



# Considerations When Applying the Consumer Functional Response Measured Under Artificial Conditions

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Since its creation, considerable effort has been given to improving the utility of the consumer functional response. To date, the majority of efforts have focused on improving mathematical formulation in order to include additional ecological processes and constraints, or have focused on improving the statistical analysis of the functional response to enhance rigor and to more accurately match experimental designs used to measure the functional response. In contrast, relatively little attention has been given to improving the interpretation of functional response empirical results, or to clarifying the implementation and extrapolation of empirical measurements to more realistic field conditions. In this paper I explore three concepts related to the interpretation and extrapolation of empirically measured functional responses. First, I highlight the need for a mechanistic understanding when interpreting foraging patterns and highlight pitfalls that can occur when we lack understanding between the shape of the functional response curve and the mechanisms that give rise to that shape. Second, I discuss differences between experimental and real-world field conditions that must be considered when trying to extrapolate measured functional responses to more natural conditions. Third, I examine the importance of the time scale of empirical measurements, and the need to consider tradeoffs that alter or limit foraging decisions under natural conditions. Clearly accounting for these three conceptual areas when measuring functional responses and when interpreting and attempting to extrapolate empirically measured functional responses will lead to more accurate estimates of consumer impacts under natural field conditions, and will improve the utility of the functional response as a heuristic tool in ecology.

**Keywords:** functional response, laboratory experiment, mechanism, optimal foraging, scaling up

## INTRODUCTION

In 1959, Crawford Stanley Holling, an entomologist at the Canadian Department of Forestry, published two papers describing how a predator's consumption rate changes with the density of its prey (Holling, 1959a,b). These two papers described four functional responses that have become the backbone of predation ecology over the ensuing 60 years. Beyond describing

the rate of predation, the consumer functional response is now commonly incorporated into population models used to predict community dynamics (Rosenzweig and MacArthur, 1963). While Holling's initial functional responses considered prey density as the only determinant of consumption rate, additional important factors have since been identified. This has resulted in alternative forms of the functional response that account for, among other things, predator density (i.e., Beddington, 1975; DeAngelis et al., 1975), the relative abundance of predators and prey (Arditi and Ginzburg, 1989), prey size (Streams, 1994), predator size (Toscano and Griffen, 2013), and the size of both prey and predators simultaneously (Aljetlawi et al., 2004), the consumption of multiple prey species (Smout and Lindström, 2007), spatial variation in prey resources (Rincon et al., 2017) and habitat heterogeneity (Englund and Leonardsson, 2008), temperature impacts (Thompson, 1978), predator confusion (Jeschke and Tollrian, 2005), etc. In addition to the formulation of alternative models, other studies have shown the importance of experimental factors, such as arena size (Uiterwaal and DeLong, 2018; Uiterwaal et al., 2019). Recent work has also combined data across numerous studies to determine scaling rules for the functional response with temperature, body size, and experimental arena size (Rall et al., 2012).

In addition to the search for forms of the functional response that account for the appropriate ecological factors, considerable effort has also been given to improving statistical approaches to analyzing functional responses. This includes identifying appropriate methods of statistically determining which form of the Holling's functional response best describes consumption in a given system (Livdahl and Stiven, 1983; Juliano and Williams, 1987; Trexler et al., 1988; Casas and Hurliger, 1994; Juliano, 2001), accounting for prey depletion in studies where consumed prey are not replaced (Royama, 1971; Rogers, 1972), and estimating the functional response parameters (Glass, 1970; Juliano and Williams, 1987; Fan and Petitt, 1994; Bolker, 2008; Gilioli et al., 2012; Pritchard et al., 2017; Rosenbaum and Rall, 2018).

While the work cited above demonstrates consistent effort devoted to the technical aspects of developing and analyzing functional response equations, considerably less attention has been given to examining how to extrapolate and apply the functional response in ways that avoid bias. While less technical, and thus less certain, this aspect of the functional response is no less important, especially given the central role of the consumer functional response in determining expected population growth of recovering consumers (e.g., gray wolves, Van Deelen, 2009; sea otters, Chadès et al., 2012), control of pest prey species (e.g., Luff, 1983; Fernández-arhex and Corley, 2003; Liu et al., 2006; Xu et al., 2018), and understanding community stability (Murdoch and Oaten, 1975; Schmitz et al., 1997).

In this paper, I discuss three conceptual issues with the use or application of the consumer functional response. This is not the first time these issues have been noted. Indeed, many of the papers cited throughout have raised concerns with the measurement and use of the functional response. Yet the continued misuse of functional responses suggests a need for additional clarity in the way that functional responses are measured, usually in the laboratory, and then extrapolated to field conditions. I

first address the mechanistic basis of the functional response and the need for understanding the mechanisms underlying the consumption patterns and the link between behavioral mechanisms and functional response parameter estimates. Next, I address the application of functional responses measured in standard laboratory procedures to natural systems that often do not mimic the simplified laboratory setting. Finally, I address the functional response in the context of optimal foraging behavior and highlight some ways that optimal foraging can complicate the application of functional responses to natural systems.

