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The mechanics of predator–prey interactions: First principles of physics predict predator–prey size ratios

Sébastien M. J. Portalier[1] (iD) | **Gregor F. Fussmann[1]** | **Michel Loreau[2]** | **Mehdi Cherif[3]** (iD)

[1]Department of Biology, McGill University, Montreal, Quebec, Canada

[2]Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station, CNRS and Paul Sabatier University, Moulis, France

[3]Department of Ecology and Environmental Sciences, Umeå University, Umeå, Sweden

Correspondence
Sébastien M. J. Portalier
Email: sebastien.portalier@mail.mcgill.ca

Abstract

1. Robust predictions of predator–prey interactions are fundamental for the understanding of food webs, their structure, dynamics, resistance to species loss, response to invasions and ecosystem function. Most current food web models measure parameters at the food web level to predict patterns at the same level. Thus, they are sensitive to the quality of the data and may be ineffective in predicting non-observed interactions and disturbed food webs. There is a need for mechanistic models that predict the occurrence of a predator–prey interaction based on lower levels of organization (i.e. the traits of organisms) and the properties of their environment.

2. Here, we present such a model that focuses on the predation act itself. We built a Newtonian, mechanical model for the processes of searching, capturing and handling of a prey item by a predator. Associated with general metabolic laws, we predict the net energy gain from predation for pairs of pelagic or flying predator species and their prey depending on their body sizes.

3. Predicted interactions match well with data from the most extensive predator–prey database, and overall model accuracy is greater than the allometric niche model.

4. Our model shows that it is possible to accurately predict the structure of food webs using only a few mechanical traits. It underlines the importance of physical constraints in structuring food webs.

KEYWORDS
body size, energy, mechanics, predation, trophic link

1 | INTRODUCTION

Predicting predator–prey interactions accurately is fundamental. The dynamics of food webs depend critically on their structure (Allesina & Tang, 2012). Moreover, the fate of native and invasive species depends on the network of interactions in which they are embedded (Romanuk et al., 2009). There is also increased awareness that ecosystem functioning itself depends on the structure of food webs (Thompson et al., 2012). It is thus important to understand what determines the occurrence of pairwise predator–prey interactions and, by extension, the structure of food webs.

Many models that predict the structure of food webs use parameters measured at the food web level (e.g. connectance). They derive rules from the regularities observed in well-studied food webs; devise probabilistic models that can reproduce these regularities; and test the capacity of these models to predict the structure of newly described food webs (Cohen & Newman, 1985; Eklöf et al., 2013; Gravel, Poisot, Albouy, Velez, & Mouillot, 2013; Williams & Martinez, 2000). While these models often succeed in faithfully replicating the patterns from which they are constructed, they do not provide clear insights into the mechanisms underpinning these patterns. Moreover, despite steady improvements in the quality and

quantity of data, most food web data are still irremediably spatially, temporally and/or taxonomically aggregated (Martinez, Hawkins, Dawah, & Feifarek, 1999). As a result, estimation of parameters at the food web level depends on sampling effort. Hence, statistical modelling approaches describe reasonably well food webs similar to those on which they have been built and trained, but they might have issues describing other food webs, knowing that discrepancies exist among ecosystems (Yvon-Durocher et al., 2011). Thus, a more detailed mechanistic approach capable of predicting species interactions based on parameters measured at the individual level and properties of the environment would be a major progress. The food web then emerges from the combination of all the potential pairwise interactions between the species present (Stouffer, 2010).

Several trait-based models exist that can be used to build food webs. Some of these models use abstract traits (Ito & Ikegami, 2006), while others draw trait values stochastically (Morton & Law, 1997). Such models are not suitable for the prediction of realized interactions from real food webs. On the other hand, studies that use real traits to describe species interactions are often very specific to the organisms of interest (Koehl & Strickier, 1981), which make them difficult to generalize across species and systems. Hence, there is space for mechanistic models that trade off realism, generality and simplicity by using simple traits to predict predator–prey interactions across a wide range of species and systems (in the same vein as, e.g., Petchey, Beckerman, Riede, & Warren, 2008). One trait upon which much attention has been focused, and for good reasons, is body size (Aljetlawi, Sparrevik, & Leonardsson, 2004; Cohen, Pimm, Yodzis, & Saldaña, 1993; Gravel et al., 2013; Loeuille & Loreau, 2005; Pawar,

Dell, & Savage, 2012). These studies have made great strides to reveal the role of size in structuring food webs, including its role in determining functional responses and interaction strengths (Brose, 2010). But here again, most of the patterns of prey-to-predator body size ratios are descriptive or based on statistical regressions made at the food web level, and thus, they do not offer a clear mechanistic underpinning at the species level. Hence, the factors determining the range of prey sizes that can be consumed by a predator of a given body size and the mechanisms by which these factors operate remain incompletely understood.

