# Functional responses are maximized at intermediate temperatures

Stella F. Uiterwaal [ID][1] and John P. DeLong [ID]

*School of Biological Sciences, University of Nebraska–Lincoln, 410 Manter Hall, 1104 T Street, Lincoln, Nebraska 68588 USA*

*Abstract.* Functional responses describe how consumer foraging rates change with resource density. Despite extensive research looking at the factors underlying foraging interactions, there remains ongoing controversy about how temperature and body size control the functional response parameters space clearance (or attack) rate and handling time. Here, we investigate the effects of temperature, consumer mass, and resource mass using the largest compilation of functional responses yet assembled. This compilation contains 2,083 functional response curves covering a wide range of foragers and prey types, environmental conditions, and habitats. After accounting for experimental arena size, dimensionality of the foraging interaction, and consumer taxon, we find that both space clearance rate and handling time are optimized at intermediate temperatures (a unimodal rather than monotonic response), suggesting that the response to global climate change depends on the location of the consumer's current temperature relative to the optimum. We further confirm that functional responses are higher and steeper for large consumers and small resources, and models using consumer and resource masses separately outperformed models using consumer:resource mass ratios, suggesting that consumer and resource body mass act independently to set interaction strengths. Lastly, we show that the extent to which foraging is affected by temperature or mass depends on the taxonomic identity of the consumer and the dimensionality of the consumer–resource interaction. We thus argue that although overall body size and temperature effects can be identified, they are not universal, and therefore food web and community modeling approaches could be improved by considering taxonomic identity along with body size and unimodal temperature effects.

*Key words: Arrhenius; body size; consumer; database; foraging; functional response; handling time; predator; prey; resource; space clearance rate; temperature.*

## Introduction

Foraging interactions between consumers and their resources generate the structure of food webs and are thus a core feature of ecological systems. Although these interactions can be quantified in numerous ways (Wootton and Emmerson 2005, Novak and Wootton 2010), functional responses are widely used to formalize feeding interactions. Functional responses describe how the foraging rates of consumers (predators or parasitoids) change with resource (prey or host) density (Holling 1959). In addition to informing species interactions in a general sense, functional responses are commonly used to interpret food web links (McCann 2011), understand population dynamics (Yodzis and Innes 1992), and inform biocontrol (Uiterwaal and DeLong 2018). Quantitative variation in functional responses has consequences for the stability, dynamics, and abundances of consumers and resources of all types (Yodzis and Innes

1992, Weitz and Levin 2006, Petchey et al. 2008, Gilljam et al. 2011, McCann 2011, DeLong and Vasseur 2012, Pawar et al. 2012, Brose et al. 2019). Identifying the sources of variation in functional responses is therefore key to understanding variation in the structure and function of food webs and broader ecological systems.

The most commonly used form of the functional response is the Type II, which rises as prey density increases and then saturates at an asymptote. This form of the functional response is given by

$$f_{pc} = \frac{aN}{1 + ahN} \tag{1}$$

where $f_{pc}$ is the per capita consumer foraging rate (resources/time), $a$ is the space clearance rate (also known as attack rate or attack efficiency) ([space/time], where the units of space depends on the foraging dimensionality), $N$ is resource density (resources/space), and $h$ is handling time (time/resource) (Holling 1959). A high space clearance rate indicates that the consumer is adept at quickly removing resources from the areas or volumes the predator is searching. Because space clearance rate sets the initial slope of the Type II functional response,

[1] E-mail: suiterwaal@huskers.unl.edu

this parameter largely determines foraging rates at low prey densities. Handling time describes the time lost from searching per resource consumed. This parameter primarily determines foraging rates at high prey densities, as the inverse of handling time is the asymptote of the foraging rate. Although Type II is the standard functional response model, other types are used, including Type I, for which handling time is zero, and Type III, for which space clearance rate is an increasing function of resource density.

Because of the broad applicability of functional responses, there is a large body of literature focused on what factors influence the parameters of functional responses both across and within species (Spitze 1985, Yodzis and Innes 1992, Gergs and Ratte 2009, Englund et al. 2011, Rall et al. 2012, Kalinoski and DeLong 2016, Schröder et al. 2016, Uiterwaal et al. 2017, Uiterwaal and DeLong 2018). Effects of body mass are among the most studied of these factors, with strong evidence showing that consumer mass, resource mass, or consumer:resource mass ratio affect both space clearance rate and handling times. Typically, space clearance rate increases and handling time decreases as consumer size or consumer:resource mass ratio increases (Gergs and Ratte 2009, Vucic-Pestic et al. 2010, DeLong and Vasseur 2012, Rall et al. 2012, Kalinoski and DeLong 2016, Hirt et al. 2017, Uiterwaal and DeLong 2018, DeLong and Belmaker 2019). This is generally attributed to the increased ability of larger consumers to cover ground, detect resources from farther away, and successfully attack resources (McGill and Mittelbach 2006). Metabolism is also a critical consideration here, as larger consumers demand more energy and thus may forage more to fuel that demand. Although allometric scaling of functional response parameters has been presented as universal or likely to have power-law–type scaling that is conserved across taxa (Yodzis and Innes 1992, McGill and Mittelbach 2006, Otto et al. 2007, Rall et al. 2012), analyses of individual taxonomic groups suggest that functional responses may scale with consumer body mass differently across taxa (Wahlström et al. 2000, Kalinoski and DeLong 2016, Uiterwaal and DeLong 2018).

Temperature is another powerful modifier of functional responses, but there are conflicting thoughts about how temperature affects the functional response parameters. Although analyses of specific taxonomic groups suggest that functional response parameters respond monotonically to changes in temperature (Thompson 1978, Dell et al. 2011, Moayeri et al. 2013, Burnside et al. 2014, Kalinoski and DeLong 2016, Uiterwaal and DeLong 2018), a compilation of functional responses by Englund et al. (2011) shows unimodal responses of space clearance rate and handling time to temperature, indicating that there are optimal temperatures at which foraging rates are maximized. Some evidence suggests that this may be more apparent at smaller taxonomic scales, as Rall et al. (2012) found

responses that were both unimodal (within taxonomic groups) and linear (across taxa). Both unimodal and monotonic responses are supported by theoretical evidence. The Arrhenius equation, which describes how heat speeds up chemical reactions, has provided a framework for explaining exponential temperature effects in consumer–resource interactions (Burnside et al. 2014). On the other hand, resource-based theoretical work suggests that foraging rates may show a hump-shaped response to temperature (Uszko et al. 2017).

