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PERSPECTIVE
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Predation in Many Dimensions: Spatial Context Is Important for Meaningful Functional Response Experiments

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For simplicity and to minimize variation, functional response experiments frequently use environments of simple physical structure and small size. Less attention is paid to similarity of the experimental environment to the natural environment where predation occurs. Assumptions about predator and prey use of space are often implied in the choice of experimental environment. We illustrate how these assumptions may affect conclusions with an experiment testing how arena size affects a functional response. *Toxorhynchites rutilus* preyed upon larval *Culex restuans* in containers differing in volume by 15x, but spanning a similar range of prey/liter. The most plausible Type II model included attack rates that were statistically indistinguishable, but in the larger volume, had handling time that was lower by > 30x compared to the smaller volume, suggesting a major change in predator behavior with container volume. When we altered our assumption that predation scales with prey/liter, assuming instead that aggregation causes predation to scale with prey/area of surface or bottom, the conclusions changed: neither attack rate nor handling time differed with container size. Thus, our assumption about how predator and prey used space altered the conclusions of the experiment. We then summarize recently published experiments showing that spatial context affects estimated functional responses. We suggest that functional response experiments would be improved by using larger experimental spaces that represent physical complexity of environments where predation occurs. Greater spatial extent and complexity are likely to cause aggregation of predation. Effects of more realistic spatial context are likely to yield more complete understanding of quantitative aspects of predation.

Keywords: aggregation, area, edge effects, environmental complexity, predation, prey density, spatial dimensions, volume

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INTRODUCTION

Since Holling's thorough development of the quantitative treatment of the functional response of a predator to the density of its prey (Holling, 1959, 1965, 1966), functional responses have remained one of the most prevalent concepts in biological study of consumer-resource interactions. The quantitative relationship of consumption vs. resource density figures prominently in many investigations in biology, ecology, and behavior. Functional response models are commonly used in investigations of animal behavior, in attempts to understand the behavioral processes limiting feeding by predators and mortality of prey (e.g., Juliano, 1989; Jeschke et al., 2002).

Functional responses also form the basis of theory of foraging behavior predicting choices made by consumers while foraging (e.g., Stephens and Krebs, 1986; Cressman et al., 2014) and in resource-based models of competition and predation (e.g., Grover, 1997; Chase and Leibold, 2003). Empirically determined functional responses have been used in developing predictive models of predator-prey interactions for biological control (e.g., Madadi et al., 2011), predictions of potential for introduced species to become problematic invasive species (e.g., Dick et al., 2017; McCard et al., 2021), quantification of how multiple predators impact prey populations (e.g., McCoy et al., 2012; Hossie and Murray, 2016; Sentis and Boukal, 2018), and in evaluations of stability of species interactions and their effects on community diversity (e.g., Buxton et al., 2020; Kratina et al., 2021). A central idea in all the uses of functional responses is that individual behavioral interactions of consumers and their resources can be scaled up across different levels of biological/ecological organization, from behavioral choices and interactions of individuals, to population dynamics of consumers and victims, to community level interactions as they effect coexistence and diversity. Scaling up requires that functional responses are quantified in ways that are meaningful and predictive of processes occurring at higher levels of organization. This creates a need to measure functional responses in spatial contexts that are appropriate for the organisms and representative of the environments in which individual interactions of consumer and resource occur, and in which those individual processes influence population dynamics and community organization.

For simplicity and to minimize experimental variation, experimental environments used in functional response experiments are frequently simple in physical structure, small in size, and otherwise designed for ease of data collection. Less attention is paid to the similarity of the experimental environment to the natural environment about which predictions will be made (Griffen, 2021). These simplifications of the environment can have consequences for the results of the experiment, and are often based on assumptions about how both predator and prey perceive and use their environment.

The purpose of this perspective is: (1) To describe a case study of how assumptions about animal behavior in different spatial contexts can affect conclusions of functional response experiments; we do this via a simple example manipulating spatial context, and alternative analyses of the data under different assumptions about how predator and prey aggregate in the space in which the experiment was run. (2) To summarize recent examples of how different spatial contexts, and what is assumed about how predator and prey use experimental space, can change the conclusions and predictions of functional response experiments, often because of aggregation.

