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PRIMARY RESEARCH PAPER

Effects of habitat complexity on giant water bug (*Belostoma*) functional response to rams-horn snail prey (*Helisoma*)

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Abstract Outcomes of predator–prey interactions depend on biotic and abiotic factors. Habitat complexity, for example, mediates predator functional response type and parameters (attack rate and handling time). However, the relationship between habitat complexity and functional response varies across ecosystems. We assessed interactions between the giant water bug, *Belostoma* sp., and its prey, rams-horn snails, *Helisoma trivolvis*, across four prey densities ($N = 2, 4, 8, 16$ snails) and three habitat complexity levels (No-complexity, Low-complexity, High-complexity) to understand how complexity affected the functional response. We also tested effects of predator and prey body size on number of prey killed. *Belostoma* exhibited a Type III functional response in all habitat complexity treatments. Attack rate tended to increase with increasing complexity. Handling time was different among treatments, being lowest in the No-complexity treatment and highest in the Low-complexity treatment. *Belostoma* body size was positively related, while *Helisoma* body size was inversely related, to the number of *Helisoma* killed. We show habitat complexity does not affect the shape of predator functional response but impacts response parameters in the *Belostoma–Helisoma* system. We

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reaffirm that attack rate, handling time, and mortality outcomes for prey within predator–prey interactions are affected by abiotic factors through habitat complexity.

Keywords Predator–prey interaction · Community ecology · Species interactions · Pond · Body size · Attack rate · Handling time

Introduction

Predator–prey interactions are often context-dependent (Agrawal et al., 2007; Chamberlain et al., 2014). To a large extent, the dynamics between predator and prey are dictated by the biological or functional characteristics of either species (Kotler, 2016). Traits like body size (Klecka & Boukal, 2013) and foraging strategy in predators or mobility and behavioral defense mechanisms in prey (Green & Cote, 2014) determine their survival. The abiotic environment, including physical features of habitat or overall spatial dimensionality (Pawar et al., 2012), may play an equally important role in determining survival. Identification of these context dependencies in different predator–prey interactions should be prioritized so that they can be integrated into predictive models of population dynamics, increasing realism.

Differences in predator–prey interactions in varying environments can be assessed with the focal predator's foraging response by measuring foraging parameters under increasing prey densities (Holling, 1959). Under most realistic prey density conditions, predators are commonly observed to exhibit either a Type II or Type III functional response, although their response may also be predator-dependent (Kratina et al., 2009). A Type II response occurs when the predator foraging rate (number of prey consumed) increases with increasing prey densities before eventually saturating at higher prey densities (i.e., logarithmic). In a Type III functional response, a predator's foraging rate increases until it reaches an inflection point, after which it begins to decrease as it approaches an asymptote at high prey densities (i.e., sigmoidal; Juliano, 2001). Both functional response types are defined by two parameters: attack rate, or number of prey consumed over a given period of time, and handling time, the time needed for prey processing. While the behaviors of Type II and Type III functional response models are well characterized theoretically, numerous factors can affect the type and shape of functional response curve exhibited, including direct interactions among predators (Skalski & Gilliam, 2001; Mccoy et al., 2012), nonconsumptive effects (Anderson, 2016), or food web complexity (Paterson et al., 2015).

Individual traits of both predator and prey, especially body size (Kalinkat et al., 2013), also affect the efficiency with which predators can consume prey across a range of prey densities. Body mass scales allometrically with metabolism (Peters, 1989), so predators that are large relative to available prey should experience lower handling times and should be able to consume higher amounts of prey than smaller predators (Brose, 2010). These parameters have been widely studied (Thompson, 1975; Wahlström et al., 2000; Vucic-Pestic et al., 2010) and specific body size-to-foraging relationships have been documented in multiple taxa (Gergs & Ratte, 2009; Uiterwaal et al., 2017), bringing interest to the possibility of a universal allometric relationship between body size and functional response. However, recent broad-scale analyses suggest that this relationship may be taxon-specific (Uiterwaal & DeLong, 2020) and needs to be established independently for distinct species.