As with body size, metabolism plays a critical role in determining the effects of temperature. By increasing metabolism, higher temperatures enable faster movement, facilitating increased searching and handling rates and raising the height of the functional response (Dell et al. 2011, DeLong et al. 2018). Higher metabolic rates also necessarily increase energy intake requirements, suggesting that warmer temperatures may simultaneously facilitate foraging and reduce net energy gains of successful captures. On the other hand, metabolism also shows a unimodal response to temperature (DeLong et al. 2018), further underscoring the need to understand the shape of temperature effects on functional responses.

Here, we analyze a previously compiled database of consumer functional responses (Uiterwaal et al. 2018). In addition to being the largest of its kind, the data set covers an extremely diverse set of taxa, crosses many orders of magnitude of consumer and resource body mass, spans a broad range of temperatures, and contains foragers that occupy a diverse array of habitats and forage in different dimensions of space (e.g., 2D versus 3D foragers). This breadth gives us a unique opportunity to definitively compare competing hypotheses about broad patterns of variation in functional responses. We test (1) the competing views that functional response parameters have monotonic (Arrhenius or similar) versus unimodal (e.g., quadratic) responses to temperature, (2) the alternatives that allometric effects of mass are universal versus taxon-specific, and (3) the possibility that the dimensionality of consumer–resource interactions influences the allometric or temperature dependence of functional response parameters (Pawar et al. 2012, Rall et al. 2012). Our results confirm allometric and unimodal temperature effects on functional response parameters, but our findings also indicate that taxa differ in the extent to which foraging is affected by mass and temperature. We further show that the dimensionality of the foraging interaction has a strong effect on handling time and changes the ways in which mass and temperature shape space clearance rate.

## METHODS

We used functional response data from the FoRAGE database (Uiterwaal et al. 2018).[2] FoRAGE contains

data for 2,083 functional responses, including data on experimental setup and consumer/resource traits. Consumers in this database include predators (i.e., organisms consuming live prey, dead prey, or pelleted food) and parasitoids (e.g., organisms laying eggs in hosts). The database contains original resource densities and associated foraging rates from the literature. To standardize these, all data were first converted to comparable space and time units. We then generated 200 bootstrapped data sets per functional response data set, and fit this data to either the Holling disc equation (Eq. 1) or the Roger's Random Predator equation—a modified form of the Holling disc equation that accounts for prey depletion—to provide estimates of space clearance rate and handling time across pairwise consumer–resource interactions. FoRAGE also contains reported temperatures, foraging dimensionality, and the reported or estimated body masses of consumers and resources. More details on standardization of the FoRAGE data is provided is provided in the associated data paper (Uiterwaal et al. 2018).

Handling times in FoRAGE are approximately lognormally distributed (Appendix S1: Fig. S1) but still show a pronounced negative skew extending below about $1 \times 10^{-6}$ days. We therefore excluded from our analysis 188 handling time estimates below this value because we suspect they are either indicative of a Type I functional response (where $h = 0$) or they were underestimates of the true handling time resulting from a limited prey density range. By excluding extremely small handling times, we ensure that our results are based on identifiable handling time estimates.

Then, in order to analyze the effects of experimental arena size, we excluded arena size data from field functional responses, as these "arena" sizes represent the size of the study area rather than a physically bounded arena. We updated the arena size for Sørnes and Aksnes (2004), which was reported incorrectly in the original FoRAGE database. We also set the temperature for functional responses with endotherm consumers to body temperature, 37°C for mammals (30 functional responses) and 42°C for birds (25 functional responses). We performed all analyses in Matlab.

To look at the effects of body mass on handling time and to determine whether temperature's effect on handling time is monotonic or unimodal, we constructed several linear mixed effect models. All models included handling time as the dependent variable and either temperature or temperature$^2$ as one of the predictor variables. We also included taxon as a random effect to account for simultaneous across-source and across-species variation, because most functional responses from the same source paper were conducted with the same species. We tried models with various combinations of predictor variables. We first constructed a "complete" model with temperature and all four other predictor variables (consumer mass, resource mass, dimensionality of the foraging interaction [2, 2.5, or 3 dimensional], and

experimental arena size). Foraging interactions that occur in 2.5 dimensions included orb-weaving spiders that filter a 3D volume with a 2D web, parasitoid wasps flying in search of hosts on leaves, or insects foraging on the branches of plants. In some cases, interactions which we classified as 2.5D—such as insects on plants—could be thought of as interactions on complex 2D surfaces, but we believe 2.5D to be a more accurate dimensionality given that organisms can move not just along the surface area of a leaf, but also up or down the plant stems along a third axis, yet they cannot forage in the full volume of the arena.

We systematically dropped predictor variables from the complete model to construct 15 additional models: Four models contained temperature and three of the four other predictor variables, six models contained temperature and two of the four other predictor variables, four models contained temperature and one of the four other predictor variable, and one model contained only temperature (see Appendix S1: Table S1). Then, we ran each model again using temperature$^2$ instead of temperature. We chose as the best-performing model the one with the lowest Akaike information criterion (AIC) (Burnham and Anderson 2004). To verify that adding taxon as a random effect improved this model, we confirmed that the AIC value increased when taxon was removed. Lastly, to determine whether consumer:resource mass ratio is more descriptive than both masses separately, we modified the optimal model to include this ratio rather than independent consumer and resource body masses. We used a total of 1,895 handling-time estimates for this model selection process.

