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FRAIR: AN R PACKAGE FOR FITTING AND COMPARING CONSUMER FUNCTIONAL RESPONSES

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AUTHOR CONTRIBUTIONS STATEMENT

DP authored and maintains the FRAIR package with support from RP, HB and DBO. All authors contributed critically to the drafts of this manuscript and gave final approval for publication.

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SUMMARY

1. Consumer-resource interactions (i.e. the functional response) underpin decades of ecological advancements. However, selecting, fitting and comparing functional response models using appropriate methods remains a non-trivial endeavour.
2. The R package *FRAIR* provides tools for selecting and differentiating various forms of consumer functional response models, a consistent interface for fitting and visualising response curves, and a selection of statistically robust methods for comparing fitted parameters.
3. Using real data from crustacean predator-prey systems, we demonstrate the utility of *FRAIR*, highlighting best practice and common analytical mistakes.

KEYWORDS

consumer-resource interactions; predator-prey; resource use; non-linear curve fitting; bootstrapping; maximum likelihood

INTRODUCTION

Consumer-resource interactions are at the heart of ecology because all organisms must consume resources of some kind. Functional responses describe how the per capita feeding rates of consumers change systematically with resource availability as a result of the consumer's search for, capture, and handling of resources (Holling 1959, 1966). The ubiquity and simplicity of principles underpinning the functional response continues to resonate with ecologists working at scales ranging from the behaviour of individuals (Toscano & Griffen 2014) to entire food webs (Brose 2010). Across fields—from theoretical explorations of

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stability and coexistence (Williams & Martinez 2004) to applications in biocontrol, invasions and conservation (Sinclair *et al.* 1998; Twardochleb *et al.* 2012)—functional responses remain central to much ecological research.

THE ANATOMY OF A FUNCTIONAL RESPONSE

Despite decades of refinements (e.g. Real 1977; Hassell 1978; Arditi & Ginzburg 1989; Skalski & Gilliam 2001; Okuyama 2012), the essential components of search, capture and handling outlined by Holling (1959) have remained largely unchanged. A generalised version of the Holling disc equation is (Real 1977):

$$N_e = \frac{aTN^{(q+1)}}{1+ahN^{(q+1)}} \quad (1)$$

where N is the resource density or number of prey; T is experimental time (typically hours or days); a is the instantaneous resource capture rate of the consumer, per unit area/volume per unit time; h in practice represents the time spent subjugating, ingesting and digesting each prey item, with the same units as T (Jeschke *et al.* 2002; Sentis *et al.* 2013); and q is a scaling exponent defining the extent to which the functional response changes from a decelerating hyperbola (Type II: $q = 0$ and Fig. 1a purple) to a sigmoidal form (Type III: $q > 0$ and Fig. 1a green).

When q is 0, capture rates are constant with resource density, whereas where $q > 0$, capture rates follow a power-law relationship with resource density, often implying that consumers learn as they forage (Real 1977). Type I (linear rather than saturating *sensu* Holling; Fig. 1a orange) functional responses can be described where $q = 0$ and $h = 0$. Since handling time determines the maximum consumption rate ($1/h$), doubling h suppresses the asymptote for consumers with identical capture rates (Fig. 1c: dashed *versus* solid blue curve). In contrast,

for consumers with identical handling times, doubling capture rates (a) increases consumption at low resource densities (Fig. 1c: dashed *versus* solid purple curves).

An important assumption of equation 1 is that local resource density does not decline. However, in many experiments, consumers deplete resources, rendering models in the equation 1 family inappropriate (e.g. Bollache *et al.* 2008). The family of models introduced by Royama (1971) and popularised by Rogers (1972) provide a solution to this problem by integrating instantaneous consumption over time. The modification of equation 1 assuming depletion is:

$$N_e = N_0(1 - \exp(aN_0^q(hN_e - T))) \quad (2)$$

where N_0 is the initial prey density, and other parameters are as in equation 1. Although the number of prey eaten (N_e) appears on both sides of equation 2, it can be solved using the ‘Lambert-W’ function (W). The derivation and definition of W is beyond the scope of this manuscript but it is described in detail in Corless *et al.* (1996) and with respect to ecological applications by Lehtonen (2016).