Habitat structural complexity is known to influence predator–prey interactions (Langellotto & Denno, 2004; Janssen et al., 2007; Kovalenko et al., 2012; Mocq et al., 2021), and researchers have long sought to generalize its effects in different ecosystems. Habitats with limited complexity—those with less horizontal or vertical spatial variation—are typically thought to reduce search effort by predators, resulting in improved prey detection (Gotceitas, 1990; Gingras et al., 2003; Rennie & Jackson, 2005). Therefore, in the absence of external factors, encounter rate is expected to increase indefinitely as prey densities increase (Turesson & Brönmark, 2007), and predators would be expected to exhibit a Type II functional response. In contrast, habitats with greater complexity should increase search times for predators by offering more potential refuges for prey, reducing predator efficiency (Kareiva & Sahakian, 1990; Clark & Messina, 1998; Alexander et al., 2012) and leading to a higher prevalence of Type III functional response in these habitats. Thus, predator functional responses would be expected to shift from Type II to Type III in more structurally complex habitats, as has been documented for dragonfly (Hossie & Murray, 2010), amphipod (Alexander et al., 2012), and crab predators (Moksnes et al., 1997). On the other hand, some studies have revealed other functional response patterns. For instance, Wasserman et al. (2016) and Rossi et al. (2006) always found a Type II response, and Eggleston et al. (1992) always observed a Type III response in predators; regardless of complexity treatment, foraging efficiency was unaffected by structural complexity.

The influence of habitat structure also depends on specific predator foraging mode and prey defense strategies (Winfield, 1986; Diehl, 1988) as well as the overall nature of the abiotic environment itself. Because of this, the effect of habitat complexity is often nonlinear (Mocq et al., 2021). Contrary to the expected pattern, the presence of structure may benefit predators by providing a perching site for prey ambush (Klecka & Boukal, 2014) or increase vulnerability of prey by impeding vision and movement (Manatunge et al., 2000). Many studies have suggested that there is an environmentally specific "threshold" of structural complexity necessary to have any impact on predator foraging and prey avoidance (Gotceitas & Colgan, 1989). Dimensionality of the environment, whether terrestrial and 2-dimensional or aquatic and 3-dimensional, leads to a further bias in favor of predators. Pawar et al. (2012) and Barrios-O'Neill et al. (2016) both showed that prey consumption efficiency was greater in 3-dimensional environments compared to 2 dimensions, possibly owing to increased visibility of prey. Given the inconsistent patterns in which functional response varies with habitat complexity, it becomes difficult to predict its impact on predator–prey dynamics.

Giant water bugs (*Belostoma* sp.) and rams-horn snails (*Helisoma* sp.) are a model system for understanding eco-evolutionary dynamics of predator–prey interactions. They have been previously used in studies of phenotypic plasticity, specifically trade-offs associated with survival and induced antipredator defenses in *Helisoma,* such as generation of wider shells in as little as 7 to 14 days after predator detection or an increase in size over several months (Hoverman et al., 2005; Hoverman & Relyea, 2009). *Belostoma* are often an apex predator in small water bodies lacking fish because of their large size and generalist diet (Runck & Blinn, 1994). Unlike many predators, *Belostoma* are not gape-limited; they inject digestive enzymes into their prey with a piercing mouthpart and then suck out liquified tissue (Swart & Felgenhauer, 2003; fig. S1). They are sit-and-pursue ambush predators that hunt from perches grasped with their hindlegs before launching to catch and handle prey using their forelegs (Klug & Hicks, 2014). They feed on invertebrates, small amphibians, and fish (Smith, 1997). *Belostoma* readily consume *Helisoma* and can be a substantial cause of *Helisoma* mortality (Kesler & Munns, 1989; fig. S1). *Helisoma* feed on periphyton and detritus (Smith, 1989) and are widely distributed in lentic systems around the world (Kater, 1974).

In this study, we characterized the functional response of *Belostoma lutarium* (Stål, 1856) (hereafter, *Belostoma*), with respect to their natural prey, *Helisoma trivolvis* (Say, 1817) (hereafter, *Helisoma*), under three different levels of habitat complexity and four levels of *Helisoma* density. Our goals were to assess (1) whether the type of functional response varied by habitat complexity, (2) whether the parameters of the functional response, attack rate and handling time, differed across habitat complexity, and (3) the contribution of predator and prey body size to the proportion of prey killed. We predicted that (1) *Belostoma* would forage with a Type II functional response in the absence of habitat complexity, as prey would be visible regardless of density and consumption would only be limited by handling time. *Belostoma* would shift to a Type III functional response as habitat complexity increased because *Helisoma* would be less visible at low density treatments and would require greater search effort. We also predicted that (2) attack rate would be negatively related with habitat complexity and that (3) *Belostoma* body size would be positively related with prey consumption.