MATERIALS AND METHODS

A Case Study –Role of Assumptions About Use of Space

The functional response experiment used the predatory *Toxorhynchites rutilus* larvae and *Culex restuans* larvae as prey. Both mosquitoes are native to North America, and are commonly found in man-made (e.g., tires) and natural (e.g., tree holes) water filled containers. *Toxorhynchites* spp. are obligate predators on other invertebrates in water filled containers (Steffan and Evenhuis, 1981). *Culex restuans* is a member of the *Culex pipiens* complex, and is primarily a filter feeder (Merritt et al., 1992). *Culex restuans* were collected in Normal IL as egg rafts and placed individually in small vials. After egg hatch, larvae from each raft were identified as either *C. restuans* or *C. pipiens* (Darsie and Ward, 2005) and *C. restuans* were placed into a tray holding ∼300-400 larvae. *Toxorhynchites rutilus* were from a laboratory colony originating at Tyson Research Center, Eureka MO.

The functional response experiment tested the hypothesis that the size of the experimental arena (water-filled container) affects the functional response. We used first instar *T. rutilus* as predators and first instar *C. restuans* as prey. Water-filled containers were plastic Tripour® beakers of two sizes: 50 ml beakers holding 28 ml of water and 1, 2, 5, 7, and 12 prey, replicated 3, 2, 3, 4, and 4 times, respectively, or 1000 ml tripour beakers holding 420 ml of water and 11, 37, 75, 112, and 187 prey, replicated 5, 3, 3, 4, and 4 times, respectively, each with one *T. rutilus*. The combinations of these volumes and prey numbers were designed to produce a similar range of densities of prey/L in both arena sizes. Both prey and predators were 1-2 d post hatch. Predators had not been fed mosquito prey before the experiment, and each predator was used only once. The experiment ran at 25°C for 6 h after which the predator was removed, and surviving prey larvae counted. Number eaten was quantified as the difference between the initial number and number surviving.

We chose to design this experiment using prey/L as the quantification of density as this has been the implicit assumption of functional response experiments with *Toxorhynchites* (e.g., Livdahl, 1979; Russo, 1983; Juliano, 2001; Griswold and Lounibos, 2005). An alternative assumption is that prey/dm^2 surface or bottom is the best way to quantify density. This quantification arises because both predator and prey are air-breathing insect larvae that must come to the water's surface (Clements, 1992). *Culex* species often filter feed while hanging at the surface (Yee et al., 2004; Skiff and Yee, 2014). For *T. rutilus*, some investigators have found that prey capture occurs primarily at the bottom (Russo, 1986; Juliano and Reminger, 1992), and others have suggested that captures occur primarily at the surface (Linley, 1995; Focks, 2007). Either case would result predation being spatially aggregated in approximately two dimensions, although behavioral studies show that captures do occur in all parts of the water (Juliano and Reminger, 1992). Thus, we also analyzed the functional responses expressing prey density as number/area (dm^2) based on the area of the surface of the water in the experimental arena, which also approximates the area of the arena bottom.

Although past tests for *Toxorhynchites* functional response have found Type II functional responses are most common (Juliano, 2001; Griswold and Lounibos, 2005), we used logistic regressions of proportion of prey eaten (Juliano, 2001) to test whether a Type II or Type III functional response was more appropriate. That analysis (**Supplementary Material**) confirmed that Type II functional responses were best for all analyses. Data were analyzed by non-linear regressions of number of prey eaten vs. prey density expressed as either number/L or number/dm^2 of surface area, using the implicit function method (Juliano, 2001) to fit a Type II functional response accounting for prey depletion (Rogers, 1972):

$$N_e = N_0[1 - exp(a(T_h N_e - T))]$$

Where N_e = number of prey eaten, N_0 = initial density of prey, a = attack rate, T_h = handling time per prey eaten, and T = duration of the experiment (= 6 h). Parameters estimated and compared between the two sized experimental arenas are a and T_h. An indicator variable (values of 0 or 1) was used to distinguish the two arena sizes (Juliano, 2001). Models tested for differences in both a and T_h, only a, only T_h, or neither a nor T_h, and were evaluated by AICc (Motulsky and Christopoulos, 2004; Anderson, 2008), which is a useful way to evaluate models of similar geometric complexity (Novak and Stouffer, 2021) such as those compared here. Model fits also yielded hypothesis tests for differences of parameters between the two container sizes. All analyses were conducted using PROC NLIN *SAS Statistical Software* version 9.13.