We conducted a similar model selection process using space clearance rate as the dependent variable. This parameter has a spatial component that reflects the spatial dimensionality of the interaction, and therefore space clearance rate is incomparable across dimensionalities. To remedy this, we first divided the data into three smaller data sets by the dimensionality of the foraging interaction. For each of these data sets, we constructed a "complete" model using temperature and all three other predictor variables: consumer mass, resource mass, and arena size. We then constructed seven additional models: three models contained temperature and two of the three other predictor variables, three models contained temperature and one of the three other predictor variable, and one model contained only temperature (see Appendix S1: Table S2). In all models, we included taxon as a random effect. Then, we ran each model again using temperature$^2$ instead of temperature. We selected the best model for each dimension, verified that including taxon as a random effect improved the models, and tested modified optimum models with mass ratio. We used 723, 269, and 1,091 space clearance rate estimates for our 2D, 2.5D, and 3D space clearance rate models, respectively.

Because arena size typically has a large effect on space clearance rate, and because larger arenas are necessarily

used for larger organisms (Uiterwaal and DeLong 2018), we suspected that collinearity may be at play in our space clearance rate models. To determine if our results are robust to this arena size–consumer mass relationship, we fit a regression between consumer mass and arena size for each dimensionality (2D: $R^2 = 0.62$, $P = {<}0.001$; 2.5D: $R^2 = 0.17$, $P = {<}0.001$; 3D: $R^2 = 0.45$, $P = {<}0.001$). We substituted residuals from these regressions for consumer mass in the best models to determine whether body mass, having corrected for arena size, remains a significant predictor of space clearance rate.

To account for the possibility that some of the FoR-AGE data sets were better characterized as a Type III functional responses (in which space clearance rate increases with prey density) than a Type II, we repeated the fitting process as described in Uiterwaal et al. (2018) using equations modified to allow a Type III response (i.e., we included a fitted exponent on prey density). We performed this fitting process on all but one functional response, to which we were unable to fit a Type III equation. We calculated an AIC for both the Type II and Type III fits for each functional response and then removed from our analysis functional responses for which a Type III fit was supported over a Type II fit based on a $\Delta$AIC $\geq 2$. We repeated our model selection process to determine whether our results were sensitive to the presence of Type III responses.

We then constructed several additional models to determine if there are taxonomic differences in how temperature, consumer mass, and resource mass affect functional responses. To construct these models, we made two modifications to the best models for each parameter. First, these models did not include taxon as a random effect. Instead, they included an interaction between taxon and either temperature, consumer mass, or resource mass. Second, these models included only a linear term for temperature, as we were unable to include a squared temperature term. Functional responses from the literature typically do not cover temperature ranges that are broad enough to allow such an analysis within taxonomic groups. We ran these models on abridged versions of the data set with only well-represented taxa (greater than ~10 functional responses per taxon). Thus, our taxon-inclusive handling time model was based on 1,795 functional responses and our taxon-inclusive space clearance rate models were based on 665, 263, and 1,051 functional responses for 2D, 2.5D, and 3D interactions, respectively.

## Results

The best model for handling time included temperature[2] and all predictor variables (Table 1, Table S1). The model indicated that handling time increases when temperatures deviate from a thermal optimum of 23.4°C, decrease with consumer mass, and increase with resource mass (Fig. 1). The model further suggested that handling times are shorter in higher dimensionalities. Arena size,

TABLE 1. Results for the best linear model for handling time.

| Term | Estimate | SE | $t$ | $P$-value |
|---|---|---|---|---|
| Intercept | 0.83 | 0.85 | 0.98 | 0.327 |
| Temperature[2] | 0.005 | 0.001 | 4.42 | <0.001 |
| Temperature | −0.24 | 0.04 | −5.48 | <0.001 |
| ln(Consumer mass) | −0.25 | 0.03 | −9.44 | <0.001 |
| ln(Resource mass) | 0.34 | 0.02 | 15.59 | <0.001 |
| Dimensionality | −0.64 | 0.19 | −3.35 | <0.001 |
| ln(Arena size) | −0.01 | 0.03 | −0.38 | 0.704 |

although not a significant predictor variable, improved the model when included.

For space clearance rate, the best models were identical for all dimensionalities and included temperature[2] and all predictor variables (Table 2, Table S2). In all dimensionalities, the models suggested that space clearance rate decreases when temperatures deviate from a thermal optimum (Fig. 2). This optimum depended on dimensionality, with space clearance rate being optimized at 15.7°C, 25.6°C, and 26.7°C for 2D, 2.5D, and 3D interactions, respectively. Across dimensionalities, space clearance rate tended to increase with consumer mass and decrease with resource mass. Regardless of dimensionality, arena size had a strong positive effect on space clearance rate (Table 2). Models using residuals from an arena size–consumer mass regression produced results nearly identical to the optimum models (Appendix S1: Tables S2, S3). For both handling time and space clearance rate, and across dimensionalities, models using consumer:resource mass ratios were not supported over models using consumer and resource masses separately. We identified 939 functional responses for which a Type III fit was supported over Type II. Exclusion of these Type III responses did not affect selection of the best model for either parameter, except for the 2.5D space clearance rate model, where removal of the random taxon effect was supported (Appendix S1: Tables S1, S2).

Across taxa, there were distinct differences in the effects of temperature, consumer mass, and resource mass on functional response parameters (Figs. 3 and 4). Overall, larger consumers tended to have shorter handling times and larger resources took longer to handle, but the size of this effect varied by taxon. The effect of temperature on handling time also varied across taxa, with rotifer handling times appearing particular sensitive to temperature. Within a given taxon, the effect of temperature on space clearance rate varied depending on the dimensionality of the foraging interaction, although the effect of dimensionality was inconsistent across taxa.

