

Supplementary Material

A biomechanical approach to infer size-based functional response in aquatic and terrestrial systems

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1 MAIN FRAMEWORK

Our approach is based on the recently published biomechanical model (Portalier et al., 2019). This model uses body size and physical features of the medium, to predict predator to prey interactions.

Hence, the model requires body masses of both the predator and its prey. The physical parameters are acceleration due to gravity, body density, medium density, and medium viscosity. Then, the model computes all necessary information to predict feasible predator-prey interactions.

In the present article, only elements required for the computation of a functional response will be described. A full description of the model can be found in the original study (Portalier et al., 2019). A list of parameters computed from the biomechanical model and used in the present study can be found in table S1.

Predation implies motion, and motion is constrained by the mechanical properties of the medium. Following the idea developed by Bejan and Marden (2006), motion can be modelled as an oscillatory movement. Animal stroke propels its body upwards and forwards, then the body returns to its original vertical position, but it has moved forward. We decompose motion into two components: a vertical one and a horizontal one. Mechanical factors affect the body in different ways during the whole process (see Fig. S1).

1.1 Vertical component of motion

During stroke, the organism applies a thrust force (e.g., muscles, flagella). Part of this force is dedicated to a vertical lift. This upward motion follows Archimedes force (due to the difference between medium and body densities), but is opposed to weight (due to gravity) and drag (due to medium density and viscosity). When thrust stops, the body pursues its movement upwards by inertia, until it stops. Then, the body returns to its original vertical position by inertia, following weight, but in opposition to Archimedes' force and drag.

1.2 Horizontal component of motion

The other part of the thrust is allocated to the horizontal component of motion. The body is pushed forwards, facing drag. When thrust stops, the body pursues its motion by inertia, until drag stops it. Both vertical and horizontal components are essential: the horizontal component determines the distance travelled between two points, but it requires that the vertical component either lifts the body or the surrounding medium, allowing motion (Bejan and Marden, 2006).

1.3 Animal speed

Using this framework, the model can compute animal speed. The maximal muscular output that an organism can develop is related to its size (Marden Allen, 2002). Then, the model computes the energetic cost associated to a given motion sequence according to the initial thrust force developed in the vertical

(F_{Mv}) and horizontal planes (F_{Mh}), and the distance covered during the active phase in the vertical (x_v) and horizontal planes (x_h).

$$Work = \int_{t_0}^{t_{force}} F_{Mv} x_v dx + \int_{t_0}^{t_{force}} F_{Mh} x_h dx \quad (S1)$$

The work can then be divided by the total duration of the sequence (from t_0 to t_3) to yield a cost *per time* ($Cost_{pt}$).

$$Cost_{pt} = \frac{Work}{t_3} \quad (S2)$$

The model can then compute a species-specific speed (\bar{v}) that leads to a maximal speed to a minimal cost.

$$(F_{Mv}, F_{Mh}) \Rightarrow \text{Min} \left(\frac{Work}{\bar{v}} \right) \quad (S3)$$

The computed species-specific speed fits existing data remarkably well (Fig. 1 main text).

2 PREDATION

Predation is broken up into three successive sequences: a predator needs to search, capture and then handle its prey. Each predation sequence leads to time expenditures. Thus, predation on a given prey requires time for searching (t_s), time for capturing (t_c) and time for handling (t_h) this prey. Each predatory activity implies motion, and motion is constrained by physical factors (mentioned above).

2.1 Search sequence

During searching time, both predator and prey move at a species-specific speed (v_p for predator and v_n for prey) that scales with body size. A given predator will encounter an individual from the prey population at a rate E_r (Rothschild and Osborn, 1988) depending on prey abundance (N), and predator detection distance (D_p). Predator detection distance scales with its size (Pawar et al., 2012).

$$E_r = \frac{\pi D_p^2 (v_N^2 + 3v_P^2)}{3v_P} N \quad (S4)$$

For a given predator and a given prey, all parameters are constant except prey abundance (N). Thus, encounter rate (Eq. S4) can write

$$E_r = \beta N \quad (S5)$$

2.2 Capture sequence

Once a prey is detected, the capture sequence begins. The predator jumps and tries to seize its prey, while the prey tries to escape, the distance between the predator and the prey is assumed to be the detection distance of the prey (that scales with prey size). Relative speed at time when predator reaches the prey leads to a capture probability (P_C) using a logistic function.

$$P_c = \frac{1}{1 + \frac{v_N}{v_P}} \quad (S6)$$

If the predator cannot reach the prey, then $P_C = 0$.