APPLICATIONS OF FUNCTIONAL RESPONSES

Ecologists often seek objective comparisons between one or more groups; with functional responses this usually necessitates comparisons of fitted model parameters, though the particular methods employed remain a subject of confusion and debate (Houck & Strauss 1985; Juliano 2001). Renewed interest in consumer functional response models has driven several innovative analytical solutions, at least two of which have been widely adopted. The first involves explicitly modelling the difference fitted parameters between two (or more) groups. This approach – described in Juliano (2001) – is computationally simple, but requires reparameterisation of the underlying model. It provides a coefficient (the difference between

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groups of interest) that can be interpreted within a regression-modelling framework, and with proper formulation and sufficient data, can be extended to moderately complex hypotheses (e.g. Paterson *et al.* 2015). A second approach involves bootstrapping (resampling with replacement) of either raw data (e.g. Bovy *et al.* 2015) or modelled residuals (e.g. Médoc *et al.* 2015). This computationally intensive approach explores the likely range of fitted coefficients, and allows for direct comparison of the range of these values (e.g. via confidence intervals).

Not all analytical approaches in the recent literature are as well advised. For example, some have applied null-hypothesis significance tests to bootstrapped parameter estimates from functional response models (e.g. Dodd *et al.* 2014; Bunke *et al.* 2015) – an approach that is clearly flawed (White *et al.* 2014). We suspect that the lack of a common toolset for non-specialists to fit and examine consumer functional response models has contributed to the propagation of these methods. With research output increasing, it is critical that ecologists working on functional responses make robust analyses: we anticipate that *FRAIR* can meet this need.

THE FRAIR PACKAGE

FRAIR is a package in the R statistical environment for selection, fitting and comparisons among common functional response models and constituent parameters. *FRAIR* is available on CRAN and development is undertaken openly on GitHub (<http://github.com/dpritchard/frair>).

This tutorial is based on *FRAIR* version 0.5.100 (the most recent version available on CRAN) and outlines key functionalities whilst providing a general introduction to these analyses. The tutorial is based on two experimentally derived datasets included with the package:

`gammarus`, a subset of data from Paterson et al. (2015) and `bythotrephes`, a previously unpublished dataset.

The `gammarus` dataset describes consumption of dipteran larvae (*Simulium* spp.) by two amphipod species (*Gammarus duebeni celticus* and *Gammarus pulex*). The `bythotrephes` dataset describes consumption of three size classes of the cladoceran *Polyphemus pediculus* by the cladoceran *Bythotrephes longimanus*. Both datasets concern experimental designs incorporating prey depletion. For further examples, readers are directed to other published studies utilising *FRAIR* (<https://github.com/dpritchard/frair/wiki/FRAIR-in-use>).

```
# Gammarus
data("gammarus")
str(gammarus)

## 'data.frame':  224 obs. of  4 variables:
## $ density: int  2 2 2 2 2 2 2 2 2 2 ...
## $ eaten  : int  0 2 2 2 2 2 2 2 2 2 ...
## $ alive  : int  2 0 0 0 0 0 0 0 0 0 ...
## $ spp    : Factor w/ 2 levels

levels(gammarus$spp)
## [1] "G.d.celticus" "G.pulex"
```

```
# Bythotrephes
data("bythotrephes")
str(bythotrephes)

## 'data.frame':  72 obs. of  4 variables:
## $ density: int  1 1 1 3 3 3 2 2 2 4 ...
## $ eaten  : int  1 1 0 3 2 3 2 2 2 4 ...
## $ alive  : int  0 0 1 0 1 0 0 0 0 0 ...
## $ size   : Factor w/ 3 levels

levels(bythotrephes$size)
## [1] "small" "medium" "large"
```

The *FRAIR* workflow involves a three-step process: (1) model selection; (2) model fitting and; (3) comparison of fits and coefficients. An essential step in this process is to visually inspect the raw plotted data (Fig. 2).