## Discussion

Functional responses provide a useful quantification of interaction strengths between consumers and resources and are thus fundamental to both an
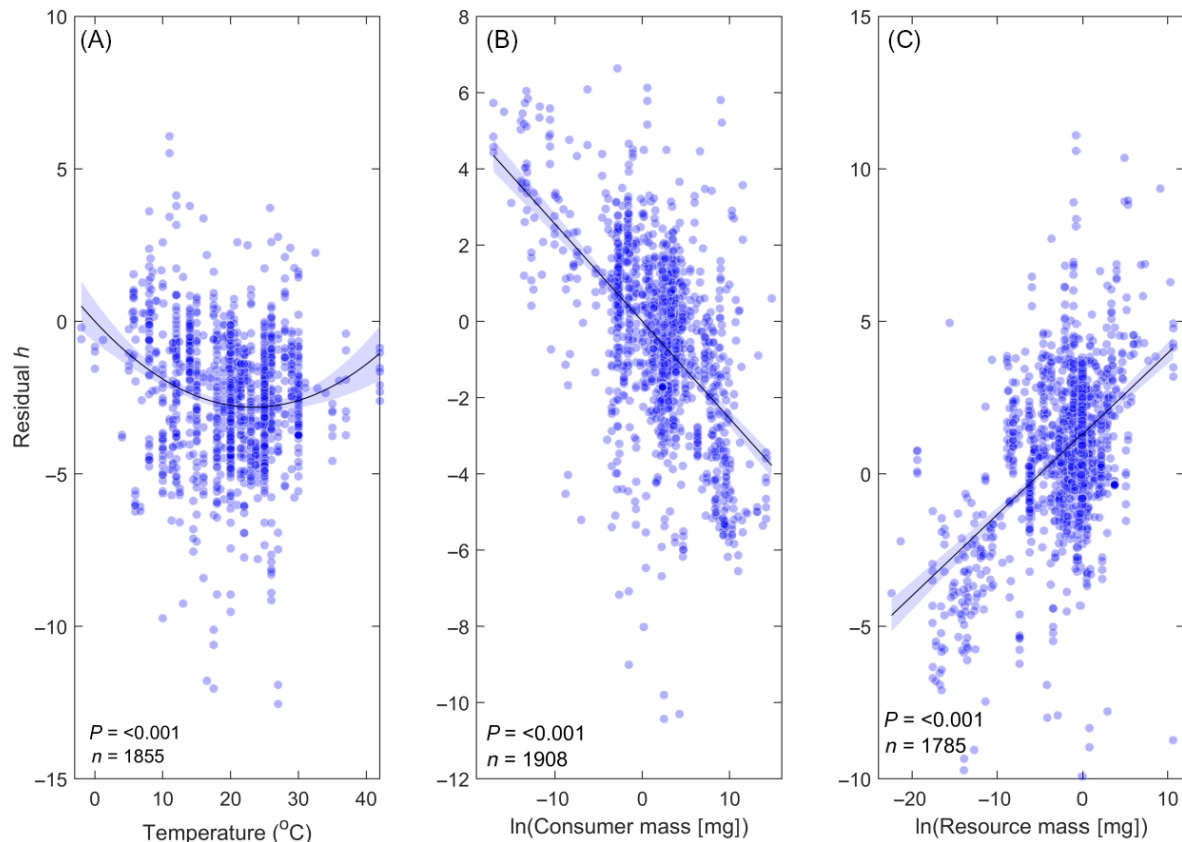
FIG. 1. Partial regression plots for the effects of temperature (A), consumer mass (B), and resource mass (C) on handling time for functional responses in all dimensionalities. Shaded areas represent 95% confidence intervals and $P$-values are given for the quadratic term (A) or slope (B) of the fit.

understanding of species interactions and our ability to model ecological communities. Simplifying the enormous variation in functional response parameters using allometric scaling or Arrhenius functions has thus been essential for making food web and other ecological community models more tractable (Yodzis and Innes 1992, Vasseur and McCann 2005, Brose et al. 2006, Otto et al. 2007, O'Connor et al. 2011, Binzer et al. 2012, Schneider et al. 2016). Our results provide the most comprehensive treatment yet for how temperature, arena size, and consumer and resource body masses influence the functional response, allowing for improved parameterization and model predictions.

Our results show clearly that the overall effect of temperature on functional response parameters is unimodal rather than monotonic. The strong quadratic effects of temperature in our best models indicate that consumers have reduced foraging ability when temperatures stray from an optimum. This result contrasts with the monotonic effects of temperature (whether using Arrhenius or simply linear effects) on space clearance rates and handling times found in other meta-analysis studies of functional responses (Rall et al. 2012, Kalinoski and DeLong 2016, Uiterwaal and DeLong 2018). It is likely

that the larger and more comprehensive nature of the FoRAGE database made it possible to detect this unimodal effect. This result also conflicts with the broad usage of Arrhenius expressions to capture the effect of temperature on consumer–resource interactions (Vasseur and McCann 2005, O'Connor et al. 2011, Binzer et al. 2012, Gilbert et al. 2014).

The optimal temperature for handling time was slightly lower than those calculated in other analyses, while our calculated optimal temperatures for space clearance rate were similar to other estimates (Englund et al. 2011, Rall et al. 2012). However, foraging is not the only biological process susceptible to temperature; metabolic demand also changes with temperature. Thus, after accounting for thermal effects on energy acquisition (foraging) and energy demand (metabolism), realized optimum temperatures for net energy intake may very well be distinct from those calculated here. Interestingly, the thermal optima found here are similar to those previously reported for maximum metabolic rates (DeLong et al. 2018), suggesting that foraging ability and metabolism may be maximized at similar temperatures.