## MECHANISMS OF THE FUNCTIONAL RESPONSE

When striving to understand how to apply the consumer functional response, it is instructive to understand the mechanisms under which it was developed. Holling (1959b) developed his ideas using a simple experiment in which his secretary (Miss Patricia Baic) tapped her fingers around the surface of a 3-ft square table while blindfolded to find small (4-cm diameter) round discs of sandpaper that were stuck to the table with thumb tacks; hence the name of the type II functional response equation (the "disc equation"):

$$C = \frac{TaR}{1 + ahR}$$

There are two parameters in the disc equation. The first is the attack rate ( $a$ ), or the rate of discovery of prey, which is influenced by the rate of searching and the probability of finding a given prey. The second is the handling time ( $h$ ), or the amount of time required to capture, subdue, consume, and digest a prey item. In addition, the equation includes the time available for foraging ( $T$ ), and the prey density ( $R$ ). Mechanistically, attack rate and handling time were determined in Holling's experiment by the rate at which his secretary probed the desk to find sandpaper discs (attack rate) and the time required to pick up each sandpaper disc once found (handling time). Appropriately estimating the value for these two parameters in the functional response equation depends on meeting the assumptions of the model. Holling (1959b) identified two assumptions, namely that both the attack rate and the handling time are constants at all prey densities (i.e., they are independent of prey density). However, this assumption does not appear to be met in many experimental systems. Instead, handling times often decrease with prey density (Okuyama, 2010), and attack rates that increase with prey density are the basis of the sigmoidal (Type III) functional response (Juliano, 2001). Frequent violation of this static-parameter assumption means that multiple combinations of attack rate and handling time can lead to the same predation rate, and may therefore require the use of models with flexible components that can accommodate parameter changes with prey density (Okuyama, 2012).

An additional assumption not highlighted by Holling is that predators are engaged in foraging, via either searching for or handling prey, throughout the duration of the experimental trial. This was always true in Holling's simplified sandpaper disc

experiment, largely because the experimental duration of each trial was only 1 min. But this assumption is rarely met with live predators. Instead, even in simplified experimental conditions, predators will often engage in other activities during the experimental trial. Functional responses are generally measured using experiments where treatments consist of chambers with different numbers of prey ( $R$ ). Predators are then added to the chambers for a set amount of time ( $T$ ) and allowed to forage. At the conclusion of this time, predators are removed and surviving prey are counted. Using this experimental design, the predator may spend non-foraging time in several ways, including exploring the experimental chamber in an attempt to escape, sitting idle at the start of an experiment until they become sufficiently comfortable to begin foraging, digesting or otherwise remaining immobile due to a lack of hunger, etc. In addition, given variation in prey defense, some prey are detected and attacked and time is spent handling them in unsuccessful foraging attempts that do not ultimately result in prey consumption.

The standard functional response model is blind to each of these aspects of “wasted” time. The model is fitted to a dataset with the assumption that all time during the experimental trial was spent either searching for or handling prey that were ultimately consumed. When the dataset includes any non-foraging behaviors, it results in rates of prey consumption that are less than what would occur if predators actually were foraging through every moment of an experimental trial. Longer experimental trials, which are more likely to include non-foraging behavior than shorter trials, therefore generally result in lower attack rate estimates and higher handling time estimates because the assumption of continual foraging described above is increasingly violated as experimental duration increases. This phenomenon has been demonstrated by the meta-analysis of Li et al. (2018) using a large database of functional response parameter estimates obtained from 648 published experiments (Rall et al., 2012). They showed that attack rate decreased as experimental duration increased, likely because as experimental duration increases, increasingly large proportions of the experimental duration are spent doing activities other than foraging.

The reality that consumers engage in non-foraging activities suggests two possible problems that may arise in the measurement of functional responses using short-duration experiments. First, time spent in non-foraging activities is normal for consumers, and these normal activities may be absent during short-duration experiments using animals that are encouraged to forage actively by providing abundant food that requires little effort to acquire or by withholding food prior to the start of the experiment to create extreme hunger. Thus, short-duration experiments will overestimate attack rates relative to attack rates under natural conditions. Second, some non-foraging activities reflect responses to handling or to being placed in an unfamiliar environment, and may reflect a fear response that, while natural, may be expressed for a greater proportion of time under experimental conditions than may be expected under natural conditions. This may especially be true when measuring functional responses of individuals with shy personalities (Toscano and Griffen, 2014). In this case,

short-duration experiments may underestimate attack rates expected under natural conditions.

The result of fitting the functional response model to a dataset that results from an experiment where predators engaged in non-foraging activities during the experimental trial, is that we take a mechanistic model and we divorce the parameterization of that model from the true mechanisms that it is meant to convey. Problems arise when we then apply the functional response for any practical purpose, such as comparing parameters (attack rates and handling times) across species, using it to predict population growth, using it to inform pest control in agroecosystems, etc. Previous work advocates a comparative functional response approach for determining the relative impacts of different consumers, especially for predicting the likely impacts of invasive species (e.g., Dick et al., 2013, 2014; Alexander et al., 2014; Paterson et al., 2015). However, this approach only works if species being compared respond similarly to the artificial conditions of the experiment (food withholding, caging, simplified habitat, laboratory conditions, food offered, etc.). The use of identical experimental techniques across species being compared is not sufficient to allow comparison; what is important is the *response* of those species to the experimental techniques employed, and how those responses compare to foraging behavior and time use under natural conditions.

The problems of non-foraging behavior during functional response experiments can be handled in three possible ways. The first approach is to explicitly build non-foraging mechanisms into the functional response model. For instance, Jeschke et al. (2002) developed a model that included both digestion time and the unsuccessful attack of prey. The result was a model that predicted that consumers consumption rates would be limited (i.e., the asymptote of the functional response curve would be determined) by either handling time or digestion time, whichever of the two took longer to complete. This first method has the potential to fully address the problem arising from the expression of non-foraging behavior by consumers during experimental trials, but it may result in complicated functional response models that are challenging to fit to data and are difficult to interpret.

