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

# **Abstract**

First derivations of the functional response were mechanistic, but in practice, the subsequent uses of these first mechanistically-derived functions were mostly phenomenological and, to a large degree unsatisfactory. However, a better understanding of mechanisms underpinning functional response would lead to novel insights on predator-prey relationships within natural systems. We propose to return to the mechanistic approach, and we try to push it by including an explicit consideration of the movement of the organisms involved, and hence of mechanics. Living organisms are constrained by the physical properties of the surrounding medium. Hence, ability of moving is an essential aspect of most predator-prey interactions, and motion is affected by physical properties such as density or viscosity. Most predators have to move to search for a prey, then to capture this prey. Search and capture efficiencies are key elements of attack rate. Physical properties of the medium, in relation with body size, constrain predator and prey ability to move, thus affecting functional response. Considering mechanical effects from the medium grounds the functional response within its physical, local environment, and makes its parameterisation dependent on measurable morphological and physical traits of organisms. As an example of this kind of approach, we provide a model that derives classical parameters of a functional response (i.e., attack rate and handling time) from body size and physical factors. We use a recently published biomechanical model, and compute parameter values for the functional response. The novelty of this approach is that parameters are not estimated from observational data. The model only needs body sizes and physical properties of the medium, which can be easily measured.

Several ways for potential improvement are discussed. Further studies may include more physical factors such as temperature that affects physical properties and/or organism metabolism, or light that may be of importance for visual predators. This approach also provides easy ways to validate of falsify hypothesis. Hence, discrepancies between predictions and real data point immediately towards an error in the modelling, or means that important mechanisms are missing. Using this approach, functional response becomes an emerging property of the system. It opens a promising avenue for new approaches that would merge the biological part and the physical part of the medium. The strength of this kind of approach is to derive patterns at the community level from measures done at the individual or species level.

# **Introduction**

The study of the consumption rate of prey by a given predator (i.e., the functional response) began several decades ago (Gause, 1934; Gause et al., 1936). Quickly, the need of a theoretical framework emerged, and several mechanistic approaches were proposed (Lotka, 1923; Volterra, 1926; Beverton and Holt, 1957; Watt, 1959).

The model proposed by Holling (1961; 1966) is one of the best known. This mechanistic model defines parameters such as attack rate (the rate at which a predator encounter and capture prey) and handling time (the time needed by the predator to subdue, ingest and digest the captured prey, and during which the predator cannot attack another prey). These parameters can be measured concomitantly, and they give information about factors that constrain predation on a given prey, which is the strength of this mechanistic approach.

However, since Holling proposed the type-I, II and III models of functional responses, the subsequent uses of these mechanistically-derived functions have been, in practice, mostly phenomenological and, to a large degree unsatisfactory. Hence, many studies investigating functional response use a type-II or a type-III model, or any subsequently derived model (e.g., Rogers (1972)) as an *a priori* framework from which authors derive the values of attack rate and handling time from the data (e.g., Andresen and van der Meer, 2010; Farhadi et al., 2010; Papanikolaou et al., 2011)). They usually do not provide any mechanistic model to derive how the factors considered could affect the functional response. These approaches give valuable information on the studied systems, and they allow for hypothesis testing: for example, the effects of temperature (Archer et al., 2019) or predator satiation (Li et al., 2018) on functional response. However, they do not provide a real explanation on the mechanisms constraining attack rate, handling time, and therefore the functional response. Moreover, these studies are mostly carried out in laboratory, where many external factors do not apply (Abrams, 1982).

Coming back to the mechanistic roots of the functional response approach, several studies investigated the role played by factors known to affect the functional response. These models emphasized different features of predator-prey relationships, such as feeding saturation (DeAngelis et al., 1975)⁠, or interaction between predators (Wasserman et al., 2016)⁠. Among them, the body sizes of predator and prey is known to strongly affect the functional response (Aljetlawi et al., 2004; Vucic-Pestic et al., 2010)⁠. It appears that body size is a good predictor of trophic position (Williams et al., 2010)⁠ and affects the overall dynamics of the interaction (Yodzis and Innes, 1992).

However, the surrounding physical medium remain absent or at least implicit in most models, despite its ubiquity in real ecosystems. Although in his pioneer work Tansley (1935) stated that organisms should not be separated from their “special environment, with which they form one physical system”, the role played by the physical medium in constraining the functional response remains largely unexplored. Including physical features into predator-prey models would lead to novel insights about species interactions.