RESULTS AND DISCUSSION

Analyses Based on Volume

AICc for this analysis (**Figure 1A**) led to the conclusion that the most plausible model has the same attack rate (a) in both experimental arena sizes, but different handling times (T_h) in each arena size. For this model, handling times differed significantly (**Figure 1A**), with the handling time in small experimental area considerably greater than that in the large experimental arena. This is evident in the plot of the predicted values of number eaten N_e vs. initial density/L N_0 (**Figure 1A**).

Analyses Based on Surface Area

AICc for this analysis (**Figure 1B**) led to a different conclusion: that the most plausible model has the same attack rate (a) and handling time (T_h) in both arena sizes. In this analysis, handling times were also not significantly different ($T_{h(large)}$-$T_{h(small)}$ = −0.098 h, 95% CI = [−0.484, 0.288] h). The plot of the predicted values of number eaten N_e vs. initial density/dm^2 N_0 from the most plausible model suggests little difference in the functional responses in the different experimental arena sizes (**Figure 1B**).

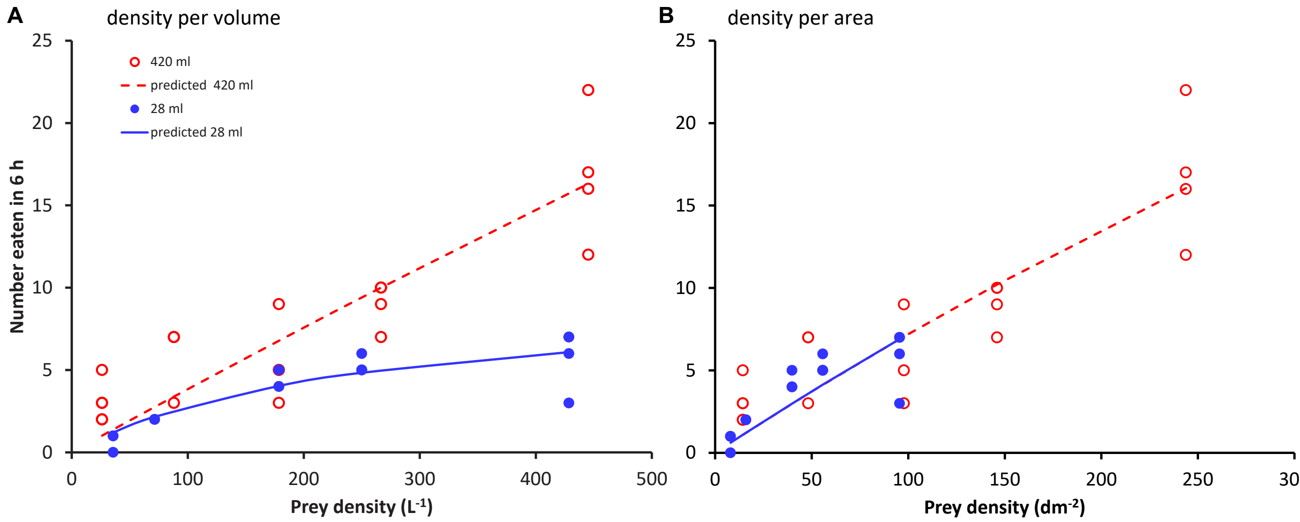
Thus, what is assumed about how the predator and prey use space affects the conclusion about the effects of container size on predation. Under the assumption of interactions over volume, one might conclude predator behavior changes with container size. Predator processing time of victims appears to decrease greatly in the large experimental arena, yielding a prediction that does not reach an asymptote (**Figure 1A**). Uiterwaal et al., 2019 suggested that arena size is most likely to affect apparent attack rates, rather than handling time, when prey and predator are non-randomly distributed in space (see also **Table 1**). Aggregation of predator and prey would have the effect rendering our prey densities expressed per liter inaccurate and suggested to us an alternative assumption of interactions over area may be more appropriate.