The second approach for dealing with non-foraging behavior during trials is to increase the complexity of experiments used to measure the functional response to include behavioral observations during each trial. When fitting the functional response equation to the data, the foraging time ( $T$ ) is then adjusted to be the time actually spent actively foraging rather than the duration of the experimental trial. This second method provides an estimate of the attack rate while actively foraging, and the application of this rate in population models or for any applied purpose therefore requires knowledge of the proportion of time that consumers spend foraging under natural conditions.

The third approach for dealing with non-foraging behavior when measuring the functional response is to conduct longer experimental trials. Experimental trials should be sufficiently long so that the fear response is a relatively small portion of the overall experimental duration, and so that digestion, resting, and other normal non-foraging behaviors are expressed during the trial. The goal is for the trial to encompass or capture a realistic time budget of the experimental animal. Following this

reasoning, researchers often use experimental durations of 24 h; however, longer experimental periods are likely necessary for many organisms. This type of experiment is likely most feasible and successful under natural field conditions rather than in highly artificial lab conditions that are commonly used in functional response trials. Ultimately, the value of this approach must be balanced with the tradeoffs in replication that come with longer experiments conducted under natural field conditions.

In summary, while attack rates and handling times can be estimated by fitting the functional response model to any experimental data, this does not ensure that the parameter estimates will be ecologically meaningful. Thus, future studies either need a greater focus on measuring attack rates and handling times to ensure that these mechanisms are accurate and useful, or they need to abandon the pretense that they have produced metrics that can be scaled up to field settings. In this case, researchers should simply report the consumption rates observed under the set of experimental conditions used, without trying to infer anything about the searching efficiency or the handling time of consumers. Additionally, results of functional response experiments can be most usefully applied when we understand the mechanisms that give rise to the parameter estimates, and whether those same mechanisms are relevant under more natural field conditions. For example, it is possible that response asymptotes in the lab are determined by gut fullness due to the short duration of experiments and the ease of finding food, while under field conditions, upper limits of consumptions may be determined by prey handling time, interactions with other consumers such as kleptoparasitism, or constraints that limit foraging time (Jeschke, 2007). Similarly, in the lab, attack rate may conceivably be determined by search image or simply by the time required to move across an empty tank to the next prey item, while in the field, it could instead be determined by diet choice based on optimal foraging strategies. Thus, if we want to apply functional responses outside the conditions where they were measured, a firm understanding of the underlying mechanisms is essential.

## EXTENDING RESULTS OF SIMPLIFIED LAB TESTS TO COMPLICATED NATURAL SYSTEMS

Above, I discussed the need for understanding the mechanistic basis of the measured functional response if that relationship is to have applied utility. In this section, I explore this topic in more depth by providing examples of the pitfalls of blindly applying laboratory-measured functional responses to field situations, especially when trying to scale up from individual level consumption to the population level impacts of consumers. Scaling up from individual phenomena to population patterns is complicated for any ecological process (Thrush et al., 1997; Underwood et al., 2005) and multiple approaches have been developed to accomplish this task (Denny and Benedetti-Cecchi, 2012).

The process of scaling up the functional response can yield counterintuitive results, such as changes in the form of the

functional response. For instance, Cordoleani et al. (2013) found that when type I and type II functional responses measured at the small scale (i.e., the scale of most experiments) are scaled up to the entire system, nonlinearities in the system resulting from spatial heterogeneity in prey abundance shift the functional response to a type III instead. Further, the likelihood of this switch in the form of the functional response increases as the size of the system, and thus the amount of scaling, increases. This provides a cautionary tale for directly scaling functional responses as measured on individuals in the lab to consumer populations in the field. The temptation is to use the average prey density in an environment, together with the per capita consumption rate of a predator at that prey density as determined from the functional response, and the density of the predator to simply multiply through to get an estimate of the consumptive impacts of the predator populations. But performing such a simplified calculation can yield very misleading results. I provide two examples below to illustrate. These examples are indicative of widespread approaches, and my intent is not to malign either of these two studies. Both provide valuable insights into their respective study systems.

New Zealand mud snails *Potamopyrgus antipodarum* are invasive to the western United States where they can reach extremely high densities exceeding 500,000 individuals  $m^{-2}$  in streams (Hall et al., 2006), thus dominating ecosystem function (Hall et al., 2003). The signal crayfish *Pacifastacus leniusculus* has the potential via consumption to provide biotic resistance to the spread of this invader, and Twardochleb et al. (2012) combined functional response experiments with a population growth estimate to examine this potential. Their functional response experiments included methods that are used broadly across studies, including withholding food prior to feeding trials to increase hunger levels and thus ensure feeding during the trials, conducting experiments in simplified chambers where predators do not have to search for prey, and the use of fairly short feeding trials that ranged from 15 min. to 12 h. In their experiments, crayfish at times consumed >900 snails in a 12 h period. Based on these results, their population model projected that crayfish could indeed provide biotic resistance to the invader.

The Asian shore crab *Hemigrapsus sanguineus* is invasive to the eastern coast of the United States, where they reach densities that often exceed 100 ind.  $m^{-2}$  (O'Connor, 2014). Lohrer and Whitlatch (2002) measured the functional response of the Asian shore crabs consuming mussel prey, also in small laboratory experiments over short time intervals where crabs did not have to search for prey and did not have alternative prey available to them. As with the crayfish study above, this study too resulted in high consumption rates, with individual crabs consuming up to 125 mussels per day. Based on the type II functional response reported, the densities of crabs, and the prey densities in the field, Griffen et al. (2021) calculated that the crabs would be able to deplete the entire mussel population along the shore in less than 7 h.