Perhaps the most surprising finding is that the optimal temperatures for functional response parameters occur

TABLE 2. Results for the best linear models for space clearance rate for 2D, 2.5D, and 3D functional responses.

| Dimensions | Term | Estimate | SE | $t$ | $P$-value |
|---|---|---|---|---|---|
| 2D | Intercept | −8.45 | 1.05 | −8.08 | <0.001 |
| | Temperature$^2$ | −0.003 | 0.001 | −3.67 | <0.001 |
| | Temperature | 0.10 | 0.03 | 3.05 | 0.002 |
| | ln(Consumer mass) | 0.05 | 0.03 | 1.92 | 0.056 |
| | ln(Resource mass) | −0.0005 | 0.02 | −0.02 | 0.982 |
| | ln(Arena size) | 0.98 | 0.05 | 20.04 | <0.001 |
| 2.5D | Intercept | −16.35 | 1.20 | −13.58 | <0.001 |
| | Temperature$^2$ | −0.01 | 0.002 | −4.92 | <0.001 |
| | Temperature | 0.53 | 0.08 | 6.33 | <0.001 |
| | ln(Consumer mass) | −0.10 | 0.07 | −1.50 | 0.131 |
| | ln(Resource mass) | −0.14 | 0.06 | −2.47 | 0.015 |
| | ln(Arena size) | 0.73 | 0.06 | 12.05 | <0.001 |
| 3D | Intercept | −15.92 | 1.19 | −13.42 | <0.001 |
| | Temperature$^2$ | −0.01 | 0.002 | −2.52 | 0.012 |
| | Temperature | 0.32 | 0.08 | 3.78 | <0.001 |
| | ln(Consumer mass) | 0.54 | 0.04 | 14.25 | <0.001 |
| | ln(Resource mass) | 0.05 | 0.03 | 1.69 | 0.062 |
| | ln(Arena size) | 0.55 | 0.06 | 9.48 | <0.001 |
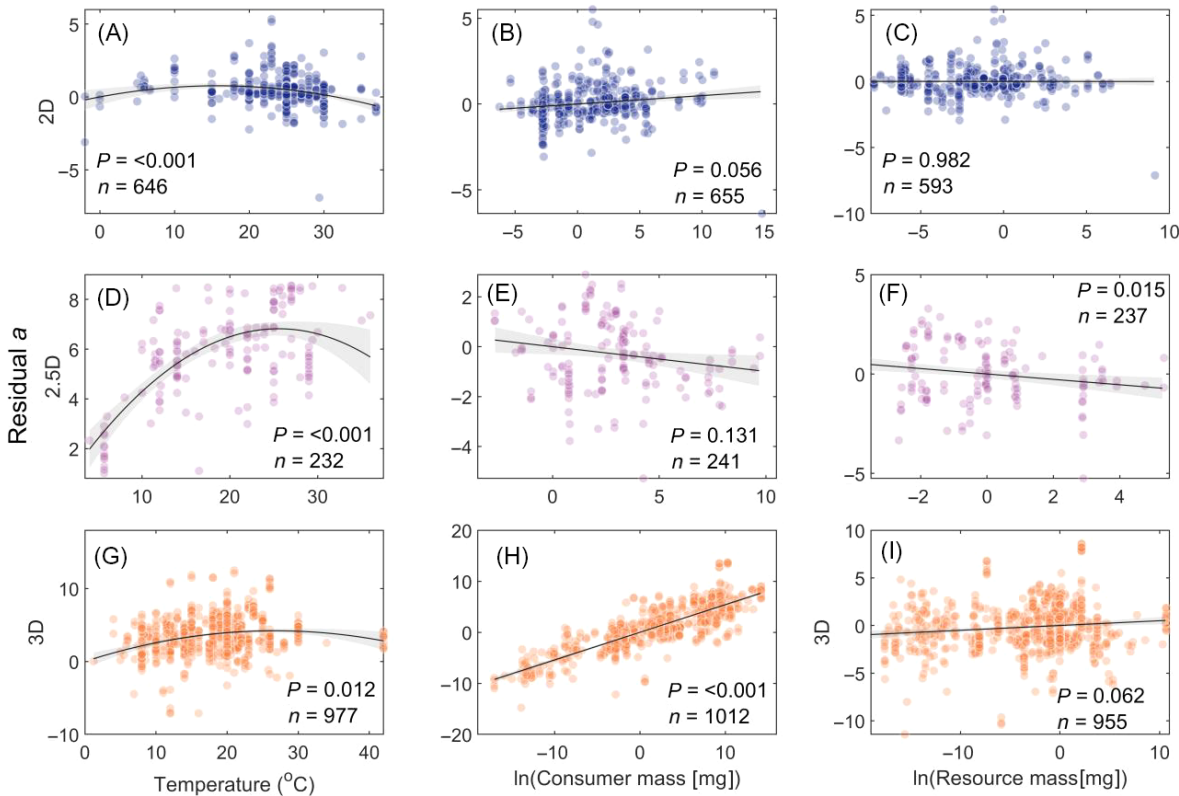


FIG. 2. Partial regression plots for the effects of temperature (A, D, G), consumer mass (B, E, H), and resource mass (C, F, I) on space clearance rate for functional responses in each of the dimensionalities. Shaded areas represent 95% confidence intervals and $P$-values are given for the quadratic term (A, D, G) or slope (B, C, E, F, H, I) of the fit.