To answer this question, we decided to adopt a mechanistic approach based on traits measured at the individual level to predict the occurrence of predator–prey interactions. Our approach focuses on the core of predator–prey interactions, the act of predation itself, represented by the local searching, capturing and handling of one prey item by one given predator. This study considers that predation by essence implies motion (Rosen, Winship, & Hoopes, 2007): the predator must set itself in motion to search and capture the prey, while the prey moves to avoid capture (Figure 1). The act of handling involves mechanical motion as well since the predator must maintain its position in the water or air column while eating its prey. The originality of our approach is to start from traits at the individual level to model the mechanics of searching, capturing and handling prey. Then, the model can predict processes occurring at the food web level (i.e. predator–prey interactions). We used Newton's laws of mechanics as a basis to estimate encounter rates, capture probabilities and handling times for all predator–prey pairs within a realistic range of body sizes. Combined with general empirically derived relationships between body size and
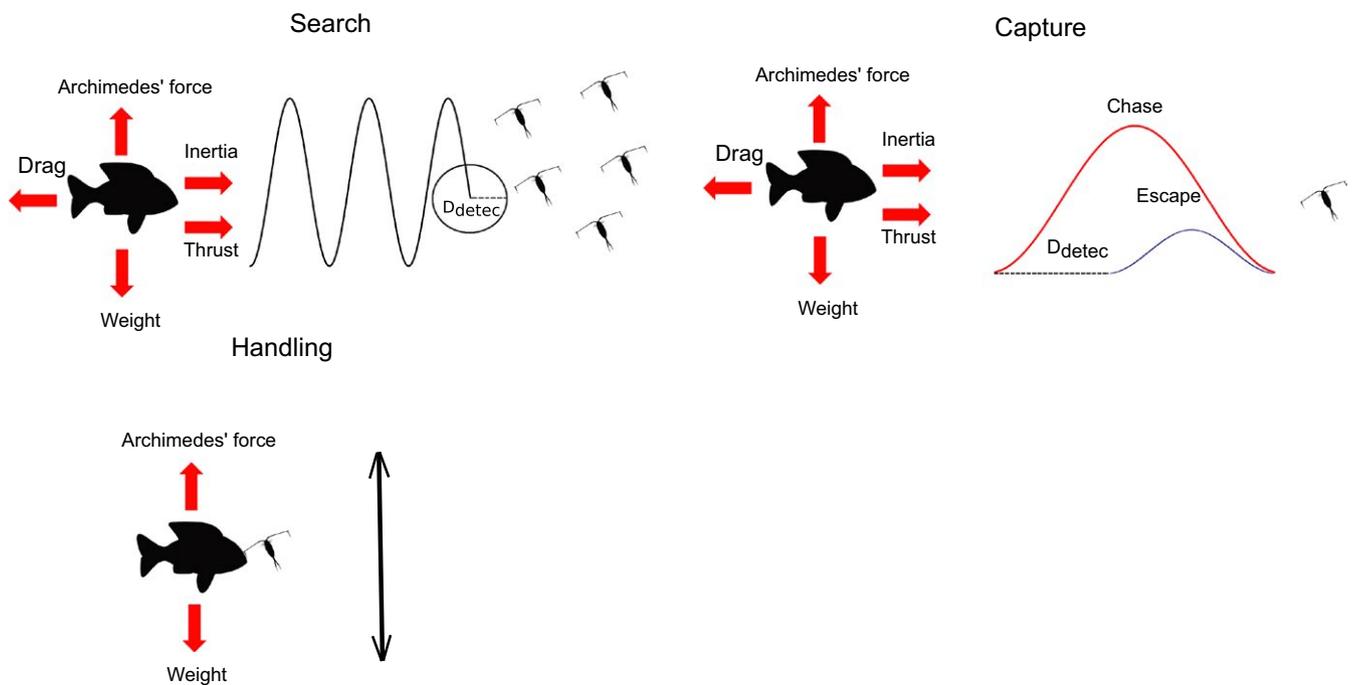

FIGURE 1 Main features of the model. The predator needs to spend energy against its weight to hover, but it benefits from Archimedes' force. Predation is split into three sequences. First, the predator searches for its prey, moving in a cyclic fashion. Motion implies interplay between mechanical thrust, inertia and drag. Encounter is constrained by predator's detection distance (D_{detec}) and prey abundance. A successful encounter leads to the capture sequence: the predator moves to seize the prey, while the prey tries to escape. In case of a successful capture, the predator needs to maintain hovering (lifting itself and the prey) during handling time (consumption and digestion)

metabolic expenditure, the model then calculates an energy budget for the predator during predation, and thus determines prey profitability, which can be used to predict which pairwise interactions are mechanistically feasible and energetically rewarding.

For the sake of simplicity, the model assumes that organisms move unhindered in a homogeneous three-dimensional medium, which is either air or water. As a result, the model is at this stage adapted to pelagic and some flying predators, which still represent a large number of predators. The next steps needed to generalize the model to bottom-dwelling predators are further discussed in the article. At any rate, including mechanics in our model allowed unifying approaches and comparisons between pelagic and aerial habitats rather than being restricted to a specific habitat (Webb, 2012). We use a general approach to include mechanical factors in our model; we define a given species only by its body size, which allows for generalization across a wide range of body sizes and ecosystems. Our model opens the door to a bottom-up prediction of the structure of food webs in diverse physical habitats, based only on a few mechanical traits of both predators and their prey.

2 | MATERIALS AND METHODS

The model calculates a net energetic gain (G) for one predator consuming one prey item:

$$G = E - (C_s + C_c + C_h) \quad (1)$$

where E is energy received from the prey, C_s, C_c and C_h are the costs for searching, capturing and handling the prey, respectively. Most of parameters used in the model scale with body size. M_{pred} refers to predator mass, while M_{prey} refers to prey mass. The model is static and only includes energy allocation related to predation (i.e. no predator growth or reproduction) at a given moment in time. Predators from the same species but different life stages would be considered as predators of different sizes.

If the predator is able to find, capture and consume the prey, this predator will receive energy, which depends on the prey ash-free dry mass:

$$E = M_{prey} R_{dm} R_{ed} \quad (2)$$

where R_{dm} is the ash-free dry mass to wet mass ratio, set as 0.16 (Ricciardi & Bourget, 1998), and R_{ed} is energy to ash-free dry mass ratio, set as 23 × 10^6 J/kg (Salonen, Sarvala, Hakala, & Viljanen, 1976).

2.1 | Framework for calculation of speed and work

Predation is broken down into three different processes (searching, capturing and handling) involving motion, which lead to three different costs (one for each process). Calculations of these costs are all based on the same framework, where speed and cost are estimated using classical laws of Newtonian mechanics and fluid dynamics. However, the model assumes that species optimize different parameters for each predation process.