Under the assumption that predator-prey interactions are aggregated in two dimensions, our analysis suggests that there is no change in predator behavior. The conclusion of no difference in handling time might be criticized as a product of low statistical power, but power was adequate to detect a significant difference in handling time under the assumptions of the alternative analysis using volume. Resolving these issues would require additional experiments, e.g., experiments at different water volumes in the same containers, so that surface area remains the same and determining if the functional responses remain consistent as volume changes. A factorial experiment manipulating surface area and volume independently and quantifying functional responses in all combinations of surface and volume would also be useful. Direct observations of *T. rutilus* hunting and capturing mosquito prey would also be useful to determine if predators, prey, and captures are aggregated, either at the bottom, at the water's surface, or in another location. Nevertheless, this simple experiment illustrates how the spatial context and assumptions about how predator and prey interact in space can have a major effect on the interpretation of predator functional response data.

Review of Evidence for Spatial Context Dependence of Functional Responses

We chose published empirical studies of functional responses of invertebrate predators, comparing different spatial contexts in two clear categories: effects of experimental arena size; and effects of environmental complexity, including arena shape, physical structure, and prey spatial heterogeneity. Effects of spatial context on functional response parameters are common in published work, changing one or both parameters of Type II functional responses, or changing the form of the functional response from Type II to Type III (summarized in **Table 1**). These effects occur in both terrestrial (largely 2 dimensional) systems and in aquatic (potentially 3 dimensional systems).

Uiterwaal et al. (2019) reported the most thorough analysis of the effect of arena size because they showed convincingly in several experiments that their spider predator and its prey do not uniformly occupy two-dimensional arenas of various sizes, but rather show positive thigmotaxis, aggregating near the walls. This can be interpreted as the animals using 1 dimensional space (i.e., linear, but circular wall of the arena), even though the arena is 2 dimensional. Similar aggregation in space at walls in experimental arenas of different sizes was demonstrated for mysid shrimp preying on cladocerans, and this aggregation affected the attack rate by concentrating encounters of predator and prey (Bergström and Englund, 2004). The difference in functional responses in the two analyses of our experiment is consistent with similar aggregation of predator and prey, perhaps



Using volume	k	AICc	ΔAICc	w_i	E	Using area	k	AICc	ΔAICc	w_i	E
***T_h* differ**	3	57.965	0	0.683	1	***a* & *T_h* equal**	2	58.963	0	0.471	1
***a* & *Th* differ**	4	60.501	2.536	0.192	3.55	***a* & *Th* differ**	4	60.501	1.539	0.218	2.16
***a* differ**	3	61.362	3.397	0.125	5.47	***T_h* differ**	3	61.024	2.061	0.168	2.80
***a* & *T_h* equal**	2	90.255	32.290	$6.7\text{x}10^{-8}$	$1.0\text{x}10^{7}$	***a* differ**	3	61.362	2.399	0.142	3.32

FIGURE 1 | Number of prey eaten per predator per 6 h experiment vs. prey density based on **(A)**. water volume and **(B)**. surface or bottom area. Points are observed values and lines are the predicted functions for the most plausible model in each analysis. For comparisons of the different models: k is the number of parameters, w_i is the Akaike weight for each model, and E is the evidence ratio (Anderson, 2008). Estimated parameters (95% confidence interval): **(A)**. Volume: Equal *a*, T_h differ: a = 0.0066 (0.0040, 0.0092) L/h, $T_{h(small)}$ = 0.6302 (0.2852, 0.9753) h, $T_{h(large)}$ **-**$T_{h(small)}$ **=** −0.6088 (−0.9039, −0.3138) h. **(B)**. Area: Equal *a*, equal T_h: a = 0.0133 (0.0091, 0.0176) dm^2/h, T_h = 0.0558 (−0.0748, 0.1864) h.