# **Physical features of the medium and size-related constraints**

Previous studies that considered the surrounding medium usually focused on specific aspects of predation or on specific taxa (Domenici et al., 2011)⁠, or investigated specific aspect of the medium such as dimensionality (Pawar et al., 2012)⁠ or complexity (Barrios-O’Neill et al., 2016)⁠. However, the role played by the surrounding medium acting at the individual level on predator-prey relationship, driving the functional response, remains to be explored.

Hence, living organisms are constrained by the physical properties of the surrounding medium (Denny, 1993; Denny, 2016; Vogel, 1996)⁠. These properties affect the way organisms move and/or interact with each other in different ways. For example, in aquatic systems, turbidity is an essential factor that constrains predator or prey that rely on visual cues to detect each others (Martens et al., 2015). Another example is turbulence that controls many planktonic organisms suspension within the water column (Rodríguez et al., 2001), and affects contact rate between predators and prey (Kiørboe and Saiz, 1995).

An important aspect is the role played by mechanical factors (i.e., gravity, density and viscosity) in constraining motion. Aquatic organisms do not experience the effects of gravity as terrestrial organisms usually do because medium density is much higher in water than in air, which creates higher buoyancy. Since predation usually implies motion, these factors create mechanical constraints acting differently on predators in different physical environments. These mechanical factors are ubiquitous and affect small predators (Kiørboe and Saiz, 1995), as well as large predators (Howland, 1974; Domenici et al., 2007)⁠. Actually, these effects are usually size-dependent: especially, the effects of medium viscosity and density on species motion through drag. Hence, motion of planktonic organisms has very different features than motion of larger organisms. Metrics such as Reynolds number are commonly used to discriminate between organisms that experience huge drag (low Reynolds number) and those that experience more inertia (high Reynolds number). These features affect the species according to their size and shape (Koehl and Strickier, 1981; Koehl, 1996). Hence, incorporating mechanical constraints into models would lead to a better understanding of the size-based relationship between predators and prey, and even of the size-structure of food webs.

Models incorporating physical (including mechanical) factors into predation model would merge size-related biological and mechanical constraints within classical predator-prey systems. In the past, several studies began to investigate this promising avenue. The complexity and dimensionality of the physical medium was shown to constrain predator-prey interactions since pelagic and flying predators would be more likely to contact prey than benthic and terrestrial predators (Pawar et al., 2012). Some studies coupled physical properties of the medium (constraining predator-prey encounter rate) with biological model (Baird and Emsley, 1999), or coupled models constraining nutrient diffusion and predator-prey contact rate with biological laws (Baird et al., 2006). But these models were limited to planktonic systems. This kind of approach was later extended to marine food webs using a oceanographic models (Baird and Suthers, 2007). Similarly, the effects of size on organismal moving ability was also investigated (Wilson et al., 2015). However, the effects of the physical medium of the specific aspect of the functional response have not yet explicitly been investigated.

The main advantage of many models coupling physical and general biological laws is that parameters in the models would be (mostly) related to predator and prey sizes, a trait that is commonly measured, which makes conclusions from the models easily testable. Applying this approach to the study of functional response would allow for a real novelty since the parameters of the functional response would not be measured at the community level, but would be derived from the individual (or species) level. Hence, classical parameters such as attack rate and handling time would become emerging properties of the model. Another strength of this approach is to allow for hypothesis testing, since discrepancies between predicted and observed patterns would point out to incomplete or erroneous hypothesis.

In order to illustrate this novel approach, we propose to include some of these mechanical factors related to body size into a theoretical model that predicts the functional response for a given predator and a given prey.

# **A case study as an example of new mechanistic approaches**

In a recent study, Portalier et al. (2019)⁠ provided a biomechanical model that uses general laws of mechanics and well-known biological laws, all related to body size, to predict predator to prey interactions. This model fits data remarkably well (Portalier et al., 2019)⁠. The model provides a detailed mechanism for predation, where predators have to move for searching, capturing and handling their prey. All these aspects depend on the body masses of both the predator and its prey. The parameters of the functional response can be immediately computed from the biomechanical model. Hence, this model provides a novel method to parameterize a functional response based on individual traits, and using mechanical laws. According to the biomechanical model assumptions, it is well-suited for pelagic organisms.

## **Main framework**

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.

