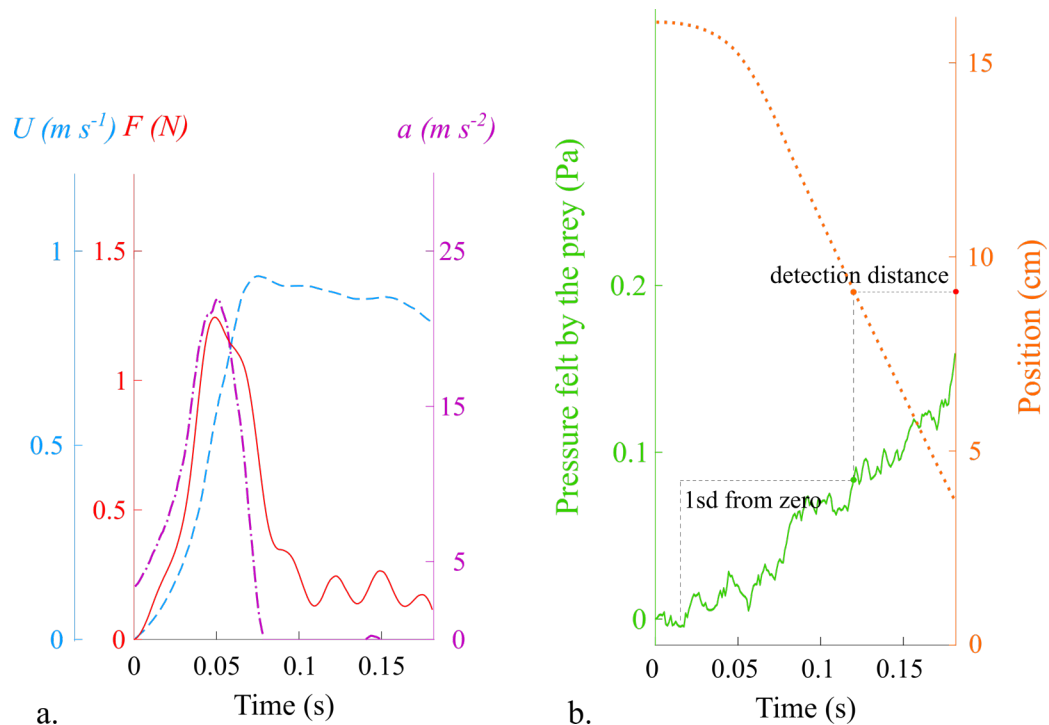
<i>Model</i>	<i>m (mass; g)</i>	<i>S (frontal surface; m²)</i>	<i>V (volume; m³)</i>
Aquatic	0.047	0.0012894	0.000073398
Non-aquatic	0.041	0.0014715	0.000057877

205 **Table 1: Characteristics of each model.**

206 *Detection distance*

207 To compare the effect of the head shape on the detection by a prey, we used the output
 208 of the second force sensor (sensor 2, Fig. 1b.). To estimate the position at which the prey could
 209 detect the predator, we defined the detection distance as the position at which the force detected

210 by sensor 2 deviates from the resting value by more than one standard deviation (Fig 2b., Fig.
 211 5.).



212

213 **Figure 2: Example of the data obtained from one strike. a. Velocity (U ; blue, dashed line)**
 214 **acceleration (a ; purple, dashed and dotted line) and force applied on the model (F , sensor 1,**
 215 **Fig 1b.) according to time (s). Between 0-0.05 sec, the springs relax, therefore velocity,**
 216 **acceleration and force increase. After approximately 0.05 sec, the springs are fully extended**
 217 **and the acceleration decreases. When the acceleration is null, the velocity reaches its**
 218 **maximum (U_{max}) and the force recorded by the sensor corresponds to the steady drag ($F =$**
 219 **F_d , Eq (3)). b. Pressure recorded by the ‘prey sensor’ (sensor 2, Fig 1b.) and position of the**
 220 **model (orange, dotted line) according to time (s). When the model gets closer to the prey**
 221 **sensor, the pressure increases. Once the pressure deviates of 1 standard deviation from 0, we**
 222 **consider the prey triggered by the attack and defined the corresponding distance as the**
 223 **detection distance.**