at the surface or bottom. A different mechanism was postulated for attack rates of damselflies that increase with arena size (Uiterwaal et al., 2017): damselfly behavior and search were inhibited in small aquatic environments that do not represent the typical habitats occupied by these predators. A previous review of functional responses of 23 coccinellid beetle predators on multiple different types of prey (Uiterwaal and DeLong, 2018) also showed a general pattern of arena size having a consistently strong positive effect on attack rate, but not on handling time, though arena size often interacted with predator size or predator stage to affect both attack rate and handling time. Aggregation imposed by investigators also can change functional responses from hyperbolic with uniformly distributed prey to sigmoid with aggregated prey (Hossie and Murray, 2016). Greater arena size, and associated greater spatial heterogeneity, are likely to result in greater prey aggregation, and thus may generally shift functional responses from Type II to Type III (Griffen, 2021). Experiments have found effects of arena size without considering the behavioral mechanism involved (e.g., Yaşar and Özgar, 2005). Explicit consideration of arena size in experiments testing for effects of predator-predator interactions on the functional response is also likely to be important, as arena size is postulated to affect how predators interact (e.g., Cuthbert et al., 2020).

Environmental complexity in the form of physical structures within aquatic and terrestrial environments has multiple potential effects, some of which are likely related to aggregation of predation. There were complex effects on Type II functional responses of *Aeshna* to the physical structure of the experimental aquatic environment, with most plausible models postulating some combination of quadratic changes in handling time, first declining, then increasing with habitat complexity, and stepwise increases in attack rate from no to some structural complexity (Mocq et al., 2021). Behavioral data implicated behavioral change of the predator in the presence of habitat complexity, but the authors also postulated that aggregation of pelagic prey in open-water spaces as another mechanism that may contribute to altered functional responses (Mocq et al., 2021). Effects of habitat complexity on predation by notonectids (Wasserman et al., 2016; Buxton et al., 2020) show a trend of decreasing predation at highest habitat complexity, which they attributed to changes in predator behavior (Buxton et al., 2020). Buxton et al. (2020) also showed that habitat complexity could impact predator dependence in functional responses, enhancing multipredator effects that increase predation for some predators (*Anisops*) and having no impact on multipredator effects for others (*Einithares*). Fractal complexity of walls of two-dimensional arenas reduced attack rates of predatory thrips and was interpreted to be a result of escape from predation by thrips prey occupying vertices in complex walls which served as a refuge from predation (Hoddle, 2003). This implies that habitat complexity may stimulate aggregation of prey in refuges, aggregating successful predation away from those refuges. Similar hypotheses were stated to account for effects of

TABLE 1 | Summary of recent functional response experiments investigating the effects of spatial context on functional response type and parameter estimates.

