Complexity reduces feeding strength of freshwater predators (CRITTER)

Supplemental Statistics Report

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Contents

Overview

Summary

This statistics report is a supplement of the upcoming publication of Aranbarri et al. (unpublished) investigating the effect of habitat complexity on the feeding functional response of two freshwater invertebrate predators. Find below information on related works and the location of the data and code.

Note that the report is still under construction!

License

Related Works

- Data on Zenodo (Flores et al., 2025)

- Data on GitHub

- R-Code on Zenodo (Rall et al., 2025b)

- R-Code on GitHub

- Statistical Report on GitHub

- Statistical Report on Zenodo (Rall et al., 2025a)

- Scientific Preprint Paper (link tba)

Methods

Theoretical Background

The feeding functional response describes how a consumer's feeding rate reacts to its resource density (Holling, 1959a). The most basic shape of the feeding functional response is a hyperbolic curve, also called the **type II functional response** (Jeschke et al., 2002). The attack rate, a, controls the initial increase in the feeding rate, F, with increasing resource density, N (Holling, 1959a), and the handling time, T_h controls the satiation of the curve:

$$F = \frac{aN}{(1 + aT_hN)}. \tag{1}$$

If the attack rate is a function of resource density, the functional response becomes s-shaped (Holling, 1959b; Kalinkat et al., 2023). In the simplest form of this **type III functional response**, the attack rate is a linear function of resource density (Juliano, 2001):

$$a = bN, \tag{2}$$

with b being the attack coefficient. The functional response becomes:

$$F = \frac{bN^2}{(1 + bT_hN^2)}. \tag{3}$$

(Real, 1977, 1979) presented an alternative formulation of the functional response inspired by chemical reactions and the Michaelis-Menten kinetics Barcroft & Hill (1910). By substituting $T_h = \frac{1}{F_{max}}$ and $a = \frac{F_{max}}{N_{half}}$ the **type II functional response** becomes:

$$F = \frac{F_{max}N}{N_{half} + N}. \tag{4}$$

Here, the curve's satiation is controlled by the maximum feeding rate, F_{max}, and the half saturation density, N_{half} controls the steepness of the functional response curve. The **type III functional response** written in this style is as follows:

$$F = \frac{F_{max}^2 N}{N_{half}^2 + N^2}. \tag{5}$$

The above-described **type III functional response** model has a linearly increasing attack rate, but the attack rate can also be a more complex function of resource density (Juliano, 2001; Kalinkat et al., 2023). A commonly used version is when the attack rate a is a power law function of the resource density (Kalinkat et al., 2023; Williams & Martinez, 2004):

$$a = b^q. \tag{6}$$

The Holling-style functional response becomes (Vucic-Pestic et al., 2010):

$$F = \frac{bN^{1+q}}{(1 + bT_h N^{1+q})}, \tag{7}$$

and the Real-style functional response becomes (Williams & Martinez, 2004):

$$F = \frac{F_{max}^{1+q} N}{N_{half}^{1+q} + N^{1+q}}. \tag{8}$$

We will refer to these functional response models as Holling/Real **generalized functional response** models. Note that many other functional response models exist, but the ones presented above are most practical and most often used to analyze laboratory functional response experiments (Jeschke et al., 2002; Juliano, 2001; Kalinkat et al., 2023). In our analyses, we will focus on the **generalized functional response** models and, if statistically appropriate, on the **type II or type III functional response**.

Functional Response Statistics

Independence of variables

Scientific laboratory experiments are designed to manipulate one or more external variables (the **independent variables**) and record the response of the system (the **dependent variable**). In functional, the main **independent variable** is the resource density, N, and the **dependent variable** is the feeding rate, F. Commonly used statistical methods (e.g., a linear regression model) require that the **independent variable** must be free of statistical noise (a.k.a. error-free) and fixed (**CITATION NEEDED**). In the case of most laboratory functional response experiments, however, the resource density decays over time due to the process of feeding. This means the independent variable is not independent anymore. To account for the decay of resource density, we set up a differential equation, describing the temporal process:

$$\frac{dN}{dt} = -F. \tag{9}$$

The **change of resource density** (dN) over a given **time span** (dt) is described by the negative of the feeding rate F. F can be any of the functional response models introduced above (or described elsewhere). This differential equation model can not be fitted directly to data, but it needs to be solved beforehand. The solution of this differential equation model depends on the type of the functional response. For a **type II functional response**, the solution is (Rogers, 1972; Rosenbaum & Rall, 2018; Royama, 1971):