at relatively mild temperatures (~15–25°C). Thus, although it has become commonplace to ignore the potential unimodality of functional response links to temperature with the argument that only the left-hand side of the curve represents the biologically relevant temperature range, our results suggest that warming may in many instances push functional response parameters over their optima. Furthermore, the unimodal response
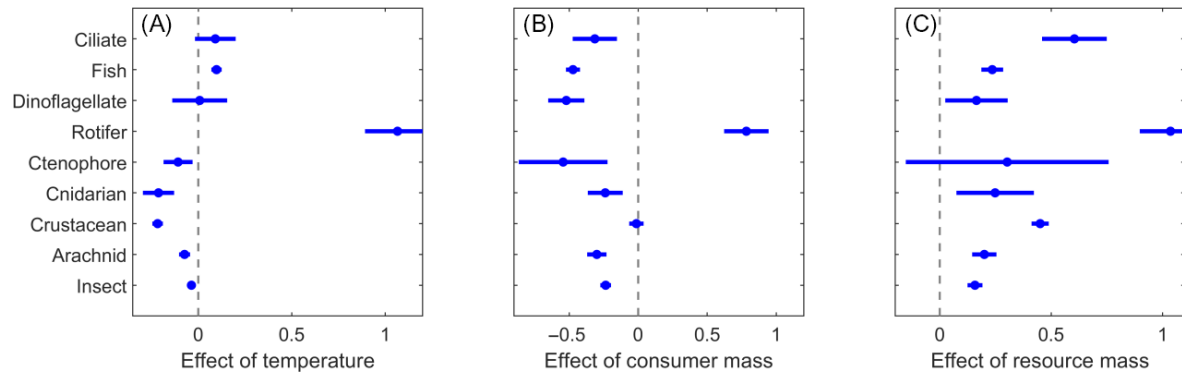
FIG. 3. Linear effects of temperature (A), consumer mass (B), and resource mass (C) on handling time for consumers of various taxa. Points represent taxon * temperature or taxon * mass estimates from modified best-performing models (see Methods). Error bars represent standard error. Number of functional responses in each taxon are shown in Appendix S1: Table S4.
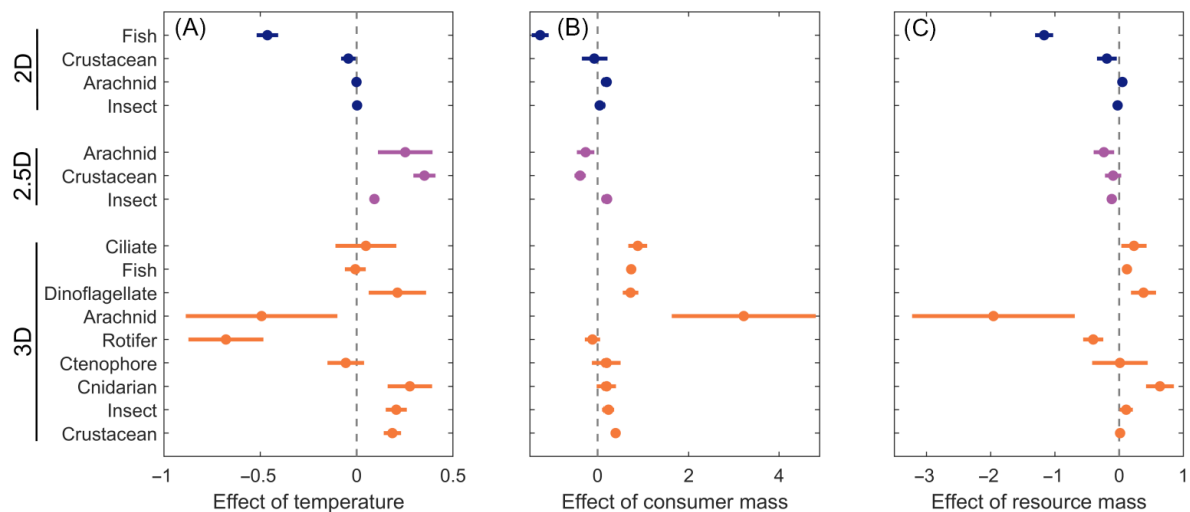


FIG. 4. Linear effects of temperature (A), consumer mass (B), and resource mass (C) on space clearance rate for consumers of various taxa. Effects are separated by the dimensionality of the foraging interaction. Points represent taxon * temperature or taxon * mass estimates from modified best-performing models (see Methods). Error bars represent standard error. Number of functional responses in each taxon are shown in Appendix S1: Table S5.

indicates that warming's effect on foraging depends on the location of the consumer's current temperature relative to the optimum temperature for each parameter (Uszko et al. 2017, Amarasekare 2019). Although some consumers may indeed forage more rapidly at warmer temperatures if they are currently at a temperature cooler than the optimum, those currently beyond the optimum may experience a decrease in foraging, reducing interaction strengths. Alternatively, consumers who are foraging at temperatures slightly below the optimum may simply experience a transverse shift across the curve's vertex and experience little to no effect of climate change on foraging rates.

Furthermore, because space clearance rate largely sets the foraging rate at low densities while handling time limits foraging at high densities, and because the two parameters have different optimum temperatures, the optimum temperature for foraging depends also on resource density. Thus, as resource population sizes change, the location of the optimum temperature of the interaction can shift relative to the current temperature. For 2D interactions, for example, the optimum temperature at low prey densities is 15.7°C and at high prey densities is 23.4°C. Thus, if current temperatures fall between these two optima, warming may decrease foraging rates at low resource densities and increase foraging rates at high resource densities as the temperature moves away from the optimum space clearance rate temperature but towards the handling time optimum. This means that the effect of warming on functional responses may depend largely on whether resource populations tend to be relatively low or high. This also means that the cycling of resource population levels has the potential to change the direction of the effect of warming.

These complex and context-specific implications of warming imply that, going forward, an increased focus on the temperature dependence of species interactions is crucial. We were unable to look at unimodal responses within taxa, so we cannot make taxon-specific predictions of how warming will influence consumer–resource interactions. This calls attention to the urgent need to test functional responses across broader temperature ranges wherever logistically and ethically possible, both to enable comparison of unimodal and monotonic models and to determine the direction and strength of changes in species interactions under warming conditions. Until then, a nuanced understanding of the effects of warming on individual consumer–resource interactions will remain elusive.

Such a focus on the shape of temperature dependence within taxonomic groups would likely uncover surprising diversity across taxa. Even our simplified taxon-inclusive models, which included only linear temperature dependence, show striking variation in the extent to which temperature constrains consumers (Figs. 3A and 4A). Indeed, even closely related taxa, such as arachnids, insects, and crustaceans (all arthropods), respond differently to temperature. Thus, although all foraging is adversely affected by suboptimal temperatures, biological traits appear to determine how consumers are impacted. Furthermore, although space clearance rates cannot be compared directly across dimensions, it is clear that the dimensionality of the foraging interaction modifies how space clearance rate changes with temperature. In crustaceans, for instance, temperature's effect on space clearance rate is negative in 2-dimensional interactions but positive in interactions that are 2.5- or 3-dimensional. These results suggest that habitat plays a role in mitigating internal temperature-dependent rates (such as locomotion speed) that help determine space clearance rate (Hurlbert et al. 2008). Interestingly, handling times are shorter when dimensionality is reduced, although the mechanism for this is unclear, as handling time does not have an explicit spatial component. This effect could arise because of separation of some taxa along dimensions. Differences across dimensionalities also may be due to factors not considered here, such as hunting strategy (e.g., ambush, filter feeding) or search medium (e.g., water, air). Search medium may also somewhat account for differences in optimum temperatures, as water and air have different thermal properties.