Spatial context compared Prey density units	**Predator**	**Prey**	**Functional response parameters sig. affected**	**References**
TERRESTRIAL				
Arena size (3 areas)[1] Prey/area	*Schizocosa ocreata* (Araneae: Lycosidae)	*Drosophila melanogaster* (Diptera: Drosophilidae)	Attack rate	Uiterwaal et al., 2019
Arena size (3 areas)[2] Prey/area	*Oenopia conglobate* (Coleoptera: Coccinellidae)	*Hyalopterus pruni* (Hemiptera: Aphidiidae)	Attack rate	Yaşar and Özgar, 2005
Arena shape (Circular, Annular)[1] Prey/area	*Schizocosa ocreata* (Araneae: Lycosidae)	*Drosophila melanogaster* (Diptera: Drosophilidae)	Attack rate	Uiterwaal et al., 2019
Arena shape (Perimeter complexity)[3] Prey/area	*Franklinothrips orizabensis* (Thysanoptera: Aeolothripidae)	*Scirtothrips perseae* (Thysanoptera: Thripidae)	Handling time	Hoddle, 2003
Arena shape (Perimeter complexity)[3] Prey/area	*Franklinothrips orizabensis* (Thysanoptera: Aeolothripidae)	*Heliothrips haemorrhoidalis* (Thysanoptera: Thripidae)	Attack rate & Handling time	Hoddle, 2003
Substrate (2 grass species) Prey/plant	*Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae)	*Diuraphis noxia* (Hemiptera: Aphididae)	Type II vs. Type III	Messina and Hanks, 1998
Substrate (petri dish vs. Sitka spruce) Prey/experimental arena	*Aphidecta obliterata* (Coleoptera: Coccinellidae)	*Elatobium abietinum* (Hemiptera: Aphididae)	No differences	Timms et al., 2008
Substrate (petri dish vs. Sitka spruce) Prey/experimental arena	*Adalia bipunctata* (Coleoptera: Coccinellidae)	*Elatobium abietinum* (Hemiptera: Aphididae)	Lower consumption at high prey density, but no parameter differences	Timms et al., 2008
Substrate (1, 2, 4, 8 g Beech leaves) Prey/area	*Lithobius mutabilis* (Lithobiomorpha: Lithobiidae)	*Heteromurus nitidus* (Collembola: Entomobryidae)	Attack rate & Handling time[4]	Kalinkat et al., 2013
Substrate (1, 2, 4, 8 g Beech leaves) Prey/area	*Lithobius mutabilis* (Lithobiomorpha: Lithobiidae)	*Heteromurus nitidus* (Collembola: Entomobryidae)	Handling time[5]	Kalinkat et al., 2013
Substrate (2-dimensional cucumber leaf vs. 3-dimensional cucumber seedling) Prey/experimental arena	*Hippodamia variegata* (Coleoptera: Coccinellidae)	*Aphis gossypii* (Hemiptera: Aphididae)	Attack rate & handling time[6]	Madadi et al., 2011
Obstacle densities (1, 23, 52 obstacles) Prey/area	*Pergamasus crassipes* (Mesostigmata: Parasitidae)	*Folsomia candida* (Collembola: Isotomidae)	Attack rate	Hauzy et al., 2010
AQUATIC				
Arena size (2 volumes) Prey/volume	*Neomysis integer* (Mysida: Mysidae)	*Polyphemus pediculus* (Diplostraca: Polyphemidae)	Attack rate	Bergström and Englund, 2004
Arena size (3 diameters) Prey/volume	*Enallagma* & *Ischnura* (Odonata: Coenagrionidae)	Copepods, *Daphnia, Chydorus*	Attack rate	Uiterwaal et al., 2017
Prey distribution (Clumped, Even) Prey/experimental arena	*Anax junius* (Odonata: Aeschnidae)	*Lithobates clamitans* (Anura: Ranidae)	Type II (even) vs. Type III (Clumped)	Hossie and Murray, 2016
Structural complexity (0, 1, 2, 4, 8 plastic plants) Prey/experimental arena	*Aeshna cyanea* (Odonata: Aeschnidae)	*Chaoborus obscuripes* (Diptera: Chaoboridae)	Attack rate & Handling time	Mocq et al., 2021
Structural complexity (0, 2, 4 *Cyperus* stalks) Prey/experimental arena	*Enithares sobria* (Hemiptera: Notonectidae)	*Daphnia longispina* (Diplostraca: Daphniidae)	Attack rate & Handling time[7]	Wasserman et al., 2016
Structural complexity (0, 2, 4 *Cyperus* stalks) Prey/experimental arena	*Anisops sardea* (Hemiptera: Notonectidae)	*Culex pipiens* (Diptera: Culicidae)	Attack rate & Handling time[8]	Buxton et al., 2020

(Continued)

TABLE 1 | (Continued)

Spatial context compared Prey density units	**Predator**	**Prey**	**Functional response parameters sig. affected**	**References**
Structural complexity (0, 2, 4 *Cyperus* stalks) Prey/experimental arena	*Enithares chinai* (Hemiptera: Notonectidae)	*Culex pipiens* (Diptera: Culicidae)	Attack rate[8]	Buxton et al., 2020
Structural complexity (without, with moss) Prey/experimental arena	*Prionchulus muscorum* (Mononchida: Mononchidae)	*Caenorhabditis elegans* (Rhabditida: Rhabditidae)	Type III attack rate for small prey; Handling time for large prey	Kreuzinger-Janik et al., 2019
Structural complexity (0, 2, 8 pieces of screen) Prey/experimental arena	*Belostoma lutarium* (Hemiptera: Belostomatidae)	*Helisoma trivolvis* (Hygrophila: Planorbidae)	Type III attack rate and handling time	Gunn et al., 2021
Structural complexity (0, 14.1, 63.5 g oak leaves) Prey/experimental arena	*Anax junius* (Odonata: Aeschnidae)	*Lithobates pipiens* (Anura: Ranidae)	Type II (0, 14.1 g leaves) vs. Type III (63.5 g leaves)	Hossie and Murray, 2010

Type II functional responses fit using Rogers' integrated form of the disk equation, except as noted.