224 *Particle Image Velocimetry*

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

227 the tank (Fig. 1b.). Water was seeded with polyamid particles of 20 μm in diameter and a
228 Quantronix® Darwin-Duo laser was used to produce the light sheet. Image acquisition was
229 performed at 733 Hz. We choose to record three different planes on each head to obtain a
230 complete picture of the fluid flow around the head during the attack (see Supplementary Material
231 3). These planes were obtained by rotating the model around the aluminum rod. We applied the
232 same compression to the springs (i.e. maximal compression) to get an equivalent comparison
233 for the different shapes. Acquisition was performed using the Dantec DynamicStudio 2015a
234 software. The PIV vector computation was performed using LaVision 7.2 with a 16 x 16 pixel
235 interrogation window and 50% overlap. Additional post-processing and analysis was done in
236 Matlab using the PIVMat toolbox³⁸. The flow features can be characterized by examining the
237 vortex structures formed at the corner of the mouth and on both tips of the jaw and of the skull.
238 We created videos of the vortex formation during a strike, obtained from PIV in three planes
239 (see Materials and Methods section) to compare both models (see Supplementary videos SM4-
240 5-6). A more quantitative analysis was performed by computing the overall primary
241 circulation $\Gamma = \int \omega^+ dA$ in each PIV plane (ω^+ being the positive vorticity in Fig. 6b.). The
242 evolution of the dimensionless circulation Γ/UL as a function of time, where L is the
243 characteristic length scale of the acceleration regime of the strike maneuver (which is constant
244 for all experiments) and U is the velocity of the strike is plotted in Fig. 6b.

245 *Statistical analyses*

246 To compare the detection distance, we ran an ANCOVA with the distance as the
247 response variable, the model as a factor, and the acceleration as covariate as a snake strike is an
248 accelerated motion. All the variables were Log₁₀-transformed and the statistical analyses were
249 performed using R³⁹. The significance level was set at 5%.

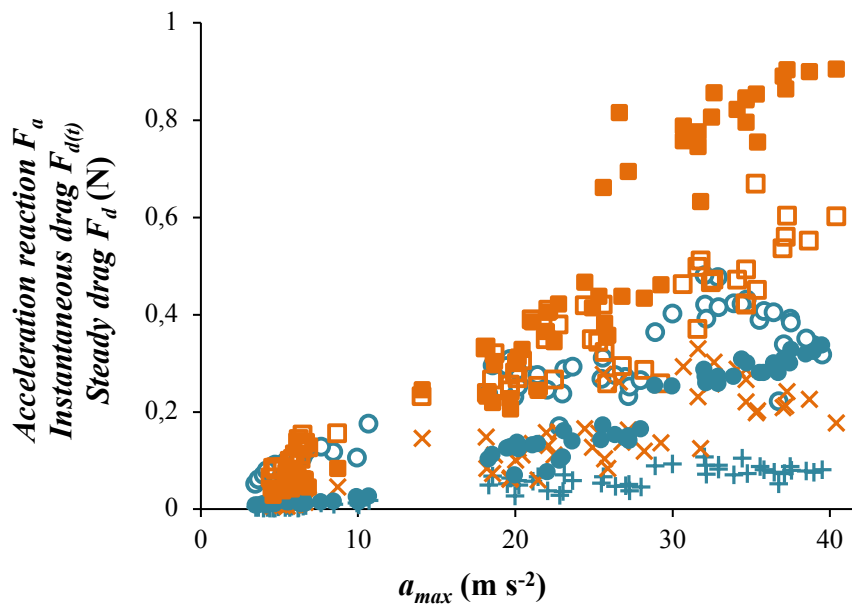
250 **Results**

251 *Drag and added mass*

252 The range of kinematics of our experiments fits the range of velocity and acceleration
253 observed in live snakes during frontal strikes (U_{max} : live snakes: 0.24 – 1.7 m s⁻¹, experiments:
254 0.22 – 1.5 m s⁻¹; a_{max} : live snakes: 8.3 – 75 m s⁻², experiments: 3.4 – 40.4 m s⁻²)^{14,16,40,41}. The
255 duration of the acceleration (0.05 – 0.1 s) also fits in the range of duration of a real snake strike⁴².