MODEL SELECTION

FRAIR offers a range of commonly used functional response models that can be viewed using `frair_responses()`. Basic models assume constant resource density throughout experimental trials (resources are replaced). For experiments where resources are depleted (so-called non-replacement experiments), models are provided (suffixed with `nr`) with Rogers (1972) modifications and solved using the ‘lambertW’ function (Bolker 2008).

Although equations 1 and 2 imply consumer functional responses can be described on a linear (Type I) to sigmoidal (Type III) continuum, the original categorical descriptions of Holling remain prominent (e.g. Denny 2014). This is likely because deviations from Type II towards Type III functional responses can stabilise otherwise chaotic consumer-resource dynamics (Williams & Martinez 2004; Barrios-O’Neill *et al.* 2016).

Juliano (2001) advocates fitting polynomial logistic functions to proportional consumption data to determine functional response Type. Type II is characterised by a negative first-order term (declining proportional consumption with increasing resource density; Fig. 1b), in contrast to a positive first-order term of Type III (initial increase and subsequent decrease in proportional consumption; Fig. 1b). Using this logic, the `frair_test` function uses forward selection based on the sign and significance of first-order (`density`) and second-order (`density^2`) terms in logistic regressions.

```
# Gammarus
frair_test(formula = eaten~density, data = gammarus)
## FUNCTIONAL RESPONSE TEST
##
```

```

## Evidence for type-II response:  Yes
## Evidence for type-III response:  -
##
## Type-II logistic regression output:
##           Estimate Std. Error z value Pr(>|z|)
## density -0.0792704  0.0044298 -17.895 < 2.2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

```

# Bythotrephes
frair_test(formula = eaten~density, data = bythotrephes)

## FUNCTIONAL RESPONSE TEST
##
## Evidence for type-II response:  No
## Evidence for type-III response:  Yes
##
## Type-III logistic regression output:
##           Estimate Std. Error z value Pr(>|z|)
## density      0.3646093  0.1009794  3.6107 0.0003053 ***
## I(density^2) -0.0206557  0.0051263 -4.0293 5.593e-05 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

Although this approach provides a statistical test to distinguish between Type II and Type III, it is considered phenomenological in that it describes only the general shape of the response, without determining whether a particular mechanistic model is appropriate. An alternative approach involves fitting a generalised form of the functional response model with a scaling exponent (q) parameterised such that $q = 0$ represents a Type II response (equation 1 or 2), thus exposing a useful null-hypothesis test (i.e. $q \neq 0$) via a regression output and allowing for comparison of models using information criteria (e.g. AIC, BIC, AICc). For example, with the `bythotrephes` dataset:

```

# Bythotrephes
# Fit a model where  $q$  can vary:
b_flex <- frair_fit(eaten~density, data=bythotrephes,
                  response='flexpnr',
                  start=list(b = 1, q = 0, h = 0.08),
                  fixed=list(T = 12/24))
# Fit a model where  $q$  is fixed to zero:
b_II <- frair_fit(eaten~density, data=bythotrephes,

```



```
response='flexpr',
start=list(b = 1, h = 0.08),
fixed=list(T = 12/24, q = 0))
summary(b_flex$fit) # q != 0 : Type III preferred
AIC(b_flex$fit, b_II$fit) # The model including q is preferred
```

The usefulness of these tests depends on the quality of data at low resource densities (Barrios-O'Neill *et al.* 2015) and some authors recommend that proportional relationships are visually inspected with locally weighted regression (Juliano 2001).

The experimental designs of our datasets indicate that depletion models are required as prey are not replaced during the experiment. Plots of the raw data and these analyses suggest that for the *gammarus* dataset, a Type II model is sufficient, however a Type III—or flexible model—may be most appropriate for the *bythotrephes* data.