$$N_{eaten} = N_{inital}(1 - e^{a(N_{eaten}T_h - Pt)}). \tag{10}$$

The number of resources eaten, N_{eaten} at the time t (e.g., the end of the experiment) depends on the initial number of resources, $N_{initial}$. All other parameters are as described above. This equation is commonly known as **Roger's Random Predator Equation** (RRPE). By substituting $T_h = \frac{1}{F_{max}}$ and $a = \frac{F_{max}}{N_{half}}$ into Roger's Random Predator Equation, we get the version for the Real-style functional response model:

$$N_{eaten} = N_{inital}(1 - e^{\frac{N_{eaten}}{N_{half}} - \frac{Pt}{F_{max}}}). \tag{11}$$

Model parameters are as described above.

These equations share the issue that N_{eaten} appears on both sides of the equation. Traditionally, this problem is solved using Newton's method, an iterative numerical procedure (Juliano, 2001; Vonesh & Bolker, 2005), but Bolker (2008) found that the Lambert **W** function (Corless et al., 1996) allows for an analytical solution:

$$N_{eaten} = N_{inital} - \frac{W(aT_h N_{initial} e^{-a(Pt - T_h N_{initial})})}{aT_h}. \tag{12}$$

The Real-style version is:

$$N_{eaten} = N_{inital} - \frac{W(\frac{1}{N_{half}} N_{initial} e^{-\frac{F_{max}}{N_{half}}(Pt - \frac{N_{initial}}{F_{max}})})}{\frac{1}{N_{half}}}. \tag{13}$$

All parameters are as described above.

Neither the type III nor the generalized functional response can be solved analytically and must be solved using numerical simulations (Rosenbaum & Rall, 2018). We follow the methods published by Rosenbaum & Rall (2018), but find more details in the section "Brief Code Description" below.

Data Distribution

So far, we described the mathematical model describing the average number of resources eaten throughout the experimental trials. Each experimentally derived replicate, however, can deviate from this overall model mean. Our dependent data, N_{eaten}, has the following characteristics: integer numbers (0, 1, 2,..., n), and the number of prey eaten cannot exceed the number of initially available resource items ($N_{initial}$). Data following these characteristics are known as proportion data and well described by a binomial probability distribution; see Crawley (2012) chapter 16 for example. We also apply this distribution to our data, as it is commonly used for functional response fitting (Bolker, 2008; Rosenbaum & Rall, 2018). Please read the "Brief Code Description" section and the code itself for further details.

Functional Response Type Selection

First, we analyze which functional response type describes our data best (Juliano, 2001). We used two methods: (1) the phenomenological test after Juliano, implemented in the `frair` package (Juliano, 2001; Pritchard, Paterson, et al., 2017)[1]; and (2) by fitting the the Real-style **generalized functional response model** and test if q is significantly different from zero (Rosenbaum & Rall, 2018; Vucic-Pestic et al., 2010; Williams & Martinez, 2004).

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[1]see "Phenomenological Test Rationale" for details on this method.

If the tests suggest, that at least one functional response treatment is not of type II, we will analyze our data further using the **generalized functional response** model. If the tests suggest, that **all** treatments are type II, we will analyze our data further using the **Roger's Random Predator Equation** models. We do so, as fitting simulations to data is computationally expensive, meaning it increases the time of the fitting dramatically.

Habitat Complexity as an Independent Variable

The main scientific question of this project is to figure out how habitat complexity affects the interaction strength of two freshwater invertebrate predators (the consumers) on their prey (the resources). We have three different ways to address this question available in the data: (1) the absence and presence of habitat; (2) the number of habitat pieces (either 0, 2, or 3 plastic ring structures); (3) five levels of complexity (0 to 5). The complexity levels originate from different spatial arrangements of the artificial ring structures, where 0 rings are complexity level 0, 2 rings comprise complexity levels 2 and 3, and 3 rings comprise complexity levels 4 and 5. See Flores et al. (2016) for further details. Contrasting the above-described analysis of the functional response type, we use here all data at once, separated by predator species. Each functional response parameter can react to habitat independently of the other parameter(s). For example, the attack rate can be different for all five complexity levels, whereas the handling time is a function of ring number. For each parameter, we can formulate the following hypotheses:

- H_0: Habitat has no effect on the functional response parameters.

- H_1: The sheer presence of habitat changes the functional response parameters.

- H_2: The amount of habitat structure (number of rings, continuous) alters the functional response parameters.