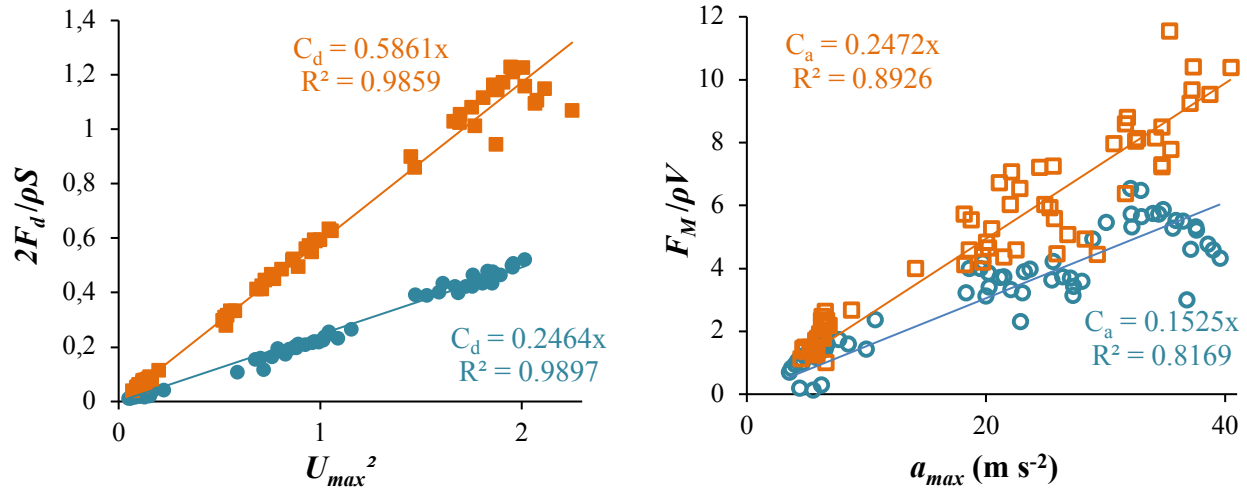
256 For each model, the instantaneous drag $F_{d(t)}$ has a smaller contribution to the peak force
 257 (i.e. during the acceleration phase) than the acceleration reaction F_a (Fig. 3.). The acceleration
 258 reaction is the predominant force for the aquatic model whereas, for the non-aquatic model, the
 259 steady drag is dominant. Force values between models are not directly comparable in Figure 3.
 260 as the specific characteristics of the models (e.g. frontal surface, volume...) are not considered.
 261 Only the drag and added mass coefficient allow to compare the impact of the shape on the forces.

262 The drag coefficient of the non-aquatic shape is larger than the coefficient of the aquatic
 263 model, respectively 0.58 and 0.24 (Fig. 4.). The mean added mass for the aquatic model is 12.67
 264 g, which represents 26.9% of the mass of the model versus 15.48 g for the non-aquatic model
 265 which represent 37.7% for the mass of the model. The added mass coefficients obtained from
 266 the linear regression on Fig. 4. are 0.15 for the aquatic model and 0.24 for the non-aquatic model.



267
 268 *Figure 3: Respective contribution of the acceleration reaction (F_a ; empty signs), the*
 269 *instantaneous drag during the peak force ($F_{d(t)}$; cross symbols for the non-aquatic, plus*
 270 *symbol for the aquatic model) and the steady drag (F_d ; filled signs) according to the maximal*
 271 *acceleration (a_{max}) for each strike, for the non-aquatic (squares) and aquatic (circles)*
 272 *models.*

273



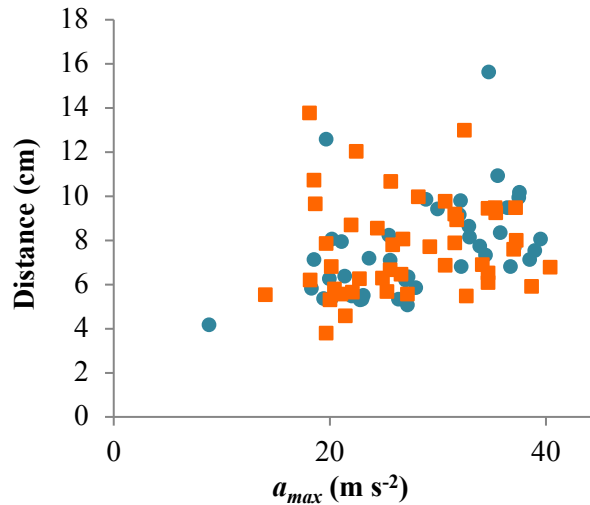
a.

b.