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 and requires motion. Following the idea developed by Bejan and Marden (2006), motion can be modelled as an oscillatory process that is decomposed into three sequences. First, organismal stroke leads to a thrust that propels the body upwards (facing gravity and drag due to density and viscosity, but following Archimedes’ force) and forwards (facing drag). Second, when stroke ends, the body pursue its ascending movement by inertia until its stops. Third, the body returns by inertia to its original vertical position. During this vertical oscillation, the body moved forward compared to its original horizontal position (which represents the distance covered during the sequence) (see supplementary material for more details). Then, another sequence can begin. The model computed the thrust force needed to propel the body (that is constrained by body size), the horizontal distance covered, the speed and the associated energetic cost. Predicted speeds fit data remarkably well (see supplementary material). Both predator and prey follow the same framework.

Predation on a given prey requires time for searching, time for capturing and time for handling this prey. Knowing speeds of both predator and prey, one can determine encounter rate (Rothschild and Osborn, 1988). Relative speed between the predator and the prey at the time of capture also determines the probability of capture (and therefore the total time for searching a prey that leads to a successful capture), and time for capture. Search time (*ts*) represents the time needed by a predator to contact a prey that leads to a successful capture (e.g., if the capture probability is 0.5, then the predator needs to contact a prey twice on average to successfully capture it) . Capture time (*tc*) is the time needed to moves towards a prey and seize it. Last, handling time (*th*) is the time needed to consume, and digest the prey (handling time is the only component of the functional response that is independent of physical factors). The functional response (*f(N)*) is defined as the inverse of the time needed for searching, capturing and handling one unit of prey of abundance *N*. The function may be written as follows (see supplementary material)

*βPc* represents attack rate, where *β* is encounter rate (constrained by search time, and so by species speed), and *Pc* is capture probability. Capture time and handling time are taken into account instead of handling time only. Under this form, one can recognize a modified version of Holling's disk equation (1961).

Given the assumptions made on the encounter rate (see Supplementary Material), the functional response behaves as a type-II one. All parameter values change according to both predator and prey sizes, while attack rate, capture probability and capture time also vary with mechanical features of the medium.

## **Validation of the model**

Data were collected in order to test predictions from the model. Most data comes from meta-analysis⁠. To be pertinent, data has to mention predator and prey sizes explicitly. Most data is individual-based, which means that two individuals from the same species, but with different sizes are treated separately.

Attack rate and handling time were compared to real data coming from aquatic systems (Fig. 1). It appears that the model fits data quite well for attack rate. Linking mechanical features from the medium and body size allows a good estimate of attack rate for pelagic predators. However, handling time is usually underestimated for small predators, while the model is more accurate for larger predators. This discrepancy for small predators opens the door to many hypotheses that remain to be tested. Hence, this parameter is not dependent on mechanical features of the medium, but is driven only by allometric laws. Thus, the results suggest that the relationship between predator size, prey size and handling time is not only driven by an allometric law that is valid across a wide range of sizes. It is possible that the slope of this allometry function is different between small and large predators (Emerson et al., 1994), or that other factors increase handling time for small predators. Some studies suggested that handling time might not be static for a given predator, but can vary with prey abundance (Okuyama, 2010). These are examples of hypothesis that can be inferred by the analysis of such a model.

# **Conclusion and future directions**

The proposed model uses medium mechanical properties in a mechanistic approach. It considers only some physical factors. It can be improved in several ways. Further studies may include more physical factors such as temperature that affects physical properties (Larsen and Riisgård, 2009) and organism metabolism (Brown et al., 2004). One can consider factors that affect detection such as light or chemical cues. These factors diffuse differently in air and water, and perception ability by predators seems to be related to size (Martens et al., 2015). This novel framework is promising because it provides easy ways to validate of falsify hypothesis. Hence, any discrepancy between predictions and real data points immediately towards an error in the model, or means that important mechanisms are missing (as shown for handling time in the case study). It can also suggest novel hypothesis to be empirically or theoretically tested.

The strength of this kind of approach is to derive patterns at the community level from measures done at the individual or species level. Thus, functional response becomes an emerging property of the system. One may go even further by including other aspects associated to predation such as behavioral features (e.g., predator avoidance, interference between predators, social aspects) that were already considered by Holling (1966). This approach opens a promising avenue for new studies that would merge the biological part and the physical part of the medium.

# **References**

Abrams, P. A. (1982). Functional responses of optimal foragers. *Am. Nat.* 120, 382–390. doi:10.1086/283996.