Typically, larger consumers are expected consume more, as they are better able to search space for resources and better able to overpower prey or hosts (Brose 2010). These characteristics translate into larger space clearance rates and faster handling times. Similarly, consumers typically search for and catch smaller resources more effectively and handle them more quickly. Our best models for both parameters supported these expectations. Nonetheless, substituting a consumer:resource mass ratio never resulted in a better model, and often significantly increased the AIC. Thus, although mass ratio is a commonly used metric in the study of foraging allometry (Vucic-Pestic et al. 2010, Barrios-O'Neill et al. 2016, Uiterwaal et al. 2017), our meta-analysis indicates that consumer and resource masses act independently to determine foraging rates. The impacts of this are clear when considering foraging relationships across body sizes: A large consumer foraging on a large resource may have a different interaction strength than a small consumer with a small resource, even if the mass ratio for the two consumer–resource pairs is the same. Thus, interaction strengths cannot simply be transposed from one consumer–resource pair to another, based on the relative sizes of the consumer to the resource. This is perhaps not surprising, given that metabolism—and the processes it powers—scale nonlinearly with body mass in metazoans, so consumers and resources independently face different costs and benefits associated with changes in body size.

Space clearance rate models using residuals from an arena size–consumer mass regression performed nearly identically to the optimum models (Appendix S1: Tables S2, S3). Surprisingly, this suggests that allometric effects are distinguishable, despite the necessary use of larger arenas for larger consumers. The ability to detect these allometric effects in our models accurately without residuals may be because some taxa have large arena size variation even for similarly sized consumers (Uiterwaal and DeLong 2018).

Our results also show that even extremely diverse consumers are largely subject to universal consequences of body size. However, taxonomic identity appears to mitigate or exaggerate how much consumers are constrained by these rules. Rotifers, for instance, have handling times that seem particularly sensitive to consumer mass, whereas crustaceans appear to be invulnerable to these effects. These differences in susceptibility to allometric effects suggest that prey size may play a role in diet composition across taxa. For example, generalist diets may be more accessible to taxa that are minimally affected by resource mass. Alternatively, because handling time largely determines foraging rates at high resource densities, whereas space clearance rate controls foraging rates at low prey densities, our taxon-inclusive models suggest that some taxa may be expected to switch between allometric specialism and generalism depending on resource availability. For instance, our model suggests that ctenophores have longer handling times for larger prey, indicating that they can optimize foraging rates by consuming small prey when prey is abundant. However, the effect of prey mass on space clearance rate is negligible, so at low prey densities opportunistic foraging on prey of any size would be most effective. Alternatively, some consumers may be expected to switch between large and small resources as resource availability changes. Cnidarians, for example, have optimized foraging for large prey at high prey densities and for small prey at low prey densities, as indicated by a positive effect of resource mass on both handling time and space clearance rate (Figs. 3 and 4).

However, despite the likelihood of a unimodal response to temperature within taxa, our taxon-inclusive models could not test for such a response. Because of this, care should be taken when interpreting specific results of our taxon-inclusive models. For example, our model's suggestion that crustacean handling times are unaffected by consumer mass is contradicted by experiment evidence (Toscano and Griffen 2013). Thus, our intent here is not to declare exact responses for each taxon, but to provide evidence that responses to temperature and body mass—and the resulting consequences on food webs—are as diverse as the organisms tested.

Therefore, although our analyses reveal broad trends in functional responses, including a prevalent unimodal response to temperature, we cannot consider such effects to be universal without identifying other factors around which functional responses might coalesce. It is imperative that we consider the unique characteristics of each interaction. Our ability to predict the structure, function, and stability of ecological communities with changing climates, novel invaders, and anthropogenic disturbances depends on appropriate parameterization of our community-level ecological models.

## Literature Cited

Amarasekare, P. 2019. Effects of climate warming on consumer–resource interactions: a latitudinal perspective. Frontiers in Ecology and Evolution. http://dx.doi.org/https://doi.org/10.3389/fevo.2019.00146

Barrios-O'Neill, D., R. Kelly, J. T. A. Dick, A. Ricciardi, H. J. MacIsaac, and M. C. Emmerson. 2016. On the context-dependent scaling of consumer feeding rates. Ecology Letters 19:668–678.

Binzer, A., C. Guill, U. Brose, and B. C. Rall. 2012. The dynamics of food chains under climate change and nutrient enrichment. Philosophical Transactions of the Royal Society B 367:2935–2944.

Brose, U. 2010. Body-mass constraints on foraging behaviour determine population and food-web dynamics. Functional Ecology 24:28–34.

Brose, U., et al. 2019. Predator traits determine food-web architecture across ecosystems. Nature Ecology & Evolution 3:919–927.

Brose, U., R. J. Williams, and N. D. Martinez. 2006. Allometric scaling enhances stability in complex food webs. Ecology Letters 9:1228–1236.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods & Research 33:261–304.

Burnside, W. R., E. B. Erhardt, S. T. Hammond, and J. H. Brown. 2014. Rates of biotic interactions scale predictably with temperature despite variation. Oikos 123:1449–1456.

Dell, A. I., S. Pawar, and V. M. Savage. 2011. Systematic variation in the temperature dependence of physiological and ecological traits. Proceedings of the National Academy of Sciences of the United States of America 108:10591–10596.

DeLong, J. P., G. Bachman, J. P. Gibert, T. M. Luhring, K. L. Montooth, A. Neyer, and B. Reed. 2018. Habitat, latitude and body mass influence the temperature dependence of metabolic rate. Biology Letters 14:20180442.

DeLong, J. P., and J. Belmaker. 2019. Ecological pleiotropy and indirect effects alter the potential for evolutionary rescue. Evolutionary Applications 12:636–654.

DeLong, J. P., and D. A. Vasseur. 2012. A dynamic explanation of size–density scaling in carnivores. Ecology 93:470–476.