2.1.1 | Generic model for locomotion

Although animal motion is diverse, it can be represented as an oscillatory movement (Bejan & Marden, 2006), a pattern observed in running (leg movement), flying (wing movement) and swimming (water movement above the body) animals. Following this idea, we define a general framework for species motion.

Considering one oscillation, motion can be decomposed into a vertical and a horizontal component (Figure 2). Both are essential. The horizontal component represents the distance travelled between two points. However, this horizontal motion requires a vertical motion that either lifts the body or the surrounding medium (Bejan & Marden, 2006). The muscular output creates a force that is split between these two components. A total allocation to the vertical component would be useless, since the body would then stay at the same place horizontally (it moves up and down), while a total allocation to the horizontal component is inefficient, since the organism cannot displace itself or the medium to move forward (gravity makes it sinking/falling). Hence, motion occurs simultaneously along both its vertical and horizontal components (i.e. total time t_3 and stroke period t_{force} are the same for both components). Any organism must split its muscular force between the two components.

The vertical motion sequence can be decomposed into three successive phases. The first one is the active phase during which
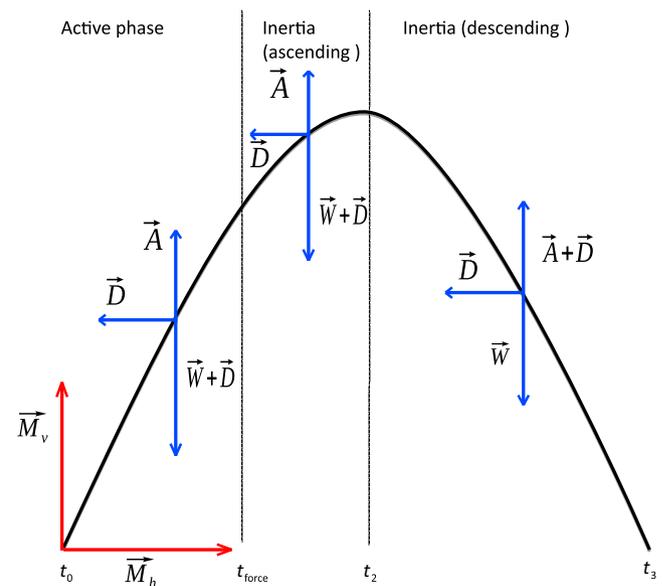

FIGURE 2 Framework for the calculation of motion cost. Motion is represented as an oscillation. An individual's body moves upwards, then downwards, while moving forward. Red arrows represent mechanical forces applied by the organism during the stroke period (from t_0 to t_{force}). Blue arrows are external forces due to the surrounding medium: Archimedes' force ($\vec{A}$), weight ($\vec{W}$) and drag ($\vec{D}$). Direction of arrows accounts for the component of motion they affect (horizontal or vertical). A given oscillation is split into three phases: an active phase, where a mechanical force is applied by the body, then an inertial phase, where the body pursues its motion upwards until its stops, and last an inertial (descending) phase, where the body returns to its original vertical position

a muscular force (F_{Mv}) is applied during the stroke period (see Equations 5 and 6). The body is lifted by this muscular force (and Archimedes' force) against its weight (due to gravity) and drag. The second phase is an inertial ascending phase: the organism pursues its lift by inertia until it stops. The last phase (inertial descending phase) occurs when the organism falls (or sinks) passively back to its original vertical position.

The horizontal motion sequence includes two phases. The first one is the active phase during which a muscular force (F_{Mh}) allows a displacement of the body. This force is applied during the stroke period. The second phase is an inertial phase: the organism pursues its motion until drag stops it.

2.1.2 | Force allocation and work

Knowing the forces ($F_{Mv} + F_{Mh}$) and the distance covered during the active phase in both the vertical (x_v) and horizontal (x_h) plans, a work can be calculated, which is the energetic cost of motion.

$$\text{Work} = \int_{t_0}^{t_{force}} F_{Mv} x_v dx + \int_{t_0}^{t_{force}} F_{Mh} x_h dx \tag{3}$$

This work can be divided by the time of a whole oscillation (from t_0 to t_3) to yield a cost per unit time (Cost_{pt}).

$$\text{Cost}_{pt} = \frac{\text{Work}}{t_3} \tag{4}$$

Organisms will optimize the costs according to the tasks carried out during each of the three sequences of predation (searching, capturing and handling (see section 2.2. and Supplementary Methods S1 in Supporting Information for full details).

2.1.3 | Physical parameters

The model considers two different media (air and water). It considers weight, Archimedes' force and drag. Parameters needed to calculate these forces are acceleration due to gravity (g), body density (ρ_b), medium density (ρ_m) and medium dynamic viscosity (μ, see Table 1, and Supplementary Methods S2).

2.1.4 | Biological parameters

Biological parameters are estimated using well-known allometric relationships (see Supporting Information Table S1). Real data points have been used to calibrate some parameters. These data points are different from those that were used to test the model predictions.

The maximal muscular output ($F_{Max} = F_{Mv} + F_{Mh}$) that a predator can develop scales with its body mass (Marden & Allen, 2002) as:

$$F_{max} \leq 55 M_{pred} \tag{5}$$

The time during which muscular forces are applied during motion, the stroke period (t_{force}), also scales with body size:

$$t_{force} = 0.35 M_{pred}^{0.25} \tag{6}$$

Stroke period was calibrated with real observations of species-specific speeds (Dodson, Ryan, Tollrian, & Lampert, 1997; Leis & Carson-Ewart, 1997; McDonald & Grünbaum, 2010). Equations 5 and 6 are similar for the prey.

2.2 | Calculation of searching, capturing and handling costs

For each predation cost (i.e. searching, capturing and handling costs), force allocation between the vertical and horizontal components is estimated using an optimization procedure based on Sequential Quadratic Programming methods (Han, 1977).