These two examples each highlight the problems that can arise if functional responses measured under simplified conditions are then scaled up to examine population level impacts. Similar arguments have highlighted the problems of scaling up to



the population level when consumer interference is important (Arditi and Ginzburg, 2012). Experiments such as these are designed to yield very high consumption rates by using starved animals, a simplified habitat where prey cannot find refuge from predators, where all prey are within the size range that is ideal for the predator so that no size selection has to occur, where no alternative food sources are available to dilute the consumption of the focal prey, and where experimental durations reveal gut capacity rather than ecologically relevant consumption rates. In the first study, while crayfish in the lab were observed consuming >900 snails in 12 h, in field locations with the highest snail density of  $4,511 \pm 1,504$  snails  $m^{-2}$  (i.e., where consumption of the invasive snail should have been highest), Twardochleb et al. (2012) report that crayfish had just  $7.9 \pm 2.8$  snail spires in their guts—more than 2 orders of magnitude less than what was predicted by the simplified functional response experiments. Similarly, while the second study on Asian shore crabs documented maximum consumption of 125 mussels per day, additional functional response experiments conducted under field conditions, over longer time periods (1 week) and with alternative prey available found that this crab species consumed just 3.9 mussels per day on average (Griffen, 2006). Further, gut content analyses conducted monthly over the entire active foraging season for this species showed that mussels were rarely found in the guts and comprised <1% of the diet (Griffen et al., 2012). Thus, while some of the mismatch between consumption in simplified experiments and natural field consumption stems from experimental issues highlighted above, some of this mismatch is attributable to ignoring the consumption of multiple prey types by using pairwise functional responses (i.e., one predator species, one prey species).

As with other fields of ecology, methods have been developed for scaling up the functional response. The primary method that has been proposed is scale transition theory (Chesson et al., 2005; Bergström et al., 2006; Melbourne and Chesson, 2006). This approach involves measuring functional responses in laboratory experiments, making small-scale measurements in the field to estimate heterogeneity, and then using these to scale up (Englund and Leonardsson, 2008). Other approaches also provide viable methods for reliably scaling up. For instance, Rincon et al. (2017) used an individual based model to scale up insect consumption from consumption in small-scale laboratory experiments to consumption on an entire tomato plant. The key to success in this method was the accurate use of search behavior by the predator that was mechanistically built into the model, together with the prey distribution in the field.

Two approaches have been implemented that provide alternatives to determining the functional response experimentally. First, DeLong and Lyon (2020) fit ordinary differential equations to time series of predator-prey populations to estimate the mechanisms of species interaction, including the functional response. The benefit of this “reverse modeling” approach is that it directly estimates the functional response at the population level and avoids the need to scale up altogether. Second, Beardsell et al. (2021) built a model of the functional response based on known or estimated mechanism, including predator speed, chasing time, attack probabilities when prey

are encountered, reaction distance, and others. The benefit of this approach is the foundation of behavioral mechanisms that build the functional response from the ground up. This type of mechanistic functional response could conceivably be applied to a broad range of conditions, depending on the quality and type of data used in its development.

In summary, per capita consumption rates must be scaled up to inform population level consequences, but care must be taken to ensure that methods used for scaling up account for ecological realities that are specific to the study system. Further, the use of appropriate methods for scaling up does not remedy inaccurate attack rates and handling times that are artifacts of experimental procedures. For instance, pre-trial starvation of experimental animals is likely to increase consumption above normal rates to compensate (Nandini and Sarma, 1999), and the meta-analysis of functional responses by Li et al. (2018) found that handling times were shorter for hungry predators than for starved predators. Thus, researchers should take steps to minimize experimental artifacts by using unstarved animals, conducting experiments over longer duration and in habitats that mimic natural habitat in terms of complexity (for example see Messina and Hanks, 1998; Anderson, 2001; Barrios-O’Neill et al., 2016; Wasserman et al., 2016), prey diversity, etc. Alternatively, researchers can conduct simplified experiments, but should then understand the real metrics that these experiments yield: gut capacity, maximum feeding rates, etc. While these types of data have value, they are less useful for application in population models because they do not reflect predation rates expected under realistic conditions.

## MISMATCHES BETWEEN MEASURED FUNCTIONAL RESPONSES AND OPTIMAL FORAGING BEHAVIOR

Above I touched on two artifacts of functional response experiments that can lead to inaccurate estimates of attack rate and handling time: time spent in activities other than foraging, and the inclusion of only a single, focal prey species in the experiment. Both of these artifacts can be problematic because of optimal foraging strategies of animals (Abrams, 1982, 1990; Stephens and Krebs, 2019). Here I explore three ways that optimal foraging may interfere with or complicate the measurement and scaling up of the functional response (Abrams, 1982). Each provides a mechanistic understanding for why we might expect non-foraging activity during an experiment or why neglecting to have alternative prey for a non-specialist consumer would be a problem.

The first issue deals with the timing of experimental trials relative to the timing of natural foraging under field conditions. Many species adopt daily to monthly foraging patterns tied to solar, lunar, and tidal patterns in order to optimize food intake in the face of fluctuating availability. For example, many species, including marine mollusks (Little, 1989), marine iguanas (Wikelski and Hau, 1995), fish (Burrows et al., 1994), and insects (Moore et al., 1989) display endogenous foraging patterns determined by tidal fluxes, daylight, or the timing of food

availability. These endogenous rhythms can remain in place for days to weeks, even after removing the environmental cue by moving the animals into static laboratory conditions (e.g., Zeng and Naylor, 1996). Consequently, ignoring these natural rhythms when designing short term feeding experiments has the potential to influence observed consumption in ways that obscure the true functional response of the study species. Similarly, abundant evidence demonstrates that animals adjust the timing of foraging activities in order to balance the competing risks of starvation and predation. For instance, blackbirds *Turdus merula* adjust their foraging throughout the day in different ways, depending on the time of year, to either increase mass gain in the early morning during winter to reduce starvation risk, or to increase mass gain later in the day during summer and autumn in order to reduce predation risk that increases with body mass (Macleod et al., 2005). The expectation that consumption rate should increase with prey density in functional response experiments is based on the assumption that it is always optimal for consumers to eat as much as they can. Yet the presence of constraints and tradeoffs that are context dependent complicates this assumption. Functional response experiments must consider consumption in light of optimal timing and amount of consumption to which the study organism has evolved. Mathematically building these tradeoffs and optimality considerations into the functional response framework would make the framework too context-dependent and would remove the generality of the model, but when trying to use the functional response in an applied, predictive way, these tradeoffs should be explicitly considered.