Materials and methods

Animal collection

We collected adult giant water bugs (*Belostoma*) of mixed sex from the University of Missouri Baskett Research Forest in Ashland, MO (38.749989 N, − 92.200476 W) and *Helisoma* prey from ponds at Fort Leonard Wood, Missouri (37.725057 N,

− 92.160930 W) by dip-netting in early fall 2018. We transported both *Belostoma* and *Helisoma* to the University of Missouri, where *Belostoma* were stored individually in 237 mL plastic cups filled with pond water and *Helisoma* were stored together in two 75 L aquaria filled with pond water and plant material. *Belostoma* were held in isolation for 24 h to standardize hunger levels before the experiment began. *Helisoma* were not fed over the duration of the experiment. Water temperatures in holding cups and aquaria were approximately 29°C.

Experimental design

We set up a factorial experiment to evaluate the effects of multiple levels of habitat complexity and prey density on predator functional response. We tested three levels of habitat complexity: high-complexity, low-complexity, and no-complexity and four levels of prey density ($N = 2, 4, 8$ or 16 *Helisoma* per tank). The combined habitat complexity and prey density conditions resulted in 12 unique treatment combinations.

We conducted trials in two temporal blocks to double the number of experimental replicates due to limited space, with each block separated by one week. Block 1 consisted of 24 clear plastic containers (dimensions = 30 × 20 × 12 cm). We randomly assigned one of our 12 treatments to each container, which allowed for two replicates of each complexity-density combination. Block 2 was similar, except there were 36 containers and three replicates of each treatment. In each block, we also included two replicates of no-predator treatments, each containing the highest prey density (16 *Helisoma*) and no habitat complexity to control for *Helisoma* mortality unrelated to predation.

Experimental set-up

The experiment was conducted inside a greenhouse under natural light. We filled each container with approximately 7 L of well water conditioned with Prime water conditioner (Seachem Laboratories, Madison, GA, USA) to remove chlorine and chloramine. Containers were filled to approximately 11 cm depth. Because *Belostoma* are known to use small perches as launching points during foraging (Swart & Taylor, 2004), we suspended a single length of white string laterally across the center of each container submerged just below the water surface to serve as a potential perch that was consistent across treatments. We placed opaque sheets of paper between all containers to minimize the effect of cross-treatment visual stimuli on predator foraging rates. To simulate habitat complexity in each container, we placed rectangular pieces of semi-transparent window screen (dimensions = 20 × 5 cm) one at a time directly in the center of each container (fig. S1), closely following the methods of Drake et al. (2014). High-complexity treatments received eight pieces, Low-complexity treatments received two pieces, and No-complexity treatments received no pieces of screen. We recorded water temperature in one container once every 24 h at the same time (1300 h) for the duration of the experiment, with the average temperature being 29°C. This reflects midsummer surface water temperatures in Missouri (Anderson et al., 2015; Jones et al., 2020). As these temperatures were representative of relatively warm conditions, our results should be interpreted as foraging rates under potentially thermally stressful conditions. However, differences among treatments would be unaffected, because all aquaria experienced the same conditions.

We assigned a density treatment to each container and added *Helisoma* to the center of each container accordingly. *Helisoma* were allowed to acclimate for 10 min. After that, one *Belostoma* was randomly assigned and introduced to each container. We secured containers with lids to prevent predator escape. The experiment lasted for a total of 96 h. Within that time, we recorded the number of *Helisoma* killed and/or consumed after intervals of 24, 48, 72, and 96 h. Intermediate counts of dead *Helisoma* were repeated twice per container to increase the accuracy of mortality estimates, though we discovered at the termination of the experiment that these counts were less accurate than when we could physically inspect snails to determine their status. Thus, we did not use these intermediate counts in formal analysis. We assumed that all *Helisoma* mortality was related to *Belostoma* predation as no *Helisoma* died during the experiment in our no-predator controls. No *Helisoma* were replaced in any treatment, which did result in complete depletion (100% mortality), and this occurred in 31% of the experimental containers (Table S1).

Body size measurement

We used total body length and shell aperture width as metrics of body size for *Belostoma* and *Helisoma*, respectively. Body length and shell aperture width were measured in the laboratory using calipers after the experiment was concluded. *Belostoma* and *Helisoma* sizes were similar among treatments (figs. S2 & S3).

Analysis

We first examined whether Type II and Type III functional responses were supported using polynomial regression (Trexler et al., 1988; Juliano, 2001). These models were generalized linear models with binomial errors. We included linear and quadratic terms of prey density: a linear term that was significant and negative would indicate a Type II response, whereas a significant positive linear term would indicate a Type III response. Our response variable in each model was proportion killed of *Helisoma*. To complement this approach, we also compared the model fit of Type II and Type III models (described below) using AICc (Burnham & Anderson, 2002), with the expectation that a difference in AICc value (ΔAICc) of > 2 would indicate separation between the two models; the model with the lower value would be more supported.