2.3 Handling sequence

Last, the predator is kept busy during the time needed to consume the prey: the handling time (t_h).

$$t_h = t_{cons} + t_{dig} \quad (S7)$$

where t_{cons} is consumption time, and t_{dig} is digestion time.

$$t_{cons} = B_t \frac{M_N}{B_s} \quad (S8)$$

where B_t is bite time, B_s is bite size, M_N is prey mass. Bite size scales with predator size (Wilson and Kerley, 2003).

$$B_s = \rho_b \frac{4}{3} \pi \left(\frac{B_0}{2} \left(\frac{M_P}{M_{Ob}} \right)^{0.32} \right)^3 \quad (S9)$$

where B_0 is bite diameter at reference size, M_P is predator mass, M_{Ob} is reference size, and ρ_b is body density. Bite time depends on bite size (Laca et al., 1994).

$$B_t = 0.1 B_s^2 \quad (S10)$$

Digestion time writes (Hendriks, 1999)

$$t_{dig} = t_{dig0} \frac{M_P}{B_s} M_N^{0.25} \quad (S11)$$

where t_{dig0} is digestion time for 1 kg of organism.

2.4 Time computation

Overall, the biomechanical model gives the total time that a predator needs to feed on a prey (for searching, capturing and handling the prey). Searching time is assumed to be the inverse of encounter rate times the probability of capture (i.e., the time needed to contact one prey that would lead to a successful capture).

$$t_s = \frac{1}{E_r P_c} \quad (S12)$$

Capture time (t_c) is the time needed for the predator to reach the prey during that jump. Last, handling time (t_h) is the time needed to consume and digest the prey.

2.5 Functional response

The functional response is defined as the inverse of the time needed for searching, capturing and handling one unit of prey.

$$f(N) = \frac{1}{t_s + t_c + t_h} \quad (S13)$$

Using equations (Eq. S5) and (Eq. S12) to replace search time, equation (Eq. S13) writes

$$f(N) = \frac{1}{\frac{1}{E_r P_c} + t_c + t_h} = \frac{1}{\frac{1}{N \beta P_c} + t_c + t_h} \quad (S14)$$

And rearranging

$$f(N) = \frac{N\beta P_c}{1 + N\beta P_c(t_c + t_h)} \quad (\text{S15})$$

Under this form, one can recognize a modified version of Hollings disk equation (Holling, 1961), where βP_c represents attack rate, and where capture and handling times are taken into account instead of handling time only.

Given the assumptions made on the encounter rate (Eq. S4), it is a type II functional response. In addition to prey abundance (N), its value changes according to both predator size, prey size and the medium (i.e., aquatic versus terrestrial).

2.6 Predicted attack rate and handling time according to body size

The model predicts attack rate and handling time according to predator and prey body masses. It allows investigating the overall trends for these parameters across a wide range of sizes. It appears that attack rate mostly varies with predator size (i.e., a larger predator attacks prey more efficiently). For a given predator, attack rate slightly decreases with increasing prey size (Fig. S2A). Predator size is bounded for very small predators since they do not move fast enough to contact and/or capture any prey. There is an upper prey size limit for all predators: due to the model assumptions, a predator cannot capture a prey larger than itself.

Handling and capture times mostly vary with prey size (a larger prey requires more time to be reached and consumed). But a larger predator will capture and consume a given prey faster than a smaller predator (Fig S2B). There is an upper prey size limit and a lower predator size limit for similar reasons as attack rate.