Aljetlawi, A. A., Sparrevik, E., and Leonardsson, K. (2004). Prey-predator size-dependent functional response: derivation and rescaling to the real world. *J. Anim. Ecol.* 73, 239–252. doi:10.1111/j.0021-8790.2004.00800.x.

Andresen, H., and van der Meer, J. (2010). Brown shrimp (Crangon crangon, L.) functional response to density of different sized juvenile bivalves Macoma balthica (L.). *J. Exp. Mar. Bio. Ecol.* 390, 31–38. doi:10.1016/j.jembe.2010.04.027.

Archer, L. C., Sohlström, E. H., Gallo, B., Jochum, M., Woodward, G., Kordas, R. L., et al. (2019). Consistent temperature dependence of functional response parameters and their use in predicting population abundance. *J. Anim. Ecol.* 88, 1670–1683. doi:10.1111/1365-2656.13060.

Baird, M. E., and Suthers, I. M. (2007). A size-resolved pelagic ecosystem model. *Ecol. Modell.* 203, 185–203. doi:10.1016/j.ecolmodel.2006.11.025.

Baird, M. E., Timko, P. G., Suthers, I. M., and Middleton, J. H. (2006). Coupled physical-biological modelling study of the East Australian Current with idealised wind forcing. Part I: Biological model intercomparison. *J. Mar. Syst.* 59, 249–270. doi:10.1016/j.jmarsys.2005.09.005.

Baird, M., and Emsley, S. M. (1999). Towards a mechanistic model of plankton population dynamics. *J. Plankton Res.* 21, 85–126. doi:10.1093/plankt/21.1.85.

Barrios-O’Neill, D., Kelly, R., Dick, J. T. A., Ricciardi, A., MacIsaac, H. J., and Emmerson, M. C. (2016). On the context-dependent scaling of consumer feeding rates. *Ecol. Lett.* 19, 668–678. doi:10.1111/ele.12605.

Bejan, A., and Marden, J. H. (2006). Unifying constructal theory for scale effects in running, swimming and flying. *J. Exp. Biol.* 209, 238–248. doi:10.1242/jeb.01974.

Beverton, R. J. H., and Holt, S. J. (1957). On the dynamics of exploited fish population. *Fish. Investig.* 11, 1–533.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., and West, G. B. (2004). Toward A Metabolic Theory Of Ecology. *Ecology* 85, 1771–1789. doi:10.1890/03-9000.

DeAngelis, D. L., Goldstein, R. A., and O’Neill, R. V (1975). A Model for Tropic Interaction. *Ecology* 56, 881–892. doi:10.2307/1936298.

Denny, M. W. (1993). *Air and Water: The Biology and Physics of Life’s Media*. Princeton University Press Available at: https://books.google.com/books?hl=en&lr=&id=XjNS6v7q130C&pgis=1 [Accessed January 11, 2016].

Denny, M. W. (2016). *Ecological Mechanics: Principles of Life’s Physical Interactions*. Princeton University Press, Princeton, New Jersey Available at: https://books.google.com/books?hl=en&lr=lang\_en&id=V2MDCwAAQBAJ&pgis=1 [Accessed December 9, 2015].

Domenici, P., Blagburn, J. M., and Bacon, J. P. (2011). Animal escapology I: theoretical issues and emerging trends in escape trajectories. *J. Exp. Biol.* 214, 2463–2473. doi:10.1242/jeb.029652.

Domenici, P., Claireaux, G., and McKenzie, D. J. (2007). Environmental constraints upon locomotion and predator-prey interactions in aquatic organisms: an introduction. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 362, 1929–1936. doi:10.1098/rstb.2007.2078.

Emerson, S. B., Greene, H. W., and Charnov, E. L. (1994). “Allometric aspects of predator-prey interactions,” in *Ecological morphology: integrative organismal biology*, eds. P. C. Wainwright and S. M. Reilly (University of Chicago Press Chicago, IL), 123–139.

Farhadi, R., Allahyari, H., and Juliano, S. A. (2010). Functional Response of Larval and Adult Stages of *Hippodamia variegata* (Coleoptera: Coccinellidae) to Different Densities of *Aphis fabae* (Hemiptera: Aphididae). *Environ. Entomol.* 39, 1586–1592. doi:10.1603/EN09285.

Gause, G. F. (1934). *The struggle for existence*. Williams and Wilkins, Baltimore.