Because we did not control for prey depletion in the experiment, we fit Type II and Type III functional response models as defined by Rosenbaum & Rall (2018). For Type II models, we accounted for depletion analytically via the Rogers random predator equation (Rogers, 1972; Bolker, 2008), with the equation:

$$N_e = N_0(1 - \exp(b(hN_e - \mathrm{TP})))$$

where N_e is the number of prey, T is temporal duration (4 days), b is attack rate (number of prey killed per unit density), h is handling time, and P is the number of predators. Solutions to the equations were then derived using the LambertW function (Bolker, 2008; Rosenbaum & Rall, 2018), using the equation below:

$$N_e = N_0 - \frac{W(bhN_0 \exp(b(hN_0 - \mathrm{TP})))}{bh}$$

For Type III models, we fit the model developed by Hassell et al. (1977), which is a sigmoidal-shaped curve that accounts for prey depletion and was the recommended method by Rosenbaum & Rall (2018):

$$N_e = \frac{bhN_0^2 + bPTN_0 + 1}{2bhN_0} - \sqrt{\left(\frac{bhN_0^2 + bPTN_0 + 1}{2bhN_0}\right)^2 - \frac{PTN_0}{h}}$$

We also attempted to use the flexible functional response model of Real (1977) also fit by Rosenbaum & Rall (2018), but it would not converge for these data, so we did not use it here.

Based on the polynomial regression and model selections steps above, the Type III model was more supported for all treatments (see “Results” section). To quantify the extent of differences in attack rate and handling time among treatments, we calculated 95% confidence intervals (CI) of each parameter using the quadratic approximation of the log-likelihood function and considered differences to be significant if 95% CIs did not overlap (Payton et al., 2003). All functional response models were fit using the ‘mle2’ function from the ‘bbmle’ package in *R* (Bolker & R Core Team, 2020).

Finally, we tested whether *Belostoma* and *Helisoma* size impacted survival rates of *Helisoma* using generalized linear models. Our response was a two-column matrix of the number of *Helisoma* killed and the number that survived, with *Helisoma* density, habitat complexity, *Belostoma* length, and mean aperture width of *Helisoma* as predictors. Block was initially included as a predictor, but was not statistically significant and was therefore removed. We used a quasibinomial error distribution to correct for overdispersion in the data (dispersion estimate of 2.6). All analyses were conducted in *R v*.4.0.2 (R Core Team, 2018).

Results

Functional response model comparison

There was support for a Type III functional response curve in the No-complexity treatment (Fig. 1a), as the linear term in the polynomial regression model was positive and significant (Table 1). We also found evidence for a Type III functional response in the Low-complexity (Fig. 1b) and High-complexity