2.2.1 | Searching cost

Searching cost represents energy spent by a predator to find its prey. It is based on a species-specific speed ($\bar{v}$), which is the average speed throughout a whole oscillation. This speed needs to be sustainable for a long period of time. Thus, it optimizes the horizontal distance travelled for a minimal cost (Bejan & Marden, 2006).

$$(F_{Mv}, F_{Mh}) \Rightarrow \text{Min}\left(\frac{\text{Work}}{\bar{v}}\right) \tag{7}$$

TABLE 1 Physical parameters

Symbol	Parameter	Value		Unit
		Water 10°C	Air 10°C	
g	Acceleration due to gravity	9.81		m/s^2
ρ_m	Medium density	1,000	1.247	Kg/m^3
μ	Medium dynamic viscosity	1.35×10^{-3}	1.768×10^{-5}	N.s/m^{-2}
ρ_b	Body density	1,080		Kg/m^3
Re	Reynolds number			Dimensionless
C_d	Drag coefficient			Dimensionless

The instantaneous speed is greater when the muscular force is applied, and then decreases. Thus, an average speed gives a fair estimate of a cyclic process.

$$\bar{v} = \frac{x_h}{t_3} \tag{8}$$

The optimization yields a species-specific speed. Simulations show that this speed increases with body size.

To be consistent throughout the study, prey population biomass is assumed to fill 1% of the total volume of the medium (White, Ernest, Kerkhoff, & Enquist, 2007). This allows small prey to be more abundant than large prey. Considering the dynamics of prey abundance would add another level of complexity and thus is not included here for the sake of simplicity. Searching time is assumed to be the inverse of the encounter rate (E_r, see Supplementary Methods S3). Searching cost is the sum of the mechanical and metabolic costs during the search of a prey.

$$C_s = \left(Cost_{pt} + C_{met}\right)\frac{1}{E_r} \tag{9}$$

The metabolic expenditure *per time* (C_{met}) scales with body mass. To allow for energetic expenditure due to muscular effort, we used the field metabolic rate (Hudson, Isaac, & Reuman, 2013; Savage et al., 2004):

$$C_{met} = 12.5 M_{pred}^{0.75} \tag{10}$$

Parameters were estimated from published data (Hudson et al., 2013).

2.2.2 | Capture cost

To keep it as simple as possible, a capture sequence is based on a unique oscillation: the predator moves and tries to seize the prey. The prey moves and tries to escape the predator. This assumption is based on the observation that many predators do not actually pursue their prey during a long period of time; predators usually try to capture the prey quickly and stop if they fail (Weihs & Webb, 1984).

The predator tries to optimize the horizontal distance (x_h) covered during a unique oscillation.

$$\left(F_{Mv}, F_{Mh}\right) \Rightarrow Max\left(x_h\right) \tag{11}$$

The prey can detect the predator if it is closer than the prey detection distance D_{prey}, which is assumed to be the distance between the predator and its prey when the sequence starts. A larger species should have a larger detection sphere. We used a published model to take this into account (Pawar et al., 2012):

$$D_{prey} = d_0 \left(\frac{M_{prey}}{M_{0d}}\right)^{\frac{1}{3}} \tag{12}$$

where d_0 is the detection distance at reference size (set at 0.225 m), M_{0d} is the reference mass (set at 0.0376 kg). d_0 and M_{0d} were estimated by regression from Pawar et al. (2012).

The predator may fail to capture the prey. Hence, a capture probability (P_{suc}) is calculated. First, the predator must cover the distance (D_{prey}) between itself and its prey (i.e. it catches the prey) before it stops, otherwise the probability of capture is 0 ($P_{suc} = 0$). Second, the relative speed between the predator (v_{Pred}) and the prey (v_{Prey}) at contact plays an essential role because if the prey is not able to move anymore, while the predator can pursue its motion, the probability of capture should be high. On the other hand, if the predator is at the end of its motion, while the prey can pursue its motion, the probability of capture should be low. We use a logistic function to describe this process:

$$P_{suc} = \frac{1}{1 + \frac{v_{Prey}}{v_{Pred}}} \tag{13}$$

We assume that if $v_{Pred} = 0$, the predator is unable to catch the prey ($P_{suc} = 0$).

The capture cost is paid by the predator no matter whether capture is successful or not. The number of attempts before a success is assumed to be the inverse of the capture probability. The metabolic expenditure is paid for the duration of each oscillation (t_c). Thus, the capture cost to effectively capture one prey is.

$$C_C = \left(Work + C_{met} * t_C\right)\frac{1}{P_{suc}} \tag{14}$$

If $P_{suc} = 0$, this predator–prey interaction is not feasible.

2.2.3 | Handling cost

The mechanical handling cost is based on the idea that a predator living in the water or air column has to maintain both itself and its prey at the same approximate position during handling, otherwise it would sink or lose its prey. Handling time depends on both predator and prey sizes (see Supplementary Methods S4).

Using the framework explained above, the predator body moves downwards due to gravity, and energy is spent periodically to lift its body to its original vertical position. The predator supports both its own mass and that of the prey. Only the vertical component of motion is used. Therefore, the cost *per time* (Equation 4) becomes.

$$Cost_{pt} = \frac{\int F_{Mv} x dx}{t_3} \tag{15}$$

Handling cost is the sum of muscular and metabolic energy expenditure during handling time (t_h):

$$C_h = \left(Cost_{pt} + C_{met}\right)t_h \tag{16}$$

If the predator cannot lift its body to its original vertical position while carrying the prey, the interaction is assumed to be not feasible.

2.3 | Size-related foraging costs and foraging limits

Each foraging cost (for searching, capturing and handling the prey) varies with predator and prey sizes (Supporting Information Figure S2). Each cost constrains the range of prey that a predator can consume, defining foraging limits. These limits can be either energetic or mechanical.