274 **Figure 4: Comparison of the hydrodynamic forces that apply on each model (squares: non-**
 275 **aquatic; circles: aquatic) depending on the kinematics of each strike (one point represents**
 276 **one strike) a. Representation of the steady drag (drag term $2F_d/\rho S$ of Eq (5)) depending on**
 277 **the squared velocity (U_{max}^2). b. Representation of the added mass force ($F_M/\rho V$ of Eq (7))**
 278 **depending on the maximal acceleration (a_{max} in $m s^{-2}$). Linear regression lines are drawn.**
 279 **The slopes correspond to the drag and added mass coefficient, respectively C_d and C_a , of each**
 280 **shape and the R^2 are the regression coefficients.**

281 *Detection distance*

282 The force signal was too noisy to obtain accurate measures of the detection distance at
 283 low velocities (i.e. $U > 0.5 m s^{-1}$). At higher speeds there is no statistical difference between the
 284 distances at which the prey could detect the presence of the snake depending on their head shape.
 285 However, this distance depends on the maximal acceleration of the strike, the higher the
 286 acceleration, the earlier the detection of the predator (ANCOVA: $F_{2,83} = 4.08$; $P = 0.02$; model:
 287 $P = 0.77$; a_{max} : $P = 0.001$) (Fig. 5.).



288

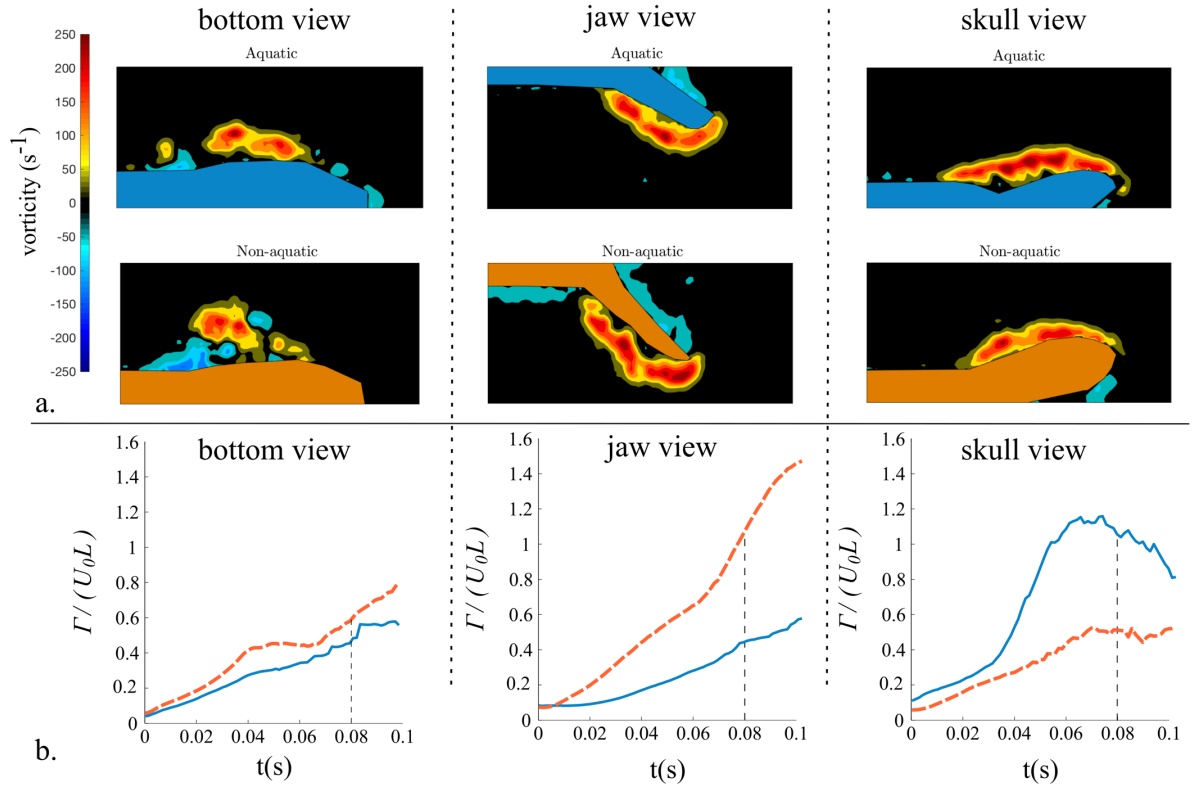
289 **Figure 5: Distance (cm) at which the prey could potentially detect the snake depending on the**
 290 **maximal acceleration ($m s^{-2}$). For each graph: squares: non-aquatic model, circles: aquatic**
 291 **model. Each point represents a strike.**