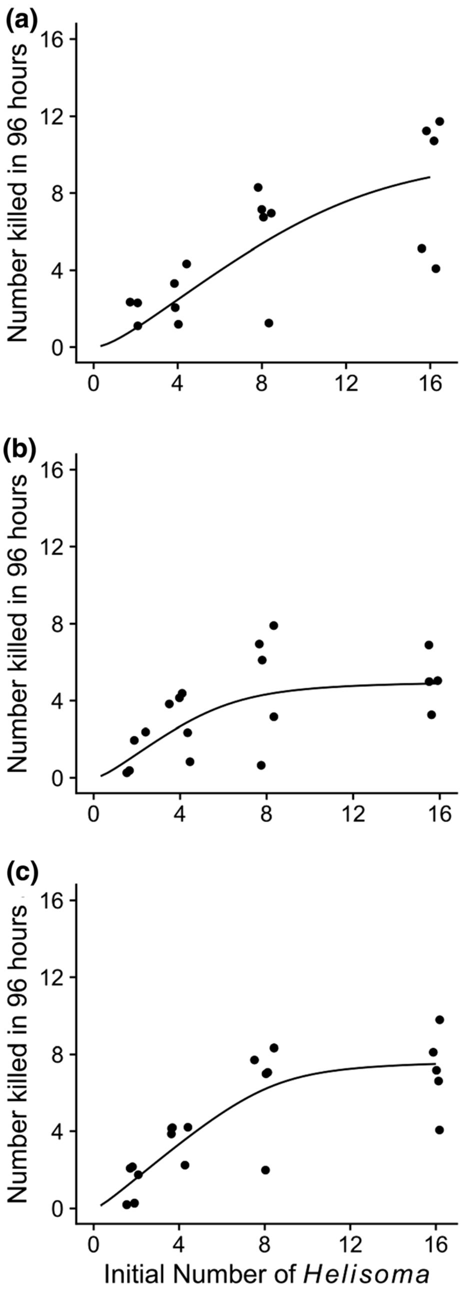

Fig. 1 Number of *Helisoma* killed versus the initial number of *Helisoma* for No- (**A**), Low- (**B**) and High- (**C**) complexity treatments over a 96-h period. Lines indicate the predicted Type III functional response curves, adjusted for prey depletion using the Rogers Random Predator Equation (Rogers, 1972)

(Fig. 1c) treatments; the linear terms were also positive, though they were not statistically significant. The AIC model comparison confirmed that the Type III model were the most supported, as ΔAICc values were greater than two between Type II and Type III models for all treatments (Table 2).

Comparison of habitat complexity treatments

We compared attack rate and handling time of predators using 95% confidence intervals of the Type III functional response parameters for all habitat complexity treatments. Average attack rates tended to increase with higher levels of habitat complexity but were not statistically different across treatments, in part because of the relatively high uncertainty in the High-complexity treatment (Table 3; Fig. 2a). Handling times were lower in the No-complexity treatment compared to the Low-complexity treatment, with the High-complexity treatment being intermediate in handling time (Table 3; Fig. 2b).

Predator and prey body size

Belostoma size did not vary by *Helisoma* density ($F_{1,49} = 0.001$, $P = 0.97$), habitat complexity ($F_{1,49} = 1.66$, $P = 0.20$) or block ($F_{1,49} = 0.78$, $P = 0.38$). Similarly, *Helisoma* size did not vary with density ($F_{1,54} = 0.28$, $P = 0.60$), habitat complexity ($F_{1,54} = 0.20$, $P = 0.82$) or block ($F_{1,54} = 0.004$, $P = 0.99$). Thus, our initial conditions were approximately equal in terms of predator and prey size (fig. S2).

Block did not affect the proportion of *Helisoma* killed and was removed from the model ($F_{1,47} = 0.87$, $P = 0.36$). *Helisoma* size showed a negative relationship with the proportion of *Helisoma* killed ($F_{1,48} = 13.58$, $P = 0.001$; Fig. 3a). For each decrease in *Helisoma* size, the odds of being killed increased by a factor of 0.02 (log-odds ratio = − 3.75). *Belostoma* size showed a positive relationship with the proportion of *Helisoma* killed ($F_{1,47} = 0.87$, $P = 0.36$; Fig. 3b), with each increase in *Belostoma* size resulting in an increase in the odds of being killed by a factor of 1.44 (log-odds ratio = 0.37).

Discussion

We tested the interplay of abiotic and biotic factors on predator–prey interactions by assessing the effect of habitat structural complexity and prey density on predator functional response. We determined the

Table 1 Summary of polynomial regression models used to distinguish Type II and Type III functional response curves, based on Trexler et al. (1988), for each habitat complexity treatment

Treatment	Parameter	Estimate	Std. Error	z value	*P* value
No	Intercept	− 1.164	0.863	− 1.348	0.178
	Linear	0.459	0.217	2.120	0.034
	Quadratic	− 0.024	0.011	− 2.225	0.026
Low	Intercept	− 0.319	0.850	− 0.376	0.707
	Linear	0.291	0.209	1.394	0.163
	Quadratic	− 0.021	0.010	− 2.087	0.037
High	Intercept	0.385	0.980	0.393	0.694
	Linear	0.331	0.247	1.341	0.180
	Quadratic	− 0.023	0.012	− 1.908	0.056

The response variable in each model was proportion killed of *Helisoma* and predictors were linear and quadratic terms of initial abundance. Significant, negative linear terms would indicate a Type II response, whereas significant, positive linear terms would indicate a Type III response

Table 2 AICc model selection results comparing Type II and Type III functional response models, each adjusted for prey depletion using the Rogers Random Predator Equation (Rogers, 1972)

Treatment	Model	AICc	df	ΔAICc
No	Type II	100.312	2	4.082
	Type III	96.230	2	0
Low	Type II	99.747	2	5.760
	Type III	93.987	2	0
High	Type II	81.803	2	6.639
	Type III	75.164	2	0

Lower AIC values are considered more supported, with ΔAICc values > 2 distinguishing between models