Table S1. List of symbols used throughout the article

Symbol	Meaning	Value	Unit
$f(N)$	Functional response		ind.s ⁻¹
N	Prey abundance		ind.m ⁻³
t_s	Search time		s
t_c	Capture time		s
t_h	Handling time		s
t_{cons}	Consumption time		s
t_{dig}	Digestion time		s
E_r	Encounter rate		ind.s ⁻¹
D_P	Predator detection distance		m
v_n	Prey speed		m.s ⁻¹
v_p	Predator speed		m.s ⁻¹
P_c	Capture probability		dimensionless
B_s	Bite size		kg
B_t	Bite time		s
M_P	Predator size		kg
M_N	Prey size		kg
B_0	Bite diameter at reference size	0.26	mm
M_{0b}	Reference size for bite diameter	2.9	kg
ρ_b	Body density	1080	kg.m ⁻³
t_{dig0}	Reference digestion time	$2.3 * 10^4$	s.kg ⁻¹

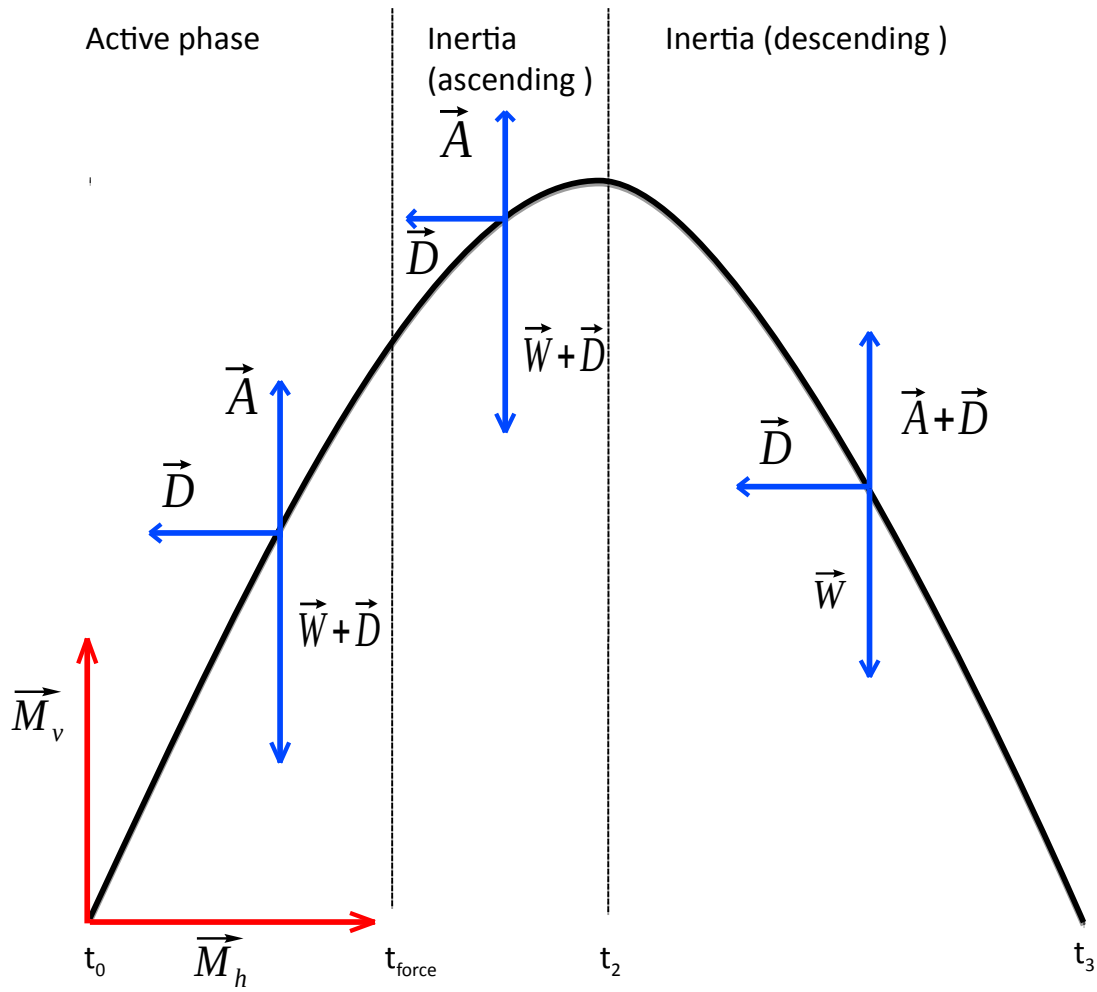


Figure S1. Framework for the computation of animal motion, represented as an oscillation. Red arrows represent thrust force due to animal stroke, and split between a vertical (M_v) and a horizontal component (M_h). Blue arrows represent forces due to mechanical factors of the medium. The sequence is decomposed into three phases. During the active phase, thrust force is applied. The body moves upwards, facing weight (W) and drag (D), but following Archimedes force (A) and forwards, facing drag, then stroke ends, the body pursue its motion by inertia. Then, the body returns to its original vertical position (descending) by inertia facing Archimedes force and drag, but following weight.