292

Flow characterization

293

The PIV measurements illustrate that the vortices are formed very early during the strike
 294 (see Supplementary videos SM4-5-6). For both models, the frontal strike maneuver involves
 295 strong flow separation due to the high shear produced by the impulsive acceleration. On the
 296 lateral side of the head (bottom view, Fig. 6a.), the number of vortices and the area they occupy
 297 and is smaller in the aquatic model, yet, the intensity of the vorticity is higher. The primary
 298 circulation in this area is slightly (~10%) lower over the whole acceleration phase for the aquatic
 299 model (Fig. 6b.). Below the jaw (jaw view, Fig. 6a.), the area occupied by the vortices is similar,
 300 yet the intensity of the vorticity is lower for the aquatic model. A much lower overall circulation
 301 is produced by the vorticity detached from the tip of the jaw in the aquatic case (around 40% of
 302 the non-aquatic value at the end of the acceleration phase). Behind the tip of the snout (skull
 303 view, Fig. 6a.), the area occupied by the vortices is larger and the vorticity is more intense for
 304 the aquatic model. The aquatic shape generates more overall circulation around the top of the
 305 head. Overall, the aquatic model seems to present smaller vortices, with slightly less overall
 306 circulation but more intense vorticity compared to the non-aquatic model.



307

308 **Figure 6: a. Snapshots of the vorticity field ω_z around the snake head models at the end of**
 309 **the acceleration phase ($t \approx 0.08$ s) for the aquatic (first line) and non-aquatic (second line)**
 310 **models, in the three measurement planes: bottom, jaw and skull views are shown on the first**
 311 **to third columns, respectively. The color bar for the vorticity field is given in s^{-1} . b. Evolution**
 312 **of the dimensionless integrated positive circulation during the acceleration phase depending**
 313 **on the time for both models (dashed line for the non-aquatic model) in each of the three views**
 314 **considered. The end of the acceleration ($t \approx 0.08$ s) is indicated on each graph.**

315 Discussion

316 The aim of this study was to characterize and measure the hydrodynamic forces involved
 317 when a snake captures a prey under water using a frontal strike, and to evaluate how head shape
 318 might affect these forces. It should first be noticed that the kinematic profile of our experiment
 319 lies within the biological range of real snake strikes. Second, we validated our hypothesis of a
 320 significant hydrodynamic advantage of the convergent head shape observed in aquatic snakes.
 321 However, we did find that shape differentially affects the steady drag and the acceleration
 322 reaction. Drag is well known for its importance during steady locomotion but it is also involved

323 in transient behaviors such as the capture maneuver studied here. Certainly, the aquatic shape
324 appears better adapted to capture aquatic prey using a frontal strike than the non-aquatic shape,
325 at least in terms of drag. The aquatic model has a drag coefficient that is more than two times
326 smaller than the non-aquatic model. The drag coefficient of the aquatic model is consistent with
327 previous fluid dynamic simulation of a prey capture in an aquatic snake, *Natrix tessellata*, at 1
328 m s^{-1} with a gape angle of 70° ($C_d = 0.25$)²⁸. The contribution of the instantaneous drag represents
329 2.7% of the peak of force for the aquatic shape whereas it is 7.6% for the non-aquatic model.
330 Additionally, figure 3 suggests that drag seems to play a larger role in the hydrodynamics of the
331 non-aquatic model as it is, quantitatively, the larger force for this model. The contribution of
332 acceleration reaction is slightly larger than the steady drag for the aquatic model. As for
333 crayfish³⁸, drag does not seem to be the major hydrodynamic constraint to overcome during a
334 transient maneuver. During crayfish escape response, 90% of the resistive force comes from the
335 mass and added mass. In our experiment, inertia-related forces represent 92.4% of the strike for
336 the non-aquatic model and 97.3% of the aquatic model. However, when the forces are rendered
337 non-dimensional (Fig. 4), the aquatic model has a more hydrodynamic profile, with a smaller
338 drag coefficient and a smaller added mass. Unlike the body of fish²⁶, the head shape of a snake
339 appears not to generate a morphological trade-off between drag and added mass. To place our
340 results in a broader context, the drag coefficient of a sphere and a circular cylinder, at the same
341 Reynolds number as our experiment, are respectively 0.47 and 1. Their added mass coefficient
342 value is close to their drag coefficient ($C_{a_sphere} = 0.5$; $C_{a_cylinder} = 1$)². Regarding the drag,
343 our aquatic model is better streamlined than a sphere, but the non-aquatic model is positioned
344 between the sphere and a circular cylinder. Whereas, for the added mass coefficient of our two
345 models are below those of both simple geometries.