A second issue deals with optimal diet selection, a subset of optimal foraging theory that predicts that consumers should pass up low quality food when higher quality food is readily available (Stephens et al., 2007). The vast majority of functional response experiments are conducted using a single prey type, even for consumers that have a broad diet. The presence of alternative prey can drastically alter the functional response (Hossie et al., 2021). Thus, for non-specialist consumers, whether the functional response measured in the laboratory on a single prey is transferrable at all to field conditions, depends on the abundance of different prey types and their relative quality as determined by energy content and handling time required. This argument applies not only to different species of prey, but to different sizes of a single prey species as well, because prey profitability depends on size-specific energy content and handling time. As predicted by optimal diet theory (Emlen, 1966), a consumer should only accept lower quality prey if the net energy gained by doing so exceeds the net energy gain from both finding and consuming the rare higher quality prey. Thus, a functional response measured using a lower quality prey in the lab will be meaningless in the field where higher quality prey are readily available and where consumers forage optimally, because only higher quality prey should be consumed. Alternatively, if the functional response is measured in the laboratory using a high quality prey, transferring this to the field where prey are likely harder to find and where alternative lower quality prey are available, could shift an observed type II laboratory functional response to a type III response in the field, because

of diet switching to lower quality prey when high quality prey are sufficiently rare.

A third issue deals with the alternative foraging strategies of rate maximization vs. time minimization (Schoener, 1971; Hixon, 1982). The measurement of the functional response using standard experimental procedures assumes that the consumer is a rate maximizer—attempting to eat as much as possible during the allotted time. But if the consumer is instead a time minimizer (i.e., a consumer that meets a given energy requirement as quickly as possible and then stops foraging), then we should expect that consumption rates will not increase substantially with prey density. Instead, foragers will seek a certain level of energy intake and will stop foraging once this level is reached. Species may not be strict time minimizers, but may show behaviors consistent with aspects of time minimization (e.g., Hughes and Seed, 1981). When time minimization influences foraging strategies, we should expect that consumption may still increase with prey density up to an asymptote; however, this asymptote may be very different than expected for energy maximizers. For time minimizers, the asymptote is set not by handling time or digestion efficiency, but by the fact that the energy intake quota has been reached. Thus, fitting functional response curves to these data for time minimizers would yield values for attack rate and handling time that are far off the mark, reflecting the time spent in activities other than foraging.

## CONCLUSION

The consumer functional response has been and will continue to be an important tool for studying and understanding consumer-resource interactions. The arguments and discussions above point to three areas where future research should place greater emphasis in order to increase the accuracy and utility of the functional response in its important role as a link between empirical and theoretical approaches. First, future empirical measurements of the functional response should strive for greater realism by conducting experiments during appropriate temporal windows that coincide with the natural foraging patterns of the study organism, and by more closely mimicking the breadth of natural prey resources available to the consumer in the field. Second, future work should collect the data necessary to ground-truth and hone model parameter estimates by measuring handling times directly and by observing the proportion of time during experiments that consumers spend actively foraging. Third, future applications of laboratory-measured functional responses to field populations should make greater effort to identify factors that lead to discrepancies between predicted and observed scaled-up consumption by identifying implicit assumptions in the use of the functional response and where those assumptions are violated by the study system, both in the lab and in the field.

## AUTHOR CONTRIBUTIONS

BG was responsible for all aspects of this work.