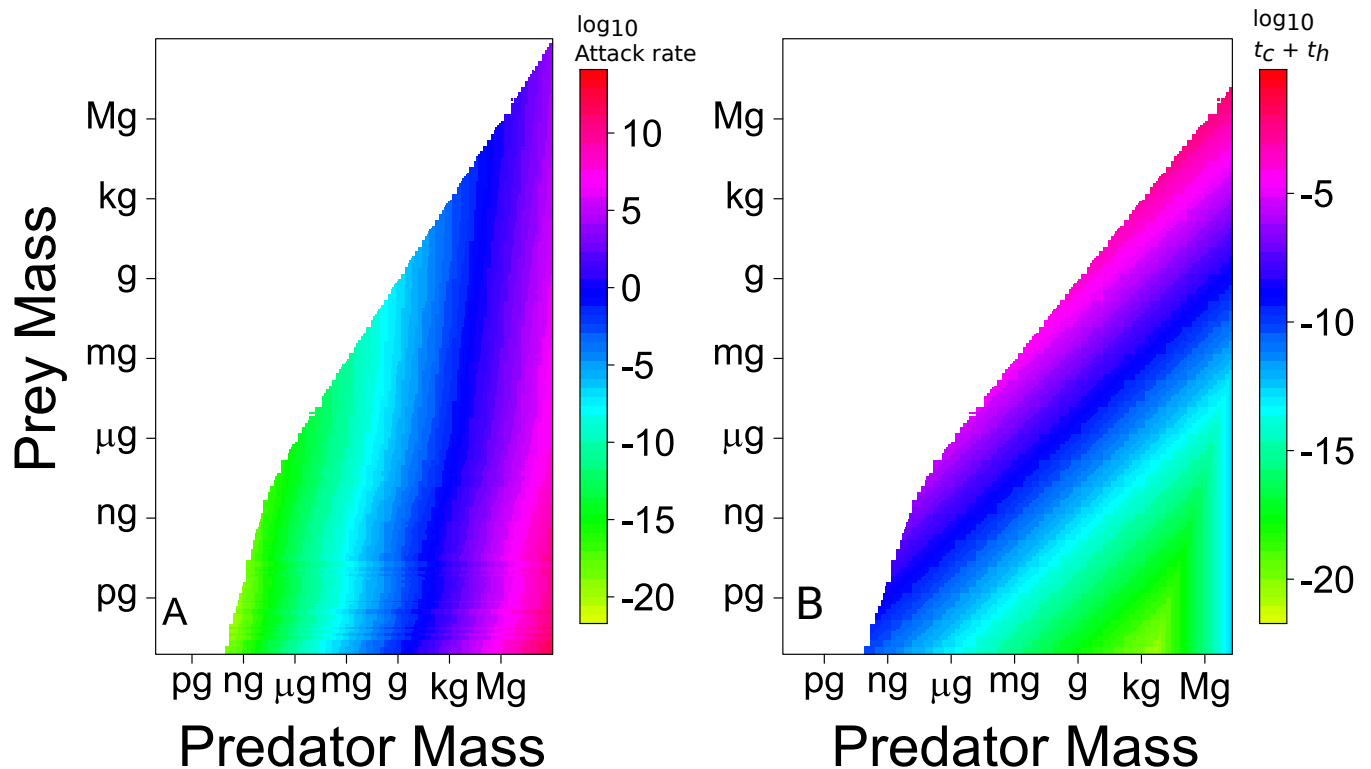


Figure S2. Predicted attack rate (A) and capture + handling times (B) according to predator and prey sizes. The white area represents cases where a predator is unable to find, capture or handle the prey, which means that the interaction is not feasible. There is a lower predator size that occurs when the predator do not move fast enough to contact and/or capture any prey. The upper prey size occurs when the predator is unable to capture the prey (due to model assumptions). Attack rate mostly varies with predator size. Capture and handling times mostly vary with prey size for a given predator.