MODEL FITTING

Essential to the optimisation of non-linear models is the provision of reasonable starting values for free parameters. There are some rules of thumb, for example, for Type II models, h can be approximated as the inverse of the maximum number eaten where T is set to 1 (Bolker 2008). An equally reliable method is a visual assessment of the data, plotting of putative starting values and trial and error (Fig. 2).

```
# Gammarus
with(gammarus, plot(density, eaten, xlab = "Prey Density",
                   ylab = "No. Prey Eaten"))
x <- with(gammarus, seq(from = min(density), to = max(density),
                       by = 0.1))
lines(x, rogersII(X = x, a = 1.2, h = 0.08, T = 40/24),
      col='grey50', lty=2)
lines(x, rogersII(X = x, a = 0.6, h = 0.16, T = 40/24),
      col='grey50', lty=2)
```

```
# Bythotrephes
with(bythotrephes, plot(density, eaten, xlab = "Prey Density",
                        ylab = "No. Prey Eaten"))
x <- with(bythotrephes, seq(from = min(density), to = max(density),
                            by = 0.1))
lines(x, flexpnr(X = x, b = 1, h = 0.04, q = 1, T = 12/24),
       col='grey50', lty=2)
lines(x, flexpnr(X = x, b = 2.4, h = 0.04, q = 0, T = 12/24),
       col='grey50', lty=2)
```

Note that all *FRAIR* functional response models take at least one fixed parameter (T), which is experimental time. Although not optimised, this value will change the units of the fitted coefficients. Many authors implicitly accept units of “experimental time” by setting $T = 1$. Unless the raw data is made available, this limits the use of parameter estimates in subsequent studies (e.g. meta-analyses, food-web models). Therefore, we recommend users adopt units of either ‘hour’ or ‘day’ and have adopted units of ‘day’ in this manuscript.

Once starting estimates and fixed values are provided, the model is optimised using maximum likelihood estimation (MLE). This robust approach to fitting non-linear models (Bolker 2008) allows for optimisation on the basis of arbitrary probability distributions. Internally, all *FRAIR* models use a binomial likelihood function, which imposes an upper (all prey eaten) and lower (no prey eaten) limit on the response. A practical limitation of this likelihood specification is that *FRAIR* can only fit curves when the density (x-axis) is specified as whole integer values (the most common situation for individual prey items).

In *FRAIR*, optimisation by MLE is provided by `frair_fit` and is implemented using `bbmle::mle2` (Bolker 2008). The resulting output (of class `frair_fit`) provides information on the fit and the maximum likelihood estimators (fitted coefficients) and a `lines` method to plot the fitted curve (Fig. 2). `frair_fit` also returns the raw output from the maximum likelihood optimisation, which provides typical regression output including asymptotic standard errors, z -statistics and p -values.

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```

# A fit to the entire gammarus dataset
g_fit <- frair_fit(formula = eaten~density, data = gammarus,
                  response = "rogersII",
                  start = list(a = 1, h = 0.1),
                  fixed = list(T = 40/24))
with(gammarus, plot(density, eaten, xlab="Prey Density",
                   ylab="No. Prey Eaten"))
lines(g_fit, lty = 1, col = "grey25")
print(g_fit)

## FUNCTIONAL RESPONSE FIT
##
## Response:          rogersII
## Description:      Roger's type II decreasing prey function
## Optimised variables: a, h
## Fixed variables:  T
##
## Coefficients:
##   a     h     T
## 1.423 0.180 1.667
##
## NOTE: It is recommended you inspect the raw fit too (see: ?frair_fit)

summary(g_fit$fit)

## Coefficients:
##   Estimate Std. Error z value    Pr(z)
## a 1.4228013  0.1314562  10.823 < 2.2e-16
## h 0.1802657  0.0098583  18.286 < 2.2e-16
##
## -2 log L: 1129.631

# A fit to the entire bythotrepes dataset
b_fit <- frair_fit(formula = eaten~density, data = bythotrepes,
                  response = "flexpnr",
                  start = list(b = 1.5, h = 0.04, q = 1),
                  fixed = list(T = 12/24))
with(bythotrepes, plot(density, eaten, xlab="Prey Density",
                      ylab="No. Prey Eaten"))
lines(b_fit, lty = 1, col = "grey25")
print(b_fit)

## FUNCTIONAL RESPONSE FIT
##
## Response:          flexpnr
## Description:      Flexible exponent, not assuming replacement
## Optimised variables: b, h, q
## Fixed variables:  T
##
## Coefficients:
##   b     q     h     T
## 0.652 1.215 0.053 0.500
##
## NOTE: It is recommended you inspect the raw fit too (see: ?frair_fit)

```