Gause, G. F., Smaragdova, N. P., and Witt, A. A. (1936). Further Studies of Interaction between Predators and Prey. *J. Anim. Ecol.* 5, 1. doi:10.2307/1087.

Holling, C. S. (1961). Principles of Insect Predation. *Annu. Rev. Entomol.* 6, 163–182. doi:10.1146/annurev.en.06.010161.001115.

Holling, C. S. (1966). The Functional Response of Invertebrate Predators to Prey Density. *Mem. Entomol. Soc. Canada* 98, 5–86. doi:10.4039/entm9848fv.

Howland, H. C. (1974). Optimal strategies for predator avoidance: The relative importance of speed and manoeuvrability. *J. Theor. Biol.* 47, 333–350. doi:10.1016/0022-5193(74)90202-1.

Kiørboe, T., and Saiz, E. (1995). Planktivorous feeding in calm and turbulent environments, with emphasis on copepods. *Mar. Ecol. Prog. Ser.* 122, 135–145. doi:10.3354/meps122135.

Koehl, M. A. R. (1996). When Does Morphology Matter? *Annu. Rev. Ecol. Syst.* 27, 501–542. doi:10.1146/annurev.ecolsys.27.1.501.

Koehl, M. A. R., and Strickier, J. R. (1981). Copepod feeding currents: Food capture at low Reynolds number. *Limnol. Oceanogr.* 26, 1062–1073. doi:10.4319/lo.1981.26.6.1062.

Larsen, P. S., and Riisgård, H. U. (2009). Viscosity and not biological mechanisms often controls the effects of temperature on ciliary activity and swimming velocity of small aquatic organisms. *J. Exp. Mar. Bio. Ecol.* 381, 67–73.

Li, Y., Rall, B. C., and Kalinkat, G. (2018). Experimental duration and predator satiation levels systematically affect functional response parameters. *Oikos* 127, 590–598. doi:10.1111/oik.04479.

Lotka, A. J. (1923). Contribution to quantitative parasitology. *J. Washingt. Acad. Sci.* 13, 152–158. Available at: http://www.jstor.org/stable/24533190.

Martens, E. A., Wadhwa, N., Jacobsen, N. S., Lindemann, C., Andersen, K. H., and Visser, A. (2015). Size structures sensory hierarchy in ocean life. *Proc. R. Soc. B* 282, 20151346. doi:10.1098/rspb.2015.1346.

Okuyama, T. (2010). Prey density-dependent handling time in a predator-prey model. *Community Ecol.* 11, 91–96. doi:10.1556/ComEc.11.2010.1.13.

Papanikolaou, N. E., Martinou, A. F., Kontodimas, D. C., Matsinos, Y. G., and Milonas, P. G. (2011). Functional responses of immature stages of Propylea quatuordecimpunctata (Coleoptera: Coccinellidae) to Aphis fabae (Hemiptera: Aphididae). *Eur. J. Entomol.* 108, 391.

Pawar, S., Dell, A. I., and Savage, V. M. (2012). Dimensionality of consumer search space drives trophic interaction strengths. *Nature* 486, 485–9. doi:10.1038/nature11131.

Portalier, S. M. J., Fussmann, G. F., Loreau, M., and Cherif, M. (2019). The mechanics of predator–prey interactions: First principles of physics predict predator–prey size ratios. *Funct. Ecol.* 33, 323–334. doi:10.1111/1365-2435.13254.

Rodríguez, J., Tintoré, J., Allen, J. T., Blanco, J. M., Gomis, D., Reul, A., et al. (2001). Mesoscale vertical motion and the size structure of phytoplankton in the ocean. *Nature* 410, 360–363. doi:10.1038/35066560.

Rogers, D. (1972). Random Search and Insect Population Models. *J. Anim. Ecol.* 41, 369–383. doi:10.2307/3474.

Rothschild, B. J., and Osborn, T. R. (1988). Small-scale turbulence and plankton contact rates. *J. Plankton Res.* 10, 465–474. doi:10.1093/plankt/10.3.465.

Tansley, A. G. (1935). The Use and Abuse of Vegetational Concepts and Terms. *Ecology* 16, 284–307.

Vogel, S. (1996). *Life in moving fluids: the physical biology of flow*. Princeton University Press, Princeton, New Jersey.

Volterra, V. (1926). Variazioni e fluttuazioni del numero d’individui in specie animali conviventi. *Mem. Acad. Lincei* 6, 31–113.