346 Looking at the flow pattern around the head models (Fig. 6), the hydrodynamic
347 advantage of the aquatic snake could potentially be related to a smaller primary vortex on the
348 side of the head, the non-aquatic snake showing a more fluctuating and disordered flow field.
349 Moreover, the vorticity produced at the tip of the jaw shows a clear quantitative difference and
350 is consistently higher for the non-aquatic model. However, the skull view shows the opposite
351 pattern of vorticity; the non-aquatic shape produces fewer vortices with an integrated primary
352 circulation that is less important than for the aquatic model. It should be noted that the 2D nature
353 of the PIV measurements presented here does not allow us to provide a quantitative link between

354 the vorticity profile of the flow around the head and the hydrodynamic forces. Nonetheless, from
355 the present results we can conjecture that a reduction of the recirculation bubble behind the jaw
356 may be one of the main physical mechanisms explaining the physical advantage of the head
357 shape observed in aquatically foraging snakes.

358 Regarding the prey detection distance, our results show that this distance does not
359 depend on the snake head shape, but rather that it increases with strike velocity. However, we
360 cannot conclude on the biological relevance of the absolute prey detection distance measured in
361 our experiment as our setup was built with as primary purpose to measure drag and added mass.
362 Snakes usually strike when the prey is close to their head (e.g. 0.5-0.8 cm for *Erpeton*
363 *tentaculatum*⁴¹; 4.87 cm for *T. couchii*; 2.81 cm for *T rufipunctatus*¹²; less than 3 cm for
364 *Hydrophis schistosus*⁴³). The detection distance measured here is around 6 to 10 cm, so we
365 could consider that the prey can possibly detect the snake almost instantaneously upon the strike
366 initiation, the reaction time of a fish being around 7 ms⁴¹. Capture success is thus more likely
367 determined by the hydrodynamic profile of the snake head than being dependent on the reaction
368 of the prey. Moreover, some snakes are known to purposefully trigger the fast escape response
369 of the prey in order to catch them⁴¹.

370 In conclusion, we investigated the role of head shape on the hydrodynamic forces
371 generated by a predator using an experimental approach focusing on a transient maneuver. We
372 were able to quantify the role and impact of head shape on the hydrodynamics of prey capture
373 in aquatic snakes. We highlighted a clear hydrodynamic advantage of the aquatic head shape
374 when capturing a prey being associated not only with a smaller drag coefficient but also a
375 smaller added mass coefficient. These results validate the hypothesis that the morphological
376 convergence of the head shape in aquatic snakes is an adaptation to an aquatic lifestyle as it
377 provides a clear hydrodynamic advantage. In this work, we focused on the shape of the head of
378 aquatically foraging snakes, as several studies have highlighted convergence therein, and as
379 shape is directly related to hydrodynamic constraints. Size could be another important feature
380 regarding the hydrodynamic constraints. However, we did not detect any allometry in our
381 morphological study, meaning that the aquatically foraging snakes are not significantly different
382 in size than their closely related non-aquatic species. Thus, the present work focuses on the
383 functional meaning of shape irrespective of size. The other factors that could play a role in the

384 hydrodynamics of the prey capture of aquatic snakes could be the gape angle and macro and
385 microscopic skin features which remains to be investigated. The versatility of snake locomotion
386 has raised the attention of engineers and spurred the development of snake-inspired robots that
387 can move both on land and in water⁴² . However, whereas most biomechanical studies have
388 focused the role of the body during steady locomotion, our results show that the head shape is
389 crucial in transient maneuvers and should thus be considered when designing underwater
390 vehicles or robots needing to perform fast transient maneuvers.