```
summary(b_fit$fit)
## Coefficients:
## Estimate Std. Error z value Pr(z)
## b 0.651730 0.258996 2.5164 0.01186
## q 1.215357 0.296077 4.1049 4.045e-05
## h 0.052912 0.005112 10.3509 < 2.2e-16
##
## -2 log L: 241.1805
```

MODEL COMPARISON

The third step in the *FRAIR* workflow includes comparisons of fitted coefficients. The two approaches currently implemented are the delta or difference method of Juliano (2001), provided by `frair_compare` and non-parametric bootstrapping of the raw data, provided by `frair_boot`. Both functions operating on objects produced by `frair_fit` (i.e. class `frfit`).

Comparisons between constituent parameters require that those parameters are equivalent. Comparisons of handling times, h , and maximum feeding rates ($1/hT$) are possible between all models in *FRAIR* (assuming consumers are handling limited), but comparisons of capture rates are often problematic. For example, there is no equivalence between capture rates as defined in `hassIIIInr` and `rogersII`, which respectively describe Type III and Type II responses (e.g. Alexander *et al.* 2012). Indeed, a Type II model assumes a prey density-independent capture rate, whilst for a Type III model capture rates typically follow a power law with prey density. Where comparing Type II and Type III models it is common to resort to comparisons of maximal capture rates, usually the steepest part of the curve (England *et al.* 2011). Often, however, responses in a dataset are of the same categorical form, making comparisons straightforward.

```

# Compare two species in the gammarus dataset
pulex <- gammarus[gammarus$spp=='G.pulex', ]
celt <- gammarus[gammarus$spp=='G.d.celticus', ]
st <- list(a = 1, h = 0.1)
fx <- list(T = 40/24)
p_fit <- frair_fit(eaten~density, data = pulex, response = 'rogersII',
                  start = st, fixed = fx)
c_fit <- frair_fit(eaten~density, data=celt, response='rogersII',
                  start = st, fixed = fx)
frair_compare(p_fit, c_fit)

## FUNCTIONAL RESPONSE COEFFICIENT TEST
##
## Response:                rogersII
## Optimised variables: a,h
## Fixed variables:        T
##
## Original coefficients:
##           a           h
## p_fit 1.47748 0.14268
## c_fit 1.41745 0.23381
##
## Test: p_fit - c_fit
##
##      Estimate Std. Error z value Pr(z)
## Da  0.05961    0.27132  0.2197  0.8261
## Dh -0.09115    0.02087 -4.3681  1e-05

```

`frair_compare` implements a difference test with the null hypothesis that fitted parameters do not differ. The fitted parameters Da and Dh estimate the differences between the capture rates and handling times of the two predators respectively. Here, we have evidence that capture rates do not differ ($Da = 0.06$, $z = 0.22$, $p = 0.826$), but that the handling time of *G. pulex* is shorter than that of *G. d. celticus* ($Dh = -0.02$, $z = -4.36$, $p < 0.001$).

Unfortunately, the difference method does not allow for direct comparisons between predicted consumption across the range of resource densities and because consumers can switch between Type II and Type III responses (Barrios-O'Neill *et al.* 2016), objective comparisons using this approach are often impossible. Therefore, *FRAIR* also provides `frair_boot`, which implements non-parametric bootstrapping and leverages `boot::boot` (Canty & Ripley 2016). This method generates multiple estimates of curves and constituent

parameters (based on a default minimum of 999 samples; Dixon 2001) and reports 95% confidence intervals (CIs) by default. We recommend using bias corrected and accelerated intervals – BCa – to account for bias, skew and bounded parameters (a and $h > 0$). It is expected that the underlying maximum likelihood estimation will sometimes fail, even with reasonable starting values, therefore `frair_boot` warns if $> 10\%$ of all bootstrapped fits fail and returns an error if $> 50\%$ of the fits fail. Because bootstrapping generates population metrics, the equivalent of a null hypothesis test is simply a lack of overlap between the CIs of model parameters.