Englund, G., G. Öhlund, C. L. Hein, and S. Diehl. 2011. Temperature dependence of the functional response. Ecology Letters 14:914–921.

Gergs, A., and H. T. Ratte. 2009. Predicting functional response and size selectivity of juvenile *Notonecta maculata* foraging on *Daphnia magna*. Ecological Modelling 220:3331–3341.

Gilbert, B., et al. 2014. A bioenergetic framework for the temperature dependence of trophic interactions. Ecology Letters 17:902–914.

Gilljam, D., A. Thierry, F. K. Edwards, D. Figueroa, A. T. Ibbotson, J. I. Jones, R. B. Lauridsen, O. L. Petchey, G. Woodward, and B. Ebenman. 2011. Seeing double: size-based and taxonomic views of food web structure. Pages 67–133 *in* A. Belgrano, editor. Advances in ecological research, The role of body size in multispecies systems. Academic Press, Cambridge, Massachusetts, USA.

Hirt, M. R., T. Lauermann, U. Brose, L. P. J. J. Noldus, and A. I. Dell. 2017. The little things that run: a general scaling of invertebrate exploratory speed with body mass. Ecology 98:2751–2757.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. The Canadian Entomologist 91:385–398.

Hurlbert, A. H., F. Ballantyne, and S. Powell. 2008. Shaking a leg and hot to trot: the effects of body size and temperature on running speed in ants. Ecological Entomology 33:144–154.

Kalinoski, R. M., and J. P. DeLong. 2016. Beyond body mass: How prey traits improve predictions of functional response parameters. Oecologia 180:543–550.

McCann, K. 2011. Food webs. Princeton University Press, Princeton, New Jersey, USA.

McGill, B. J., and G. C. Mittelbach. 2006. An allometric vision and motion model to predict prey encounter rates. Evolutionary Ecology Research 8:691–701.

Moayeri, H. R. S., H. Madadi, H. Pouraskari, and A. Enkegaard. 2013. Temperature dependent functional response of *Diaeretiella rapae* (Hymenoptera: Aphidiidae) to the cabbage aphid, *Brevicoryne brassicae* (Hemiptera: Aphididae). European Journal of Entomology 110:109–113.

Novak, M., and J. T. Wootton. 2010. Using experimental indices to quantify the strength of species interactions. Oikos 119:1057–1063.

O'Connor, M. I., B. Gilbert, and C. J. Brown. 2011. Theoretical predictions for how temperature affects the dynamics of interacting herbivores and plants. American Naturalist 178:626–638.

Otto, S. B., B. C. Rall, and U. Brose. 2007. Allometric degree distributions facilitate food-web stability. Nature 450:1226–1229.

Pawar, S., A. I. Dell, and V. M. Savage. 2012. Dimensionality of consumer search space drives trophic interaction strengths. Nature 486:485–489.

Petchey, O. L., A. P. Beckerman, J. O. Riede, and P. H. Warren. 2008. Size, foraging, and food web structure. Proceedings of the National Academy of Sciences of the United States of America 105:4191–4196.

Rall, B. C., U. Brose, M. Hartvig, G. Kalinkat, F. Schwarzmüller, O. Vucic-Pestic, and O. L. Petchey. 2012. Universal temperature and body-mass scaling of feeding rates. Philosophical Transactions of the Royal Society B 367:2923–2934.

Schneider, F. D., U. Brose, B. C. Rall, and C. Guill. 2016. Animal diversity and ecosystem functioning in dynamic food webs. Nature Communications 7:12718.

Schröder, A., G. Kalinkat, and R. Arlinghaus. 2016. Individual variation in functional response parameters is explained by body size but not by behavioural types in a poeciliid fish. Oecologia 182:1129–1140.

Sørnes, T. A., and D. L. Aksnes. 2004. Predation efficiency in visual and tactile zooplanktivores. Limnology and Oceanography 49:69–75.

Spitze, K. 1985. Functional response of an ambush predator: *Chaoborus americanus* predation on *Daphnia pulex*. Ecology 66:938–949.

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*. Journal of Animal Ecology 47:757–767.

Toscano, B. J., and B. D. Griffen. 2013. Predator size interacts with habitat structure to determine the allometric scaling of the functional response. Oikos 122:454–462.

Uiterwaal, S. F., and J. P. DeLong. 2018. Multiple factors, including arena size, shape the functional responses of ladybird beetles. Journal of Applied Ecology 55:2429–2438.

Uiterwaal, S. F., I. T. Lagerstrom, S. R. Lyon, and J. P. DeLong. 2018. Data paper: FoRAGE (Functional Responses from Around the Globe in all Ecosystems) database: a compilation of functional responses for consumers and parasitoids. bioRxiv 503334. https://doi.org/10.1101/503334.

Uiterwaal, S. F., C. Mares, and J. P. DeLong. 2017. Body size, body size ratio, and prey type influence the functional response of damselfly nymphs. Oecologia 185:339–346.

Uszko, W., S. Diehl, G. Englund, and P. Amarasekare. 2017. Effects of warming on predator–prey interactions—a resource-based approach and a theoretical synthesis. Ecology Letters 20:513–523.

Vasseur, D. A., and K. S. McCann. 2005. A mechanistic approach for modeling temperature-dependent consumer–resource dynamics. American Naturalist 166:184–198.

Vucic-Pestic, O., B. C. Rall, G. Kalinkat, and U. Brose. 2010. Allometric functional response model: body masses constrain interaction strengths. Journal of Animal Ecology 79:249–256.

Wahlström, E., L. Persson, S. Diehl, and P. Byström. 2000. Size-dependent foraging efficiency, cannibalism and zooplankton community structure. Oecologia 123:138–148.

Weitz, J. S., and S. A. Levin. 2006. Size and scaling of predator–prey dynamics. Ecology Letters 9:548–557.

Wootton, J. T., and M. Emmerson. 2005. Measurement of Interaction Strength in Nature. Annual Review of Ecology, Evolution, and Systematics 36:419–444.

Yodzis, P., and S. Innes. 1992. Body size and consumer–resource dynamics. American Naturalist 139:1151–1175.