Vucic-Pestic, O., Rall, B. C., Kalinkat, G., and Brose, U. (2010). Allometric functional response model: body masses constrain interaction strengths. *J. Anim. Ecol.* 79, 249–56. doi:10.1111/j.1365-2656.2009.01622.x.

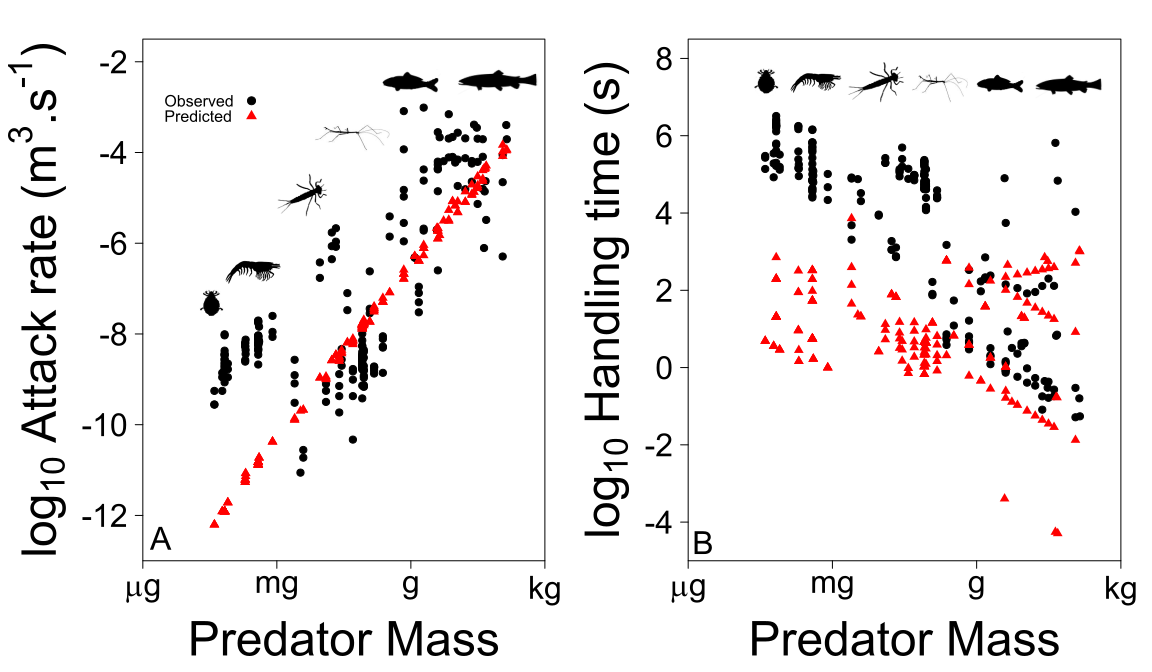
Wasserman, R. J., Alexander, M. E., Dalu, T., Ellender, B. R., Kaiser, H., and Weyl, O. L. F. (2016). Using functional responses to quantify interaction effects among predators. *Funct. Ecol.* 30, 1988–1998. doi:10.1111/1365-2435.12682.

Watt, K. E. F. (1959). A Mathematical Model for the Effect of Densities of Attacked and Attacking Species on the Number Attacked. *Can. Entomol.* 91, 129–144. doi:10.4039/Ent91129-3.

Williams, R. J., Anandanadesan, A., and Purves, D. (2010). The probabilistic niche model reveals the niche structure and role of body size in a complex food web. *PLoS One* 5, e12092. doi:10.1371/journal.pone.0012092.

Wilson, R. P., Griffiths, I. W., Mills, M. G. L., Carbone, C., Wilson, J. W., and Scantlebury, D. M. (2015). Mass enhances speed but diminishes turn capacity in terrestrial pursuit predators. *Elife* 4. doi:10.7554/eLife.06487.001.

Yodzis, P., and Innes, S. (1992). Body Size and Consumer-Resource Dynamics. *Am. Nat.* 139, 1151–1175. doi:10.1086/285380.



**Figure 1**: Predator attack rate (A) and handling time (B) according to predator mass in aquatic systems. The model fits data quite well for attack rate, although data shows variance. Predictions for handling time are more accurate for relatively large predators than for smaller predators. This suggests that more investigations are needed in order to understand which factors constrain handling time for smaller predators.

Potential figures