2.3.1 | Energetic limits

Energetic limits occur when a prey does not provide enough energy compared with the costs associated with its consumption. Limits are calculated for each foraging cost separately.

$$G_s = E - C_s \tag{17}$$

$$G_c = E - C_c \tag{18}$$

$$G_h = E - C_h \tag{19}$$

There is a limit for search (Equation 17), capture (Equation 18) and handling (Equation 19). A specific energetic limit for metabolism can be defined by assuming that metabolism is the only cost.

$$G_m = E - \left(t_s + t_c + t_h\right) C_{met} \tag{20}$$

G_m is equivalent to the net gain (Equation 1) when all mechanical works are omitted.

For each predator and for each cost, the smaller prey leading to $G > 0$ defines the corresponding energetic limit for this cost, which represents the minimal prey size that allows a given predator to fulfil its energetic expenditure for predation, when only the corresponding cost is considered.

2.3.2 | Mechanical limits

Mechanical limits are due to a lack of sufficient muscular power for the predator. The capture mechanical limit occurs when the predator is unable to reach the prey irrespective of the number of attempts (i.e. $P_{suc} = 0$). Similarly, the handling mechanical limit occurs when the predator is unable to lift the prey during handling time. In both cases, the predator–prey interaction is assumed not to be feasible, and a gain is impossible to calculate.

2.4 | Use of empirical data

We compared model predictions with empirical data on predator–prey relationships. Data come from the most extensive database of predator and prey body sizes currently published (Brose et al., 2005), supplemented with data that we collected directly from published articles (see Dataset). For our analysis and presentation in graphs, data points were sorted and grouped according to whether or not interactions fitted the model's assumptions. These assumptions were that (a) a predator captures one prey item at a time, (b) the predator tries to actively seize the prey, and the prey actively tries to escape the predator and (c) both predator and prey can detect each other without interference (i.e. the predator cannot hide itself). Points fitting these assumptions were used to compare predicted and
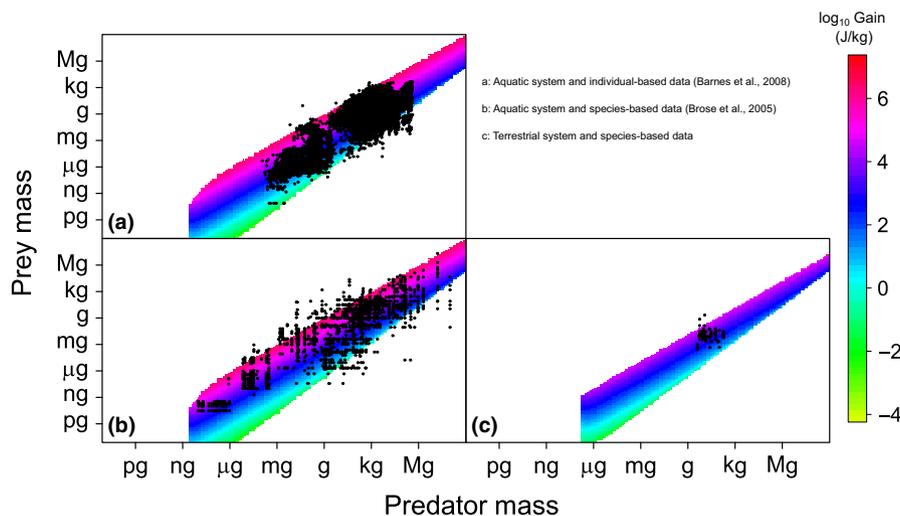
FIGURE 3 Net gains on predation for pelagic (a,b) and flying (c) predators. Heat maps show net energetic gains for predation. Gains are weighed by predator mass in order to allow comparisons between predators. The coloured zones show interactions that are assumed to be feasible (the predator can capture and handle the prey) and sustainable (the net gain is positive). Points represent real interactions that fit the model assumptions within different aquatic systems and for flying predators. In aquatic systems, data come from a food web were individual sizes are available (a), or from a meta-analysis (b) where predator size ranges from rotifers to whales. In air (c), data are restricted to insectivorous bats and birds since many flying predators come back on the ground during handling time. 90% (a), 80% (b) and 96% (c) of the points fall within the predicted range of prey sizes

observed pairwise interactions (Figure 3). A subset of these points came from 10 extensive aquatic food web studies. We used those to test the model's accuracy (see section 2.7 and Figure 4).

Data that did not fit the model's assumptions were sorted according to which assumption was violated or relaxed. If several assumptions were violated, we considered the most limiting one. Those points were used to compare observed interactions and predicted limits (Figure 5). However, the database provides average sizes of species, which can show a large variance. Hence, we also used points from another database (Barnes et al., 2008) that provides individual sizes of predators and prey to test the model (Figure 3a).

2.5 | Model accuracy

In order to evaluate to what extent the model was able to predict feasible and non-feasible interactions, the True Skill Statistics (TSS) was computed (Allouche, Tsoar, & Kadmon, 2006) on data points forming 10 aquatic food webs. For each food web, four metrics were calculated: a, the number of links predicted and observed; b, the number of links predicted with no corresponding observation; c, the number of links observed but predicted absent by the model; and d, the number of predicted and observed absence of links. TSS quantifies the amount of successful predictions relative to false predictions.

$$TSS = \frac{ad - bc}{(a + c)(b + d)} \tag{21}$$

Its value ranges between 1 (perfect prediction) and –1 (inverted prediction).