Table 3 Estimates (Est), lower (2.5%) and upper (97.5%) confidence intervals for parameters of Type III functional response models, adjusted for prey depletion using the Rogers Random Predator Equation (Rogers, 1972). Parameters include attack rate and handling time

Parameter	Treatment	Est	2.5%	97.5%
Attack rate (b)	No	0.133	0.043	0.223
	Low	0.266	0.023	0.509
	High	0.546	0.046	1.046
Handling time (h)	No	0.387	0.269	0.505
	Low	0.797	0.588	1.005
	High	0.520	0.407	0.632

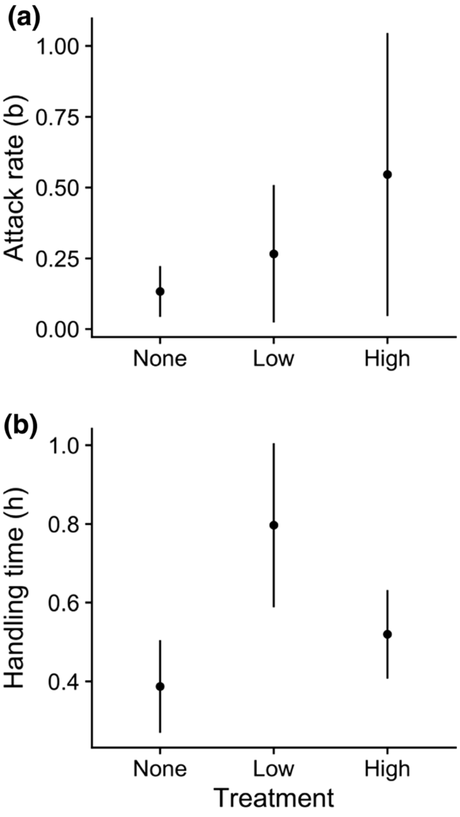

Fig. 2 Parameter estimates and 95% confidence intervals for attack rate (*b*) and handling time (*h*) based on a Type 3 functional response curve, adjusted for prey depletion using the Rogers Random Predator Equation (Rogers, 1972), in each habitat complexity treatment. Each parameter is based on foraging over a 96-h period by one *Belostoma* predator

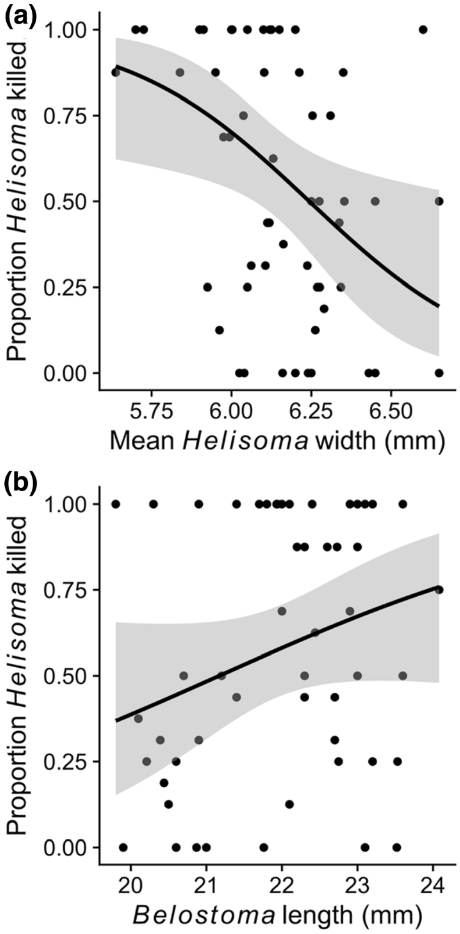

Fig. 3 Proportion of *Helisoma* killed as functions of mean *Helisoma* aperture width (**A**) and *Belostoma* total length (**B**). Lines are predicted relationships between variables, based on fitting a generalized linear model with binomial errors. Dots indicate raw data points. Shading indicates 95% confidence intervals

functional response of *Belostoma* by assessing the number of prey consumed in four levels of prey density under three different treatments associated with the amount of habitat structure. We found support for a Type III functional response curve across all three habitat complexity treatments. This result did not follow our expectation of a Type II functional response in the absence of habitat complexity. However, we found differences in the functional response parameters in *Belostoma* among complexity treatments, primarily that handling time was highest at intermediate levels of habitat complexity. Attack rate increased with complexity level, but this trend was not significant. Finally, we found that body size of both predators and prey influenced *Belostoma* predation rates. We confirmed the importance of both intrinsic biotic contributors and abiotic factors in predator foraging ability and present a clearer picture of the relationship between habitat complexity, body size, and predator–prey interactions in this system.