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483 **Videos of frontal strikes in snakes:**

484 <https://www.youtube.com/watch?v=6sC6iiCWyw4>

485 https://www.youtube.com/watch?v=4_v5THJuorw&t=53s

486 <https://www.youtube.com/watch?v=sPszRWCgJ-A>

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495 **Author contributions**

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

500 **Competing interests**

501 We have no competing interests.

502 **Data availability**

503 See Supplementary Table S5

504 **Figure and table legends**

505 **Figure 1:** a. 3D models of the head shape of aquatic (first line) and non-aquatic snakes (second
506 line) in front, side and top view (see also Supplementary Material 1). b. Experimental setup used
507 to mimic the frontal attack of a snake towards a prey (see also Supplementary Material 2). The
508 snake model is directly linked to the force sensor 1 which is itself vertically attached to the
509 mobile part of the air-bearing rail. The force sensor 2 is placed at the end of the track. It is
510 recording the pressure variation thanks to a round plate attached to the sensor (vertical grey
511 line). The directions of the positive forces of each sensor is indicated ($F > 0$). The position sensor
512 is placed at the end of the track, on the rail. The horizontal green line represents the PIV laser
513 sheet. The model is turned to obtain three different views of the flow pattern around the head
514 (see Supplementary Material 3).

515 **Figure 2:** Example of the data obtained from one strike. a. Velocity (U; blue, dashed line)
516 acceleration (a; purple, dashed and dotted line) and force applied on the model (F, sensor 1, Fig
517 1b.) according to time (s). Between 0-0.05 sec, the springs relax, therefore velocity, acceleration

518 and force increase. After approximately 0.05 sec, the springs are fully extended and the
 519 acceleration decreases. When the acceleration is null, the velocity reaches its maximum (U_{\max})
 520 and the force recorded by the sensor corresponds to the steady drag ($F = F_d$, Eq (3)). b.
 521 Pressure recorded by the ‘prey sensor’ (sensor 2, Fig 1b.) and position of the model (orange,
 522 dotted line) according to time (s). When the model gets closer to the prey sensor, the pressure
 523 increases. Once the pressure deviates of 1 standard deviation from 0, we consider the prey
 524 triggered by the attack and defined the corresponding distance as the detection distance.

525 **Figure 3:** Respective contribution of the acceleration reaction (F_a ; empty signs), the
 526 instantaneous drag during the peak force ($F_{d(t)}$; cross symbols for the non-aquatic, plus symbol
 527 for the aquatic model) and the steady drag (F_d ; filled signs) according to the maximal
 528 acceleration (a_{\max}) for each strike, for the non-aquatic (squares) and aquatic (circles) models.

529 **Figure 4:** Comparison of the hydrodynamic forces that apply on each model (squares: non-
 530 aquatic; circles: aquatic) depending on the kinematics of each strike (one point represents one
 531 strike) a. Representation of the steady drag (drag term $2F_d/\rho S$ of Eq (5)) depending on the
 532 squared velocity (U_{\max}^2). b. Representation of the added mass force ($F_M/\rho V$ of Eq (7))
 533 depending on the maximal acceleration (a_{\max} in $m\ s^{-2}$). Linear regression lines are drawn. The
 534 slopes correspond to the drag and added mass coefficient, respectively C_d and C_a , of each shape
 535 and the R^2 are the regression coefficients.

536 **Figure 5:** Distance (cm) at which the prey could potentially detect the snake depending on the
 537 maximal acceleration ($m\ s^{-2}$). For each graph: squares: non-aquatic model, circles: aquatic
 538 model. Each point represents a strike.

539 **Figure 6:** a. Snapshots of the vorticity field ω_z around the snake head models at the end of the
 540 acceleration phase ($t \approx 0.08\ s$) for the aquatic (first line) and non-aquatic (second line) models,
 541 in the three measurement planes: bottom, jaw and skull views are shown on the first to third
 542 columns, respectively. The color bar for the vorticity field is given in s^{-1} . b. Evolution of the
 543 dimensionless integrated positive circulation during the acceleration phase depending on the
 544 time for both models (dashed line for the non-aquatic model) in each of the three views
 545 considered. The end of the acceleration ($t \approx 0.08\ s$) is indicated on each graph.

546 **Table 1:** Characteristics of each model.