TSS was used to compare the results from our model to those from an allometric niche model which used the same set of aquatic food webs (Gravel et al., 2013). This model infers interactions among a pool of species from a subset of observed predator–prey
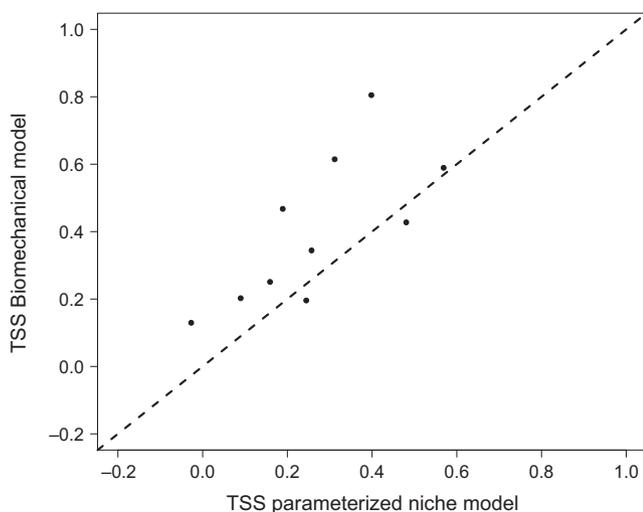
interactions from this pool. It is based on a statistical analysis of the predator–prey size ratio, which is used to infer the parameters of the niche model for each species (i.e. niche position along the niche axis, centroid and range of the niche). Then, these parameters are used to compute the predicted matrix of interactions.

3 | RESULTS

3.1 | Predicted interactions

Combining a mechanical model of predation with metabolic laws allowed us to calculate the net energy gains of a predator consuming a prey item of a given body size. Three cases can occur: (a) if an interaction leads to a positive net energetic gain, it is considered feasible and sustainable; (b) if the interaction leads to a negative net energetic gain, it is considered feasible but unsustainable; (c) if the predator cannot capture the prey, the interaction is considered unfeasible.

We found that each predator can feed on a range of prey sizes that varies with its body size. When predator size increases, prey size also increases because larger predators can capture larger prey. However, small prey do not provide enough energy, and therefore, they become not sustainable for large predators (Figure 3). The model predicts that predators should be larger than their prey, and this constraint is stronger for flying than pelagic predators. The gains of predators of similar sizes are also consistently lower in flying predators than in pelagic ones. The prey giving the highest net energetic gain is always the largest prey that a predator can consume.

Despite its simplifying assumptions, the model predicts most observed interactions across the whole range of predator sizes (from zooplankton to large vertebrates). Figure 3 shows data points that fit the model's assumptions. About 80% and 96% of pelagic and flying predators respectively fall within the predicted range of values (Figure 3b,c). The result is also robust if we consider individual body size in pelagic predatory fish (Figure 3a), where 90% of the points are predicted. Moreover, TSS shows that the model is able to predict a large part of the trophic links within food webs (Figure 4). The accuracy of the model was compared over the same data points with the allometric niche model, which represents the most advanced attempt at predicting pairwise interactions based on an empirical approach that is using body size as the only matching trait (Gravel et al., 2013). Our model often shows greater accuracy than the niche model.

3.2 | Foraging limits

In a second step, we analysed our model in detail to determine how the various mechanical and energetic components of the model constrain the size of prey that a predator can consume. The maximum prey size that a predator can eat is determined by mechanical limits. In fact, larger prey individuals can both detect a predator earlier and develop greater velocities (see Methods), resulting in successful escape. Thus, there is a maximum size for the prey that a predator of a given size can capture (solid blue lines in Figure 5). Another
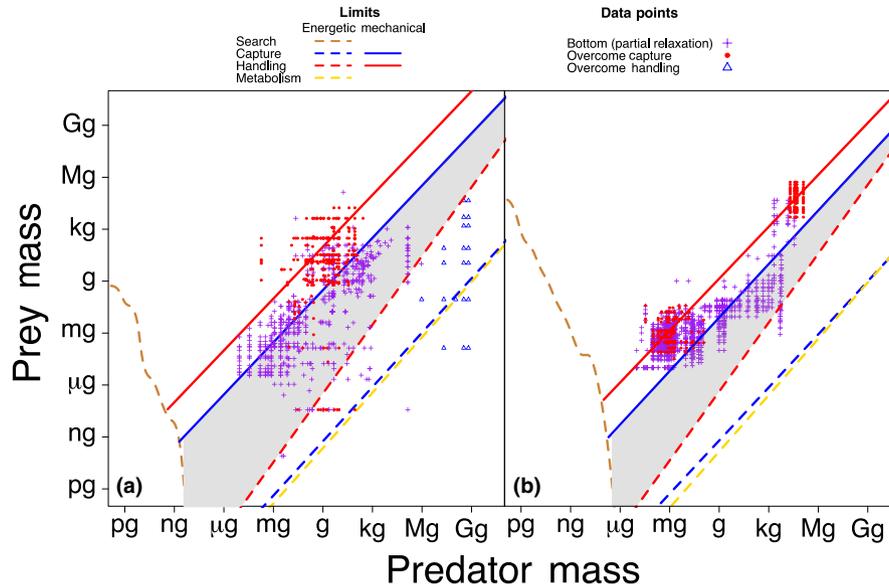

FIGURE 4 Comparison of True Skill Statistics (TSS) between our biomechanical model and the allometric niche model on ten food webs. Each point is a food web; the dashed line is a 1:1 line (i.e. similar accuracy). Most points are located above the line, which means that the biomechanical model shows greater accuracy

FIGURE 5 Limits on feeding interactions in aquatic (a) and terrestrial (b) systems. Dashed lines are the energetic limits (lower prey size allowing a positive net gain when the corresponding cost is the only one acting). Solid lines are the mechanical limits (upper prey size that a predator can capture or handle under the model assumptions). Grey areas show the predicted interactions (coloured zones in Figure 3). Upper prey size is determined by capture mechanical limit. Lower prey size is mostly constrained by handling energetic limit. Lower predator size is mostly determined by searching cost. Colour of data points shows which limit is overcome. Predators either overcome mechanical capture limit (red), handling energetic limit (blue) or both if they live on the bottom (purple). Purple points include flying predators that return to the ground to handle their prey

mechanical limit is related to handling, when the prey is too large and the predator is unable to develop sufficient mechanical power to hover while maintaining its prey (solid red lines in Figure 5). With the set of parameter values we chose, which are typical of generic pelagic and airborne food webs (Table 1 and Supporting Information Table S1), it is capture that mechanically constrains the upper prey size (Figure 5).