```
# Bootstrap the Gammarus pulex fit
p_fitb <- frair_boot(p_fit)
confint(p_fitb, cotypes = 'bca')

## Coefficient CI Type      Lower  Upper
## a          BCa          0.998  2.295
## h          BCa          0.102  0.203

# Bootstrap the Gammarus duebeni celticus fit
c_fitb <- frair_boot(c_fit)
confint(c_fitb, cotypes = 'bca')

## Coefficient CI Type      Lower  Upper
## a          BCa          0.94    2.133
## h          BCa          0.183  0.286
```

Bootstrapping outputs for the `gammarus` dataset concur with the difference method for capture rates: the 95% CIs clearly overlap. In contrast to the difference method `frair_boot` suggests no difference between consumer handling times (95% CIs for h fractionally overlap). While both methods are sensitive to underlying data quality and quantity, the difference method makes assumptions about the error structure of the fitted parameters, whilst bootstrapping reflects the likely range of values given the data provided, whilst accounting for the bounded (e.g. non-negative) nature of handling times.

Based on the output from bootstrapped fits, *FRAIR* provides visual comparisons of entire functional response curves using `drawpoly` (Fig. 3). This function plots empirical approximations of the confidence intervals using the desired quantile predictions (0.025 and 0.975 for 95% CIs). Even where estimates of 95% CIs for all fitted parameters overlap (as in this example), parameters can combine to yield differences in predicted consumption as a function of prey density (Fig. 3). Such differences cannot be addressed using the delta method, and `drawpoly` provides a means to identify where predicted consumption may differ along an axis of resource density.

LIMITATIONS

Fitting non-linear models to ecological data can be a challenging and frustrating process (Bolker *et al.* 2013), resulting from highly variable data, low replication, use of an overly complex model, a desire to test many hypotheses, or a combination of these. Although there have been computational improvements, the challenges are as real now as they were in 1988, when Trexler *et al.* noted that it may be impossible to fit a curve to data, even with 11 resource densities and 10 replicates per resource density – a quantity of data rarely attained in experimental functional response analyses (Trexler *et al.* 1988). Even after many days of laboratory work, it may be impossible to fit the desired functional response model, or distinguish between the subtleties of a Type II and Type III response. This may be an unavoidable problem that no software can solve, but accessible tools for analysis will improve understanding of the strengths and limitations of consumer functional responses. Still, even with these tools, it seems clear that there is nothing straightforward about application or interpretation.

FRAIR has been designed with the non-specialist in mind. however, for those seeking advanced analyses, *FRAIR* has some practical limitations. For example, currently *FRAIR* does not provide ratio- or predator-dependent models (e.g. Hassell & Varley 1969;

Beddington 1975), body size-dependent models (e.g. Kalinkat *et al.* 2013) or convenience functions to explore and avoid local optima, or the capacity to specify user defined models (e.g. those with arbitrary probability distributions). We aim to add these features to *FRAIR* in the future and welcome third party participation in package development (<https://github.com/dpritchard/frair>). encourage those seeking to work outside the structure provided by *FRAIR* to consider the details provided by Bolker (2008) as well as guidance in the *FRAIR* help manual (e.g. `?frair_fit`).

CONCLUSION

We have presented the *FRAIR* package and demonstrated how it provides a reproducible framework for the selection, fitting and comparison of functional response models. We anticipate that *FRAIR* will help to consolidate functional response analysis methods for non-specialists by ensuring that common mistakes are not perpetuated, and by exemplifying the current best practice for non-linear curve fitting and comparison. Consumer-resource interactions are fundamental to many aspects of contemporary ecological research and thus, we anticipate that in providing an accessible open source package for functional response analysis, *FRAIR* will provide a useful tool for many ecologists.

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DATA ACCESSIBILITY

All data used in this manuscript are included in the FRAIR package, which is available on the CRAN repository at: <https://cran.r-project.org/web/packages/frair>

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SUPPORTING INFORMATION

Appendix S1: The R Markdown document containing all code and examples used in this manuscript.