## REFERENCES

- Abrams, P. A. (1982). Functional responses of optimal foragers. *Am. Natural.* 120, 382–390. doi: 10.1086/283996
- Abrams, P. A. (1990). The effects of adaptive behavior on the type-2 functional response. *Ecology* 71, 877–885. doi: 10.2307/1937359
- Alexander, M. E., Dick, J. T., Weyl, O. L., Robinson, T. B., and Richardson, D. M. (2014). Existing and emerging high impact invasive species are characterized by higher functional responses than natives. *Biol. Lett.* 10:20130946. doi: 10.1098/rsbl.2013.0946
- 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
- Anderson, T. W. (2001). Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology* 82, 245–257. doi: 10.1890/0012-9658(2001)082[0245:prprad]2.0.co;2
- Arditi, R., and Ginzburg, L. R. (1989). Coupling in predator-prey dynamics: ratio-dependence. *J. Theor. Biol.* 139, 311–326. doi: 10.1016/s0022-5193(89)80211-5
- Arditi, R., and Ginzburg, L. R. (2012). *How Species Interact: Altering the Standard View on Trophic Ecology*. Oxford: Oxford University Press.
- Barrios-O'Neill, D., Kelly, R., Dick, J. T., 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
- Beardsell, A., Gravel, D., Berteaux, D., Gauthier, G., Clermont, J., Careau, V., et al. (2021). Derivation of predator functional responses using a mechanistic approach in a natural system. *Front. Ecol. Evol.* 9:630944.
- Beddington, J. R. (1975). Mutual interference between parasites or predators and its effect on searching efficiency. *J. Anim. Ecol.* 44, 331–340. doi: 10.2307/3866
- Bergström, U., Englund, G., and Leonardsson, K. (2006). Plugging space into predator-prey models: an empirical approach. *Am. Natural.* 167, 246–259. doi: 10.2307/3491265
- Bolker, B. M. (2008). *Ecological Models and Data in R*. Princeton NJ: Princeton University Press.
- Burrows, M. T., Gibson, R. N., and Maclean, A. (1994). Effects of endogenous rhythms and light conditions on foraging and predator-avoidance in juvenile plaice. *J. Fish Biol.* 45, 171–180. doi: 10.1111/j.1095-8649.1994.tb01091.x
- Casas, J., and Hulliger, B. (1994). Statistical analysis of functional response experiments. *Biocontrol Sci. Technol.* 4, 133–145. doi: 10.1080/09583159409355321
- Chadès, I., Curtis, J. M., and Martin, T. G. (2012). Setting realistic recovery targets for two interacting endangered species, sea otter and northern abalone. *Conserv. Biol.* 26, 1016–1025. doi: 10.1111/j.1523-1739.2012.01951.x
- Chesson, P., Donahue, M. J., Melbourne, B. A., and Sears, A. L. W. (2005). “Scale transition theory for understanding mechanisms in metacommunities,” in *Metacommunities: Spatial Dynamics and Ecological Communities*, eds M. Holyoak, M. A. Leibold, and R. D. Holt (Chicago, IL: University of Chicago Press), 279–306.
- Cordoleani, F., Nerini, D., Morozov, A., Gauduchon, M., and Poggiale, J. C. (2013). Scaling up the predator functional response in heterogeneous environment: when Holling type III can emerge? *J. Theoret. Biol.* 336, 200–208.
- 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
- DeLong, J. P., and Lyon, S. (2020). Temperature alters the shape of predator-prey cycles through effects on underlying mechanisms. *PeerJ* 8:e9377. doi: 10.7717/peerj.9377
- Denny, M., and Benedetti-Cecchi, L. (2012). Scaling up in ecology: mechanistic approaches. *Annu. Rev. Ecol. Evol. Syst.* 43, 1–22. doi: 10.1146/annurev-ecolsys-102710-145103
- Dick, J. T., Alexander, M. E., Jeschke, J. M., Ricciardi, A., MacIsaac, H. J., Robinson, T. B., et al. (2014). Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. *Biol. Invasions* 16, 735–753. doi: 10.1007/s10530-013-0550-8
- Dick, J. T., Gallagher, K., Avlijas, S., Clarke, H. C., Lewis, S. E., Leung, S., et al. (2013). Ecological impacts of an invasive predator explained and predicted by comparative functional responses. *Biol. Invasions* 15, 837–846. doi: 10.1007/s10530-012-0332-8
- Emlen, J. M. (1966). The role of time and energy in food preference. *Am. Natural.* 100, 611–617. doi: 10.1086/282455
- Englund, G., and Leonardsson, K. (2008). Scaling up the functional response for spatially heterogeneous systems. *Ecol. Lett.* 11, 440–449. doi: 10.1111/j.1461-0248.2008.01159.x