In contrast, minimum prey size is limited by net energy gain. The amount of energy given by a prey increases with its size (Supporting Information Figure S2). Hence, small prey sizes are poor energetic rewards for predators. Searching, capturing and handling and metabolic costs may further decrease prey profitability. Handling cost (dashed red lines in Figure 5) is the most limiting cost for predators larger than a few μg because the cost of hovering dominates over the other costs that are capture cost (dashed blue lines) and metabolic cost (dashed orange lines). For pelagic predators that are below the nanogram range (below the μg range for flying predators), searching cost is the limiting cost (green dashed lines in Figure 5). Small predators have short detection distances and low velocities resulting in too rare encounters under the prey densities assumed in the model (see Methods).

4 | DISCUSSION

This study presents a mechanistic and mechanical model that predicts the occurrence of an interaction between an individual predator and a prey item with specified body sizes. For each predator

size, we calculate the feasibility and energetic profitability from eating a prey of a given size, using a Newtonian, mechanical model associated with general metabolic laws. The predicted size ranges of feasible and profitable interactions compare well with observed interactions, as documented in the most extensive size-based predation database published so far (Brose et al., 2005), augmented with additional data. Since our model is mechanistic and is based on general laws, it neither needs calibration for each food web, nor any food web level metrics (such as connectance). Nonetheless, the model shows a greater accuracy than the allometric niche model (Gravel et al., 2013). Both models usually overestimate the number of predicted links, which is quite a common issue. But it is difficult to sample all links of a given food web (Martinez et al., 1999); therefore, the absence of an observation does not necessarily imply the absence of a link. Although our model uses a number of parameters that are estimated from the literature, it does not use any information extracted from the food web studied, apart from species body sizes.

Not all predators in our dataset pay the full costs of searching, capturing and handling their prey. Some predators overcome the capture mechanical limit (red points in Figure 5) by feeding on prey that do not move (e.g. sponges or corals) or that move at a lower speed than expected according to their size (e.g. gastropods). Such predators should be limited in their choice of prey by handling, the next process to act on the range of feasible prey sizes according to the model.

Other predators decrease the energetic cost of handling, which is mainly the cost of hovering in the case of small prey, by consuming

several small prey items at a time, such as strikingly performed by plankton-feeding whales (blue points in Figure 5). Finally, some predators overcome both the capture and handling limitations by living on the bottom (benthic, running or crawling predators; purple points in Figure 5). Such predators spend less energy in managing their buoyancy while handling their prey (since they cannot fall or sink anymore). Many flying predators, insects and birds, move to a hard surface during the handling of their prey and thus belong to this category of predators. Since surfaces generally bear complex landscapes, predators can hide and come closer to their prey before being detected, which increases the likelihood of capture. Such predators have potentially no limits to the maximum size for the prey they can capture, in particular if they hunt in group (Bowen, 1981). Our results however show that this category of predators targets prey with maximum prey sizes that are very close to the handling mechanical limit (solid red lines in Figure 5).

Our model would need some modifications to be generalized to the types of predators described above. A number of predators live on the bottom of the system (aquatic predators living on bottom of a lake or the sea, or terrestrial predators living on the ground), and most flying predators do not fly during handling time. These predators should pay reduced cost during handling since they do not hover. Such a reduction can be handled in a simplified version of our model (blue lines in Figure 5). But a model for bottom predators would also need to take into account the landscape complexity of bottom surfaces. Surfaces show troughs and peaks that allow the predator or the prey to hide, thus altering the search and capture sequences as well as energy expenditure. Inclusion of landscape features in a model that aims at generality is not trivial and best left for further studies.

There are a number of other mechanistic models of food webs (Carbone, Codron, Scofield, Clauss, & Bielby, 2014; Loeuille & Loreau, 2005; Petchey et al., 2008). Among these models, the allometric diet breadth model (ADBM) is the only model that, like ours, aims at predicting realized predation interactions, rather than at simulating virtual food webs (Petchey et al., 2008). ADBM adopts an approach that is similar to ours in many respects. Both models predict the diet of individual predator species based on body size as the main trait and on a mechanistic model describing the energy gain from the prey. The choice of the mechanistic underpinnings is where the two models diverge: we base our calculations on a combination of mechanical and metabolic laws; ADBM is based on optimal foraging theory (Beckerman, Petchey, & Warren, 2006). Rather than confront the two models, we see them as complementary. ADBM does not subtract energetic costs from the energy content of the prey; we account for the costs related to the searching, capturing and handling of the prey. On the other hand, our model does not offer a ranking in the choice of prey, only net gain estimates; ADBM offers a ranking of species based on optimal foraging. Thus, we see the next obvious step in the development of our model in the combination of the two modelling approaches.

Our model matches some of the common body size patterns observed in food webs (Tucker & Rogers, 2014). In particular, predators

consume smaller prey in air than in water (Figure 3), but the patterns remain similar otherwise. Thus, the model shows that constraints due to mechanical factors are stronger in air, but apply in the same way as in water. There are also a greater number of predators that handle their prey in the water column, compared with the number of flying predators that handle their prey in the air (compare numbers of data points between the two panels of Figure 3). Our model provides an explanation for this difference: hovering costs are lower in the water column than in the air, due to higher buoyancy (Table 1). Moreover, the bottom is generally farther from the vertical position of pelagic predators (in oceans and large lakes), requiring a significant energy expenditure to be reached. In contrast, it is easier for flying predators to return to the ground during handling, to a degree that we could only find a few insectivorous bats and birds, as well as bat hawks, that matched the assumption of continuous hovering in the air (Figure 3b). More generally, according to the model, since hovering is easier in water than in air, predator motion during capture has wider amplitude in water, which leads to a greater chance for the predator to reach its prey. It explains why, in air, predators are more constrained by the capture mechanical limit than are aquatic predators.