[1] *Floor of arena only.*

[2] *All inner surfaces of covered petri dishes, when analyzed using Holling's original disk equation.*

[3] *Arenas were circular, triangular, 6-pointed star, or 18-pointed snowflake; All shapes had the same floor area, with perimeter increasing as number of vertices increased.*

[4] *Prey density m^{-2} uncorrected for added surface area of leaves.*

[5] *Prey density m^{-2} corrected for added surface area of both sides of the leaves.*

[6] *Dimensionality affects parameters for 3rd instar larvae, but not for 4th instar larvae or adult females, when analyzed using Holling's original disk equation.*

[7] *Interactive effects of complexity with temperature for both parameters.*

[8] *Based on reported estimates; formal test for significant differences in parameters not reported.*

structural complexity of host plants, which can change predator functional responses from Type II to Type III (Messina and Hanks, 1998) or produce differences in the parameters of the Type II functional response for some predators (Timms et al., 2008; Madadi et al., 2011). But greater structural complexity may alter the type of functional response by changing predator hunting efficiency or strategy, rather than by providing a prey refuge (Hossie and Murray, 2010). A similar interpretation for the effect of physical structure on functional response parameters regarded structures as obstacles that provide no refuge for prey but reduce predator movement rate (Hauzy et al., 2010), and thus reduce attack rate, and also reduce predator-predator interference. More complex effects arise for nematode predators hunting nematode prey in environments with vs. without physical structure (Kreuzinger-Janik et al., 2019), where structure affected Type III attack rate for small prey, but handling time for large prey, and mechanisms behind these changes were unclear. Adding habitat complexity in the form of leaves altered the functional response of centipedes to density of Collembola (Kalinkat et al., 2013). This change was associated with the increased two-dimensional surface area of the arena due to the dual surfaces of the leaves creating more two-dimensional space for both predator and prey, effectively reducing prey density per unit space (Kalinkat et al., 2013). As in our experiment, Kalinkat et al. (2013) conducted alternative data analyses incorporating different assumptions about how their predator and prey used the experimental environment to reach their conclusions.

What is clear from this brief review is that the spatial context used in experiments, including arena size and spatial complexity, often affects the functional response. Often the spatial context may alter the functional response through aggregation of predation away from prey refuges, in areas preferred by predator, or on edges of arenas. Functional response experiments are likely to be improved by incorporating complexity of the environment in which predator and prey interact and by considering behavioral processes that are affected by spatial context, and that result in aggregation of predation even in simple experimental arenas. Previous theoretical treatments of functional responses have included predator and prey aggregation in models (e.g., Fryxell et al., 2007; Fortin et al., 2015), often in the context of social organization of prey. But aggregation may arise even in organisms with little or no social structure when environments are spatially heterogeneous, and organisms have preferences for particular physical situations (e.g., edges vs. open spaces). Spatial extent and heterogeneity, and how predator and prey use heterogeneous space are therefore likely to be generally important for a wide array of predator-prey systems. In nature, spatial context may alter functional responses in still other ways, for example, by fostering coexistence of multiple prey species of different vulnerabilities, which can reduce predation rates and stabilize community food webs (e.g., Hammill et al., 2015).

Our perspective is that several practical recommendations for experiments on functional responses arise from this review: (1) Small arenas, relative to organism sizes, should be avoided, as smaller arenas necessarily have greater edge relative to area or volume, and many organisms seem to respond to arena edges. (2) Including experimental structural complexity in ways that represent the natural environment in which focal predators and prey interact is likely to yield more accurate predictions of predation in nature, as virtually all predator-prey interactions, with the possible exception of those of planktonic animals, occur in environments with physical structures. (3) Quantifying how animals use space in functional response arenas can help to identify spatial processes that affect functional responses, and contribute to better predictions.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

SJ and GO designed the experiment and revised the manuscript. JG and GO conducted the experiment and collected experimental data. SJ analyzed the data and reviewed the literature on functional responses. JG wrote the first draft. All authors contributed to the final written version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.845560/full#supplementary-material

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