The Type III curves associated with the presence of complexity, specifically in the Low- and High-complexity treatments, conform to the expected effects of habitat complexity and are consistent with previous experiments (Crowder & Cooper, 1982; Buck et al., 2003; Janssen et al., 2007; Stoner, 2009; Hossie & Murray, 2010; Alexander et al., 2012). At low densities and in the presence of structural complexity, prey would be expected to experience reduced mortality by using obstructions as refuge (Colton, 1987), generating a Type III predator response. The absence of complexity often confers easier access to prey and should therefore lead to higher foraging success (Heck & Crowder, 1991), which, at low prey densities, would increase the amount of prey that can be consumed and would be conducive to a Type II response.

However, the Type III curve which was supported for our No-complexity treatment did not follow expected patterns. While we observed some patterns between *Belostoma* functional response and habitat complexity, they were not significant. This result has been observed for some species interactions (Wasserman et al., 2016) but contradicts other studies showing shifts in functional response under different environmental conditions (Alexander et al., 2012). Thus, this response may demonstrate a context-dependent interaction between *Belostoma* and *Helisoma* in the absence of habitat structural variation which requires further investigation. *Belostoma* are sit-and-pursue predators, often using physical debris as a launching point to attack prey. It is possible that *Belostoma* predation may increase under higher complexity treatments where the environment may be more favorable for ambush and the prey may be impeded by more structure (Klecka & Boukal, 2014; Manatunge et al., 2000). This would explain the Type III functional response in the No-complexity treatment, but would not explain the lack of a shift to a Type II response in the higher complexity treatments. *Belostoma* may have been equally effective as a predator in all treatments, perhaps by consistently using a single perching point from which to pursue *Helisoma*. It is also possible that we did not have enough discrete treatments, particularly at low prey densities, to accurately estimate the potential nonlinear shape that would lead to misidentification of the type of functional response, though given the adequate fit of the models, we think this is unlikely. It should also be noted that we observed complete prey deletion in a number of trials, especially the lower density treatments, which could potentially affect the fitting of functional response models. Specifically, we could be underestimating the kill rate at lower densities, which would increase our chances of finding of support for Type III models.

We expected differences in attack rate between treatments because these parameters have been shown to vary with habitat complexity (Wasserman et al., 2016). Attack rates are determined by the predator's ability to find available prey, whereas handling time is associated with processing of prey (i.e., digestion). Because of this ecological distinction between attack rate and handling time, we predicted that our treatments would have greater impacts on attack rates: without the presence of structural complexity, prey have fewer places to hide and are more readily available for consumption. This negative relationship between habitat complexity and attack rate has been previously observed in aquatic insects (Cuthbert et al., 2019). However, we found that attack rate did not vary between any of our treatments. It is possible the small holes in the window screen we used as structure did not limit the search efforts of *Belostoma*, making the *Helisoma* prey always visible. We used this type of structure to be able to observe prey without invasively sampling containers, though this experimental choice should be considered in future studies. Additionally, while *Helisoma* were attached to the window screen structure, they may not have perceived it as potential structure given the likelihood of light penetration. They may not have actively used it to hide, exposing themselves to predation, though we lack behavioral observations to confirm this possibility.

In contrast to attack rate, handling time was greatest in the Low-complexity treatment and lowest in the No-complexity treatment. The mechanism for this is not clear, but it could be due to the fact that these parameters are not independent. When additional environmental coefficients, like habitat complexity, are used to shape the functional response, inaccuracies in parameter estimates become more likely (Uszko et al., 2020). Another reason that handling time may have been greatest in the Low-complexity treatment, even as attack rate was highest at low habitat complexity, might be due to some behavioral change in *Belostoma* associated with habitat complexity that would affect foraging and digestion rates. In particular, partially consuming prey could occur more frequently under certain habitat complexity treatments if those conditions increase contact rates between predators and prey (Wasserman et al., 2016). We could not evaluate that process here, though, as it was not clear if *Belostoma* partially consumed *Helisoma*. Future work on our focal taxa should combine more detailed behavioral observations, including time spent feeding on each individual prey item and the extent to which *Belostoma* use available structure for ambush predation, with functional response data, as in Hossie and Murray (2010), to completely disentangle the effects of habitat complexity on these parameters.