- Fan, Y., and Pettit, F. L. (1994). Parameter estimation of the functional response. *Environ. Entomol.* 23, 785–794. doi: 10.1093/ee/23.4.785
- Fernández-arhex, V., and Corley, J. C. (2003). The functional response of parasitoids and its implications for biological control. *Biocontrol Sci. Technol.* 13, 403–413. doi: 10.1080/0958315031000104523
- Gilioli, G., Pasquali, S., and Ruggeri, F. (2012). Nonlinear functional response parameter estimation in a stochastic predator-prey model. *Math. Biosci. Eng.* 9:75. doi: 10.3934/mbe.2012.9.75
- Glass, N. R. (1970). A comparison of two models of the functional response with emphasis on parameter estimation procedures. *Can. Entomol.* 102, 1094–1101. doi: 10.4039/ent1021094-9
- Griffen, B. D. (2006). Detecting emergent effects of multiple predator species. *Oecologia* 148, 702–709. doi: 10.1007/s00442-006-0414-3
- Griffen, B. D., Altman, I., Bess, B. M., Hurley, J., and Penfield, A. (2012). The role of foraging in the success of invasive Asian shore crabs in New England. *Biol. Invasions* 14, 2545–2558. doi: 10.1007/s10530-012-0251-8
- Griffen, B. D., van den Akker, D., DiNuzzo, E. R., Anderson, L., and Vernier, A. (2021). Comparing methods for predicting the impacts of invasive species. *Biol. Invas.* 23, 491–505.
- Hall, R. O. Jr., Dybdahl, M. F., and VanderLoop, M. C. (2006). Extremely high secondary production of introduced snails in rivers. *Ecol. Appl.* 16, 1121–1131. doi: 10.1890/1051-0761(2006)016[1121:ehspoi]2.0.co;2
- Hall, R. O. Jr., Tank, J. L., and Dybdahl, M. F. (2003). Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. *Front. Ecol. Environ.* 1:407–411. doi: 10.2307/3868137
- Hixon, M. A. (1982). Energy maximizers and time minimizers: theory and reality. *Am. Natural.* 119, 596–599. doi: 10.1086/283937
- Holling, C. S. (1959a). The components of predation as revealed by a study of small-mammal predation of the European Pine Sawfly. *Can. Entomol.* 91, 293–320. doi: 10.4039/ent91293-5
- Holling, C. S. (1959b). Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91, 385–398. doi: 10.4039/ent91385-7
- Hossie, T. J., Chan, K., and Murray, D. L. (2021). Increasing availability of palatable prey induces predator-dependence and increases predation on unpalatable prey. *Sci. Rep.* 11:6763.
- Hughes, R. N., and Seed, R. (1981). Size selection of mussels by the blue crab *Callinectes sapidus*: energy maximizer or time minimizer. *Mar. Ecol. Prog. Ser. Oldendorf* 6, 83–89. doi: 10.3354/meps006083
- Jeschke, J. M. (2007). When carnivores are “full and lazy”. *Oecologia* 152, 357–364. doi: 10.1007/s00442-006-0654-2
- Jeschke, J. M., Kopp, M., and Tollrian, R. (2002). Predator functional responses: discriminating between handling and digesting prey. *Ecol. Monogr.* 72, 95–112.
- Jeschke, M. J., and Tollrian, R. (2005). Effects of predator confusion on functional responses. *Oikos* 111, 547–555. doi: 10.1111/j.1600-0706.2005.14118.x
- Juliano, S. A. (2001). Nonlinear curve fitting: predation and functional response curves. *Des. Anal. Ecol. Exp.* 2, 178–196.
- Juliano, S. A., and Williams, F. M. (1987). A comparison of methods for estimating the functional response parameters of the random predator equation. *J. Anim. Ecol.* 56, 641–653. doi: 10.2307/5074
- Li, Y., Rall, B. C., and Kalinkat, G. (2018). Experimental duration and predator satiation levels systematically affect functional response parameters. *Oikos* 127, 590–598.
- Little, C. (1989). Factors governing patterns of foraging activity in littoral marine herbivorous molluscs. *J. Molluscan Stud.* 55, 273–284. doi: 10.1093/mollus/55.2.273
- Liu, B., Teng, Z., and Chen, L. (2006). Analysis of a predator–prey model with Holling II functional response concerning impulsive control strategy. *J. Comput. Appl. Math.* 193, 347–362. doi: 10.1016/j.cam.2005.06.023
- Livdahl, T. P., and Stiven, A. E. (1983). Statistical difficulties in the analysis of predator functional response data. *Can. Entomol.* 115, 1365–1370. doi: 10.4039/ent1151365-10