The present study merges individual traits with physical features of the medium. The contribution of the physical parameters can be extracted from a comparison of net energetic gains between pelagic predators (i.e. living in water, a dense and viscous medium; Figures 4b and 5a) and flying predators (i.e. living in air, a low-density and low-viscosity medium; Figures 4c and 5b); the differences between the predicted aquatic and aerial trophic interactions explained above are ultimately related to these physical factors.

Tucker and Rogers (2014) found that predator–prey body size ratios are generally greater for carnivores than for herbivores. Usually, herbivores consume resources that do not move or move slowly compared with their size, so that they are able to overcome the mechanical limits set by the capture process. Carnivores face stronger mechanical capture limit because the prey can escape. Thus, a carnivore has better chances to capture a small prey than a large one, which leads to a larger body size ratio. In summary, our model offers a unique opportunity for a unified understanding of the mechanistic bases to predator–prey patterns across habitats and trophic levels. It shows that each predation sequence (i.e. searching, capturing and handling) plays a different role: search constrains lower predator size, capture constrains upper prey size, and handling constrains lower prey size. To analyse the respective contribution of each factor included in the model would be a step further towards a clear understanding of the results, but it would be beyond the scope of the present study.

Despite the overall good performance of the model, we see that predators often prey on organisms that the model considers smaller than the optimal size. We think that this mainly results from our use of generic, simplified allometric equations to describe important parameters in the model, such as prey population densities, maximum accelerations and detection distances. Recent advances in the field

of allometry have shown that the effect of body size can be more complicated than previously acknowledged (Hirt, Jetz, Rall, & Brose, 2017; Pawar et al., 2012; Wilson et al., 2015), although it is still predictable (Kiørboe & Hirst, 2014). Our model's predictability would certainly benefit from an increase in the realism of the allometric equations it uses.

There are other factors that may lead to a suboptimal choice of prey in real ecosystems. The optimal prey might be absent or show defence traits that make it challenging to find, capture or handle. Several studies have shown that further functional traits besides body size are necessary for an accurate prediction of trophic interactions (Blanchard, Heneghan, Everett, Trebilco, & Richardson, 2017; Eklöf et al., 2013). However, which traits need to be included first is yet debated (Boukal, 2014). Based on our model, and in agreement with other authors (Boukal, 2014; Higham, 2007), we propose as likely candidates the traits that play critical role in predator and prey performances during motion, after accounting for the effect of body size, that is, deviations from allometries in velocities, accelerations and muscular forces.

There are also predators that feed on prey with body sizes beyond the predicted range of prey sizes. Such predators probably evolved strategies to get past the capture and handling mechanical limits. One important strategy is the ambush or sit-and-wait strategy (Kiørboe, 2011), which leads to the capture of larger prey than expected in terrestrial ecosystems (Supporting Information Figure S3). Our model suggests that the largest prey size for these predators is set by the handling mechanical limit (but not for web-weaving spiders). Predators differ in other aspects of their search (Bläßle & Tyson, 2016), capture (Higham, 2007) and handling strategies (Kiørboe, 2011). Building mechanical models with a similar approach to ours for most of the major predation strategies would certainly advance our understanding of food web structure and its predictability.

Our model describes the interaction between a predator of a given size and a prey of a given size at a given moment in time, and it looks at the energetic balance between costs and gains during the predation act. But a predator usually needs to share its time between predation and other activities such as reproduction, recovery and the avoidance of its own predators. The energy gained from the predation act must also be spent in these activities. Our model ignores these additional energetic costs for the time being. The minimum prey size resulting in a positive net energy gain should be higher when all activities of the predator are included. It is far from obvious to calculate the energy cost related to the various activities of a predator. However, some existing allometric studies open the door to such a development (Preisser & Orrock, 2012; Rizzuto, Carbone, & Pawar, 2017). Similarly, prey abundance affects encounter rate and thus searching cost. Our study assumes a constant prey abundance at a given size as a first step. A model considering the effect of predators on prey abundance would be a natural next step.

Despite the high level of reductionism of our model, it fits empirical data remarkably well. This suggests that predator–prey interactions in pelagic and aerial habitats are heavily constrained by mechanical factors despite hundreds of millions of years of evolution. It seems that numerous species follow the assumptions of the model and stay within the limits imposed by mechanical and energetic constraints, while other species have adapted to overcome these limits in a way that is consistent with our model, albeit with relaxed assumptions (Figure 5). Overall, this suggests that physical factors have played a major role in the evolution of trophic interactions. Our model offers a general framework for the study of the mechanical bases of trophic interactions across a wide range of body sizes. It also provides general conclusions and mechanisms underpinning well-known empirical patterns in the structure of food webs beyond apparent discrepancies between media. Our work strongly emphasizes the need to consider the physical medium to understand the ecology of food webs (Denny, 2016). In that sense, it is an ecosystem approach at heart, one that does not separate the organisms "from their special environments, with which they form one physical system" (Tansley, 1935).

AUTHORS' CONTRIBUTIONS

S.P. implemented the model, gathered data, performed simulations and analysis, and led the writing of the manuscript. M.C. initiated the project and provided conceptual and technical advice. G.F. and M.L. provided conceptual advice. All authors discussed the results and contributed critically to earlier drafts.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository: http://doi.org/10.5061/dryad.8c40mb0 (Portalier, Fussmann, Loreau, & Cherif, 2018). The MATLAB code used to implement the model deposited in the Zenodo Repository: http://doi.org/10.5281/zenodo.1494252 (Portalier, Fussmann, Loreau, & Cherif, 2018).

ORCID

Sébastien M. J. Portalier [ID] https://orcid.org/0000-0001-9755-5712

Mehdi Cherif [ID] https://orcid.org/0000-0003-0107-9374

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