Variation in body size is closely associated with predator foraging ability (González-Suárez et al., 2011); larger predators can generally eat more prey (Avery, 1971; Tripet & Perrin, 1994; Aljetlawi et al., 2004; Vucic-Pestic et al., 2010). We found that larger *Belostoma* were associated with an increase in the number of *Helisoma* killed. This trend is consistent with existing studies of foraging in other benthic invertebrates, which have found that ingestion rate is positively correlated with body mass (Cammen, 1979).

We also found that survival of *Helisoma* was on average higher when their mean body size was greater. *Belostoma* are not gape-limited predators and thus are less limited by prey size (Jara, 2016). Perhaps the largest adult *Helisoma* in our study were difficult enough for *Belostoma* to handle that it limited their ability to consume the *Helisoma* efficiently. Handling time is shorter for smaller *Helisoma* (Kesler & Munns, 1989; Dewitt et al., 2000), which could explain why tanks with a lower mean size were associated with higher kill rates. Our findings were also consistent with previous studies on predation of *Helisoma* by predators other than *Belostoma*. Nyström and Pérez (1998) found that crayfish preferred smaller snails because of shorter associated handling times, which allowed the crayfish to reduce their exposure time to predators. It is interesting to note that *Helisoma* are known to grow wider shells as an induced antipredator defense in the presence of *Belostoma* (Hoverman et al., 2005; Hoverman & Relyea, 2007a, 2007b, 2008). Wider shells significantly increase the distance between the snail body and the shell aperture, making it more difficult for *Belostoma* to gain access with its proboscis (Hoverman & Relyea, 2009). The induction of wider shell morphology has been shown to occur between 7 and 14 days after exposure to a predator, which is well beyond the timeframe used in our study (Hoverman & Relyea, 2009). However, this evolved response may raise the likelihood that *Belostoma* seeks out smaller, more easily accessible *Helisoma*. An interesting future area of research would be to combine the eco-evolutionary aspects of *Belostoma–Helisoma* interactions within a functional response framework.

It should be noted that the effect of predators observed in simplified experiments such as ours are not always evident in natural systems (Jara, 2016). Other biotic and abiotic factors can impact pairwise species interactions. Understanding how *Belostoma–Helisoma* interactions occur in more natural settings is needed to solidify the role of structural complexity. Of the potential factors that could be explored, predator dependence, or the effect of intraspecific predator density on predation efficiency, may play a large role in dictating *Belostoma* foraging ability (Kratina et al., 2009; Hossie et al., 2021). We examined the effect of prey density and habitat complexity on only a single predator. Including predator density as a treatment may bring clarity to functional response patterns in this species. Additionally, temperature is a critical factor for ectothermic species and is known to have an impact on functional response (Englund et al., 2011). Temperature and metabolic rates are positively related, which explains why ingestion rates are higher at warmer temperatures (Peters, 1989). The relatively constant 29°C water temperatures in our study reflect only one point in a range of temperatures experienced in natural systems and is relatively high given the time of year for our experiment (Anderson et al., 2015). Therefore, while the relationships in body size between predator and prey we observed likely remains in natural systems, the results from our study might best reflect shallow-water, summer conditions. Further investigation into whether the impact of prey density and structural complexity varies with temperature (e.g., Wasserman et al. 2016) would be an interesting avenue of future research.

Conclusions

Our study has shown that different levels of habitat complexity do not affect the type of functional response but do alter the associated response parameters in predator–prey interactions between *Belostoma* and *Helisoma*. These findings reaffirm that the influence of habitat complexity on predator–prey outcomes may be inconsistent among biological systems, necessitating tests in a variety of model predator–prey systems. To better understand how predator–prey interactions will be altered by anthropogenic influences, such as habitat degradation and climate change, we need more accurate, predictive models of predator–prey dynamics under varying conditions. Further examinations of foraging abilities combined with other components of the abiotic environment will allow for more accurate predictions of predator–prey outcomes in a variety of aquatic ecosystem contexts, leading to a better understanding of aquatic community dynamics in general.

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Authors' contributions JCG aided in project design, collected data, conducted preliminary analysis, wrote and reviewed the original draft. SJC aided in project conceptualization, collected data, conducted preliminary analysis, wrote and edited the original draft. JK aided in project design, collected data, conducted preliminary analysis, wrote and edited the original draft. JACG aided in project design, collected data, conducted preliminary analysis, wrote and edited the original draft. TLA aided in project conception, collected data, conducted formal analysis, reviewed and edited the original draft.

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Availability of data and material Data and figures will be made available in the Figshare repository.Code availability *R* code to recreate the analyses will be made available in a Figshare repository as well as the corresponding author's Github webpage.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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