- Lohrer, A. M., and Whitlatch, R. B. (2002). Relative impacts of two exotic brachyuran species on blue mussel populations in Long Island Sound. *Mar. Ecol. Prog. Ser.* 227, 135–144. doi: 10.3354/meps227135
- Luff, M. L. (1983). The potential of predators for pest control. *Agric. Ecosyst. Environ.* 10, 159–181. doi: 10.1016/0167-8809(83)90060-9
- Macleod, R., Barnett, P., Clark, J. A., and Cresswell, W. (2005). Body mass change strategies in blackbirds *Turdus merula*: the starvation–predation risk trade-off. *J. Anim. Ecol.* 74, 292–302. doi: 10.1111/j.1365-2656.2005.00923.x
- Melbourne, B. A., and Chesson, P. (2006). The scale transition: scaling up population dynamics with field data. *Ecology* 87, 1478–1488. doi: 10.1890/0012-9658(2006)87[1478:tstsup]2.0.co;2
- Messina, F. J., and Hanks, J. B. (1998). Host plant alters the shape of the functional response of an aphid predator (Coleoptera: Coccinellidae). *Environ. Entomol.* 27, 1196–1202. doi: 10.1093/ee/27.5.1196
- Moore, D., Siegfried, D., Wilson, R., and Rankin, M. A. (1989). The influence of time of day on the foraging behavior of the honeybee. *Apis mellifera. J. Biol. Rhythms* 4, 305–325. doi: 10.1177/074873048900400301
- Murdoch, W. W., and Oaten, A. (1975). Predation and population stability. *Adv. Ecol. Res.* 9, 1–131. doi: 10.1016/s0065-2504(08)60288-3
- Nandini, S., and Sarma, S. S. S. (1999). Effect of starvation time on the prey capture behaviour, functional response and population growth of *Asplanchna sieboldi* (Rotifera). *Freshwater Biol.* 42, 121–130. doi: 10.1046/j.1365-2427.1999.00467.x
- O'Connor, N. J. (2014). Invasion dynamics on a temperate rocky shore: from early invasion to establishment of a marine invader. *Biol. Invasions* 16, 73–87. doi: 10.1007/s10530-013-0504-1
- Okuyama, T. (2010). Prey density-dependent handling time in a predator-prey model. *Commun. Ecol.* 11, 91–96. doi: 10.1556/comec.11.2010.1.13
- Okuyama, T. (2012). Flexible components of functional responses. *J. Anim. Ecol.* 81, 185–189. doi: 10.1111/j.1365-2656.2011.01876.x
- Paterson, R. A., Dick, J. T., Pritchard, D. W., Ennis, M., Hatcher, M. J., and Dunn, A. M. (2015). Predicting invasive species impacts: a community module functional response approach reveals context dependencies. *J. Anim. Ecol.* 84, 453–463. doi: 10.1111/1365-2656.12292
- Pritchard, D. W., Paterson, R. A., Bovy, H. C., and Barrios-O'Neill, D. (2017). Frail: an R package for fitting and comparing consumer functional responses. *Methods Ecol. Evol.* 8, 1528–1534. doi: 10.1111/2041-210x.12784
- Rall, B. C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O., et al. (2012). Universal temperature and body-mass scaling of feeding rates. *Philos. Trans. R. Soc. B Biol. Sci.* 367, 2923–2934. doi: 10.1098/rstb.2012.0242
- Rincon, D. F., Cañas, L. A., and Hoy, C. W. (2017). Modeling changes in predator functional response to prey across spatial scales. *Theor. Ecol.* 10, 403–415. doi: 10.1007/s12080-017-0338-z
- Rogers, D. (1972). Random search and insect population models. *J. Anim. Ecol.* 41, 369–383. doi: 10.2307/3474
- Rosenbaum, B., and Rall, B. C. (2018). Fitting functional responses: direct parameter estimation by simulating differential equations. *Methods Ecol. Evol.* 9, 2076–2090. doi: 10.1111/2041-210x.13039
- Rosenzweig, M. L., and MacArthur, R. H. (1963). Graphical representation and stability conditions of predator-prey interactions. *Am. Natural.* 97, 209–223. doi: 10.1086/282272
- Royama, T. (1971). A comparative study of models for predation and parasitism. *Popul. Ecol.* 13, 1–91. doi: 10.1007/bf02511547
- Schmitz, O. J., Beckerman, A. P., and Litman, S. (1997). Functional responses of adaptive consumers and community stability with emphasis on the dynamics of plant-herbivore systems. *Evol. Ecol.* 11, 773–784. doi: 10.1023/a:1018494520794
- Schoener, T. W. (1971). Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* 2, 369–404. doi: 10.1146/annurev.es.02.110171.002101
- Smout, S., and Lindström, U. (2007). Multispecies functional response of the minke whale *Balaenoptera acutorostrata* based on small-scale foraging studies. *Mar. Ecol. Prog. Ser.* 341, 277–291. doi: 10.3354/meps341277
- Stephens, D. W., Brown, J. S., and Ydenberg, R. C. (Eds.) (2007). *Foraging: Behavior and Ecology*. Chicago IL: University of Chicago Press.
- Stephens, D. W., and Krebs, J. R. (2019). *Foraging Theory*. Princeton, NJ: Princeton University Press. doi: 10.1515/9780691206790
- Streams, F. A. (1994). Effect of prey size on attack components of the functional response by *Notonecta undulata*. *Oecologia* 98, 57–63. doi: 10.1007/bf00326090
- Thompson, D. J. (1978). Towards a realistic predator-prey model: the effect of temperature on the functional response and life history of larvae of the damselfly, *Ischnura elegans*. *J. Anim. Ecol.* 47, 757–767. doi: 10.2307/3669
- Trush, S. F., Schneider, D. C., Legendre, P., Whitlatch, R. B., Dayton, P. K., Hewitt, J. E., et al. (1997). Scaling-up from experiments to complex ecological systems: Where to next? *J. Exp. Mar. Biol. Ecol.* 216, 243–254. doi: 10.1016/s0022-0981(97)00099-3
- Toscano, B. J., and Griffen, B. D. (2013). Predator size interacts with habitat structure to determine the allometric scaling of the functional response. *Oikos* 122, 454–462. doi: 10.1111/j.1600-0706.2012.20690.x
- Toscano, B. J., and Griffen, B. D. (2014). Trait-mediated functional responses: predator behavioural type mediates prey consumption. *J. Anim. Ecol.* 83, 1469–1477. doi: 10.1111/1365-2656.12236
- Trexler, J. C., McCulloch, C. E., and Travis, J. (1988). How can the functional response best be determined? *Oecologia* 76, 206–214. doi: 10.1007/bf00379954
- Twardochleb, L. A., Novak, M., and Moore, J. W. (2012). Using the functional response of a consumer to predict biotic resistance to invasive prey. *Ecol. Appl.* 22, 1162–1171. doi: 10.1890/11-0871.1
- Uiterwaal, S. F., Dell, A. I., and DeLong, J. P. (2019). Arena size modulates functional responses via behavioral mechanisms. *Behav. Ecol.* 30, 483–489. doi: 10.1093/beheco/ary188
- Uiterwaal, S. F., and DeLong, J. P. (2018). Multiple factors, including arena size, shape the functional responses of ladybird beetles. *J. Appl. Ecol.* 55, 2429–2438. doi: 10.1111/1365-2664.13159
- Underwood, N., Hambäck, P., and Inouye, B. D. (2005). Large-scale questions and small-scale data: empirical and theoretical methods for scaling up in ecology. *Oecologia* 145:177.
- Van Deelen, T. R. (2009). “Growth characteristics of a recovering wolf population in the Great Lakes region,” in *Recovery of Gray Wolves in The Great Lakes Region of the United States*, eds A. P. Wydeven, T. R. Deelen, and E. Heske (Berlin: Springer), 139–154. doi: 10.1007/978-0-387-85952-1\_9
- Wasserman, R. J., Alexander, M. E., Weyl, O. L., Barrios-O'Neill, D., Froneman, P. W., and Dalu, T. (2016). Emergent effects of structural complexity and temperature on predator-prey interactions. *Ecosphere* 7:e01239.
- Wikelski, M., and Hau, M. (1995). Is there an endogenous tidal foraging rhythm in marine iguanas? *J. Biol. Rhythms* 10, 335–350. doi: 10.1177/074873049501000407
- Xu, J., Tian, Y., Guo, H., and Song, X. (2018). Dynamical analysis of a pest management Leslie-Gower model with ratio-dependent functional response. *Nonlinear Dyn.* 93, 705–720. doi: 10.1007/s11071-018-4219-9
- Zeng, C., and Naylor, E. (1996). Endogenous tidal rhythms of vertical migration in field collected zoea-1 larvae of the shore crab *Carcinus maenas*: implications for ebb tide offshore dispersal. *Mar. Ecol. Prog. Ser.* 132, 71–82. doi: 10.3354/meps132071

**Conflict of Interest:** The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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