- H_3: The spatial arrangements modify the functional response parameters in addition to the amount of habitat structure.

Any functional response parameter independently can fulfill one of the above-stated hypotheses. If we want to test all possible combinations, we need 4×4 models (4 hypotheses per parameter) for each functional response style (Real-style and Holling style), in the case of a **type II functional response**, resulting in 32 statistical models per predator species. In the case of **generalized functional response**, we would have to test 64 statistical models for each functional response style, resulting in 128 models per species. Note that some of these models of how habitat affects the functional response are interchangeable, but not all. We will show for which models this is true in the results part below ([Habitat Complexity]).

Data Availability

You can either download the data from our data publication on Zenodo (Flores et al., 2025), or from our GitHub Repository:

```
fr_data <- read.csv(
  "https://raw.githubusercontent.com/b-c-r/CRITTERdata/refs/heads/main/critter_data.csv"
  )
```

Code Availability

You can either download the code from our code publication on Zenodo (Rall et al., 2025b), or from our GitHub Repository:

```
gh_path <- "https://raw.githubusercontent.com/b-c-r/CRITTERcode/refs/heads/main/"

## importing functions for the phenomenological test
pt_files <- supportR::github_ls(
  "https://github.com/b-c-r/CRITTERcode",
```

```
    "functions_phen_test"
)$name

for(i in 1:length(pt_files)){
  source(paste(gh_path, "functions_phen_test/", pt_files[i], sep = ""))
}

## importing functions for the generalized functional response model
gfr_files <- supportR::github_ls(
  "https://github.com/b-c-r/CRITTERcode",
  "functions_gen_fr"
)$name

for(i in 1:length(gfr_files)){
  source(paste(gh_path, "functions_gen_fr/", gfr_files[i], sep = ""))
}
```

Results

Functional Response Type Selection

Using the phenomenological test

The following code fits the phenomenological test (Juliano, 2001; Pritchard, Paterson, et al., 2017; Pritchard, Barrios-O'Neill, et al., 2017; Rall et al., 2025b) to all treatments (two predators with each five complexity levels):

```
phen_tests <- phen_type_test(
  data = fr_data,
  name_initial = "n_initial",
  name_eaten = "n_eaten",
  name_treatments = "treatment"
)
```

Table 1: The results applying the phenomenological functional response type test to all seperate treatments.

Predator	Complexity	Linear (Q)	Quadratic (Q)	Linear (L)	Type
Ischnura elegans	0	-(n.s.)	+(n.s.)	-(*)	II
Ischnura elegans	1	-(n.s.)	+(n.s.)	-(*)	II
Ischnura elegans	2	-(n.s.)	+(n.s.)	-(***)	II
Ischnura elegans	3	-(n.s.)	+(n.s.)	-(**)	II
Ischnura elegans	4	+(n.s.)	-(n.s.)	-(**)	II
Notonecta glauca	0	-(***)	+(***)	-(***)	II
Notonecta glauca	1	-(***)	+(***)	-(***)	II
Notonecta glauca	2	-(***)	+(**)	-(***)	II
Notonecta glauca	3	-(n.s.)	-(n.s.)	-(***)	II
Notonecta glauca	4	-(*)	-(n.s.)	-(***)	II

The only case in which the results suggest a hump shaped pattern in the proportion data is *I. elegans* at the complexity level of 4 as the linear term is positive and the quadratic term is negative (table 1). However, both estimates are not significant. The complexity levels 3 and 4 for *N. glauca* show a negative quadratic term, which could also indicate a type III functional response, but both results are not significant. All other treatments have

both a negative linear and a positive quadratic term indicating in all these cases a declining proportion of eaten prey and therewith type II functional responses (table 1).

Direct shape estimation using the generalized functional response model

The following code fits the generalized functional response model (Rosenbaum & Rall, 2018; Vucic-Pestic et al., 2010; Williams & Martinez, 2004) to all treatments (two predators with each five complexity levels):

```
gen_fr_results <- gen_fr_fit_all(
 data = fr_data,
 name_initial = "n_initial",
 name_eaten = "n_eaten",
 name_treatments = "treatment"
)
```

Table 2: The significance of the shape parameter q of all ten separately fitted generalized functional response models.

Predator Name	Complexity	q	Significance	Type-o-Response
Ischnura elegans	0	0.116	n.s.	II
Ischnura elegans	1	0.047	n.s.	II
Ischnura elegans	2	-0.001	n.s.	II
Ischnura elegans	3	-0.001	n.s.	II
Ischnura elegans	4	0.193	n.s.	II
Notonecta glauca	0	-0.011	n.s.	II
Notonecta glauca	1	-0.006	n.s.	II
Notonecta glauca	2	0.194	n.s.	II
Notonecta glauca	3	-0.002	n.s.	II
Notonecta glauca	4	-0.001	n.s.	II

The shape parameter q of the generalized functional response model is not significantly different from zero (see table 2). This means that in all cases, a simpler type II functional response can be used to describe the data properly. We will subsequently use Roger's Random Predator Equation.

Funding Information

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Appendix

Phenomenological Test Rationale

Instead of fitting the number eaten prey items as depended variable as function of the initial prey density, the ratio of prey eaten and initial prey items is used as depended variable (Juliano, 2001; Pritchard, Paterson, et al., 2017; Pritchard, Barrios-O'Neill, et al., 2017). In the case of a type II functional response, the proportion of eaten prey is constantly declining with increasing prey density, whereas in the case of a type III functional response, the proportion of prey eaten increases at low prey densities and declines after a reaching a maximum proportion rate. The main trend of any functional response if looking at the proportion data is negative. This negative trend is caused by the fact, that initial prey density linearly increases, whereas the eaten prey items are leveling of. Please see Juliano (2001) for a full description. Pritchard, Paterson, et al. (2017) implemented this test using generalized linear models with a binomial distribution, a standard method to analyze proportion data based on yes/no data (i.e. a prey item is eaten or not eaten), but see Crawley (2012), chapter 16, for an introduction on this topic.

We use here the customized function `phen_type_test()` which is a wrapper around the `frair_test()` function from the `frair` package (Pritchard, Barrios-O'Neill, et al., 2017). `phen_type_table()` creates a high quality pdf-report table based on the output of `phen_type_test()`. Both functions are located in the project's sub-folder `functions`.

Project Settings

Last but not least: the system's and R installation's information:

```r
print(sessionInfo(), locale = FALSE)
```

```
## R version 4.4.2 (2024-10-31)
## Platform: x86_64-pc-linux-gnu
## Running under: Linux Mint 22.1
##
## Matrix products: default
## BLAS:   /usr/lib/x86_64-linux-gnu/openblas-pthread/libblas.so.3
## LAPACK: /usr/lib/x86_64-linux-gnu/openblas-pthread/libopenblasp-r0.3.26.so;  LAPACK version 3.12.0
##
## attached base packages:
## [1] stats     graphics  grDevices utils     datasets  methods   base
##
## other attached packages:
## [1] foreach_1.5.2 dplyr_1.1.4
##
## loaded via a namespace (and not attached):
##  [1] rappdirs_0.3.3     generics_0.1.3     xml2_1.3.6
##  [4] stringi_1.8.4      lattice_0.22-5     digest_0.6.37
##  [7] magrittr_2.0.3     evaluate_1.0.3     grid_4.4.2
## [10] bookdown_0.42      iterators_1.0.14   mvtnorm_1.3-3
## [13] fastmap_1.2.0      doParallel_1.0.17  jsonlite_1.8.9
## [16] Matrix_1.7-2       supportR_1.4.0     purrr_1.0.4
## [19] viridisLite_0.4.2  scales_1.3.0       frair_0.5.100
## [22] codetools_0.2-20   numDeriv_2016.8-1.1 httr2_1.1.0
## [25] cli_3.6.3          rlang_1.1.5        bbmle_1.0.25.1
## [28] gitcreds_0.1.2     munsell_0.5.1      withr_3.0.2
## [31] yaml_2.3.10        tools_4.4.2        parallel_4.4.2
## [34] bdsmatrix_1.3-7    colorspace_2.1-1   boot_1.3-31
## [37] kableExtra_1.4.0   curl_6.2.0         vctrs_0.6.5
## [40] R6_2.5.1           stats4_4.4.2       lifecycle_1.0.4
```

```
## [43] stringr_1.5.1         MASS_7.3-64      pkgconfig_2.0.3
## [46] RcppParallel_5.1.10 pillar_1.10.1    glue_1.8.0
## [49] gh_1.4.1             Rcpp_1.0.14      systemfonts_1.2.1
## [52] xfun_0.50            tibble_3.2.1     tidyselect_1.2.1
## [55] rstudioapi_0.17.1    knitr_1.49       htmltools_0.5.8.1
## [58] svglite_2.1.3        rmarkdown_2.29   lamW_2.2.4
## [61] compiler_4.4.2
```