

# Fitting functional responses: Direct parameter estimation by simulating differential equations

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## Summary

1. The feeding functional response is one of the most widespread mathematical frameworks in Ecology, Marine Biology, Freshwater Biology, Microbiology and related scientific fields describing the resource-dependent uptake of a consumer. Since the exact knowledge of its parameters is crucial in order to predict, for example, the efficiency of biocontrol agents, population dynamics, food web structure and subsequently biodiversity, a trustful parameter estimation is of utmost importance for

scientists using this framework. Classical approaches for estimating functional response parameters lack flexibility and can often only serve as approximation for a correct parameter estimation. Moreover, they do not allow to incorporate side effects such as resource growth or background mortality. Both call for a new method to be established solving these problems.

2. Here, we combined ordinary differential equation models (ODE models), that were numerically solved using computer simulations, with an iterative maximum likelihood fitting approach. We compared our method to classical approaches of fitting functional responses, using data both with and without additional resource growth and mortality.
3. We found that for classical functional response models, like the often used type II and type III functional response, the established fitting methods are reliable. However, using more complex and flexible functional responses, our new established method outperforms the traditional methods. Additionally, only our method allows to analyze experiments correctly when resources experience growth or background mortality.
4. Our method will enable researchers from different scientific fields that are measuring functional responses to estimate parameters correctly. These estimates will enable community ecologists to parameterize their models more precisely, allowing for a deeper understanding of complex ecological systems, and will increase the quality of ecological prediction models.

## Keywords

emdbook, feeding interaction, functional response fitting, generalized functional response, interaction strength, Michaelis-Menten, plant-herbivore, predator-prey, R, Rogers

Random Predator Equation, Holling's Disk Equation

## 1 Introduction

2 Understanding the interactions between organisms is crucial to understand patterns of  
3 stability and biodiversity of whole communities (McCann, 2000). Theory suggests that  
4 especially antagonistic interactions, such as feeding interactions, may have negative ef-  
5 fects on stability (May, 1972) and subsequently on biodiversity (e.g. Rall, Guill & Brose,  
6 2008). Moreover, a good knowledge on interactions may allow ecologists to create real-  
7 istic predictions of empirical communities ranging from microcosms to whole lakes (Boit  
8 *et al.*, 2012; Schneider, Scheu & Brose, 2012; Fussmann *et al.*, 2014). It is therefore of ut-  
9 most importance to have reliable methods for quantifying interaction strength amongst  
10 organisms, especially consumer-resource pairs such as predators and their prey.

## 11 The functional response models

12 The functional response (Solomon, 1949; Holling, 1959b) is one of the oldest and most  
13 commonly-used mathematical frameworks to describe and estimate the feeding interac-  
14 tion between a consumer and a resource (see Jeschke, Kopp & Tollrian (2002) for an  
15 overview). It describes the resource density-dependent feeding rate of a consumer on  
16 its resource (Holling, 1959b). Despite the plethora of possibilities, the most important  
17 functional response models used today are the type II and the type III functional re-  
18 sponses (Skalski & Gilliam, 2001; Jeschke, Kopp & Tollrian, 2004). The type II response  
19 is a hyperbolic satiating curve (Fig. 1, blue line) where the *per capita* feeding rate,  $F$ ,  
20 depends on the number of prey in the environment,  $N$ :

$$21 \quad F(N) = \frac{aN}{1 + ahN}. \quad (1)$$

22 Here,  $a$  is the instantaneous rate of discovery (Holling, 1959b), commonly known and  
23 subsequently used here as attack rate (note that in dependence of the scientific field  
24 you may also know it as capture rate (e.g. Kalinkat *et al.*, 2011), maximum clearance  
25 rate (e.g. Hansen, Bjornsen & Hansen, 1997), maximum per capita interaction strength  
26 (e.g. McCann, Hastings & Huxel, 1998), or others); and  $h$  is the handling time (Holling,  
27 1959a). See Jeschke, Kopp & Tollrian (2002, 2004) for a comprehensive introduction and  
28 discussion of the ecological meaning of these parameters. The attack rate,  $a$ , controls  
29 mainly the initial increase of feeding at low densities (Fig. 1a, gray dashed line) whereas  
30 the handling time,  $h$ , controls mainly the feeding at high densities where the feeding  
31 curve satiates (Fig. 1a, gray dotted line). The inverse of the handling time is often  
32 referred to by the maximum feeding rate,  $F_{\max}$ , but also by the maximum ingestion rate  
33 (e.g. Hansen, Bjornsen & Hansen, 1997), the handling rate (e.g. Englund *et al.*, 2011),  
34 or similar terms.

35 If the attack rate is not a constant but depends linearly on the resource density  
36 ( $a = bN$ ), the functional response becomes a sigmoid curve (e.g. Juliano, 2001, see  
37 Fig. 1b, red line) that can be described by:

$$38 \quad F(N) = \frac{bN^2}{1 + bhN^2} \quad (2)$$

39 where  $b$  is the attack coefficient (please see Juliano (2001) for more possibilities to model  
40 a type III functional response). As for the type II functional response, the attack rate,  
41  $a$ , controls the feeding rate at low prey densities (Fig. 1b, gray dashed line) and the  
42 handling time,  $h$ , controls the feeding rate at high prey densities (Fig. 1b, gray dotted  
43 line).

44 Real (1977, 1979) incorporated a possibility to gradually shift between the above  
45 mentioned fixed two types of the functional responses by using the enzyme kinetics  
46 model by Barcroft & Hill (1910). In Real's adaptation, the attack rate depends with an

47 power law on resource density ( $a = bN^q$ ), leading to functional response model that can  
48 be written as:

$$49 \quad F(N) = \frac{bN^{1+q}}{1 + bhN^{1+q}} \quad (3)$$

50 where  $q$  is a exponent influencing the shape of the functional response from a hyperbolic  
51 type II functional response ( $q = 0$ ) to a strict type III functional response ( $q = 1$ ) and  
52 also beyond these borders (Fig. 1c). Note that the original formulation of this functional  
53 response is  $F(N) = F_{\max}N^{1+q}/(N_{\text{half}}^{1+q} + N^{1+q})$ , were  $F_{\max}$  is the already above men-  
54 tioned maximum feeding rate ( $h = 1/F_{\max}$ ), and  $N_{\text{half}}$  is the half saturation density - the  
55 prey density at which the predator consumes half the amount of its maximum possible  
56 feeding rate ( $b = F_{\max}/N_{\text{half}}^{1+q}$ ; Fig. 1c, gray dotted-dashed line, please see the supplement  
57 (Sec. 1) for the equivalence of both parametrisations and [Real \(1977\)](#)). Moreover, the  
58 attack exponent,  $q$ , is often not used directly but in its transferable version, the Hill  
59 exponent,  $H$  ( $H = q + 1$ ). This kind of functional response is also often referred to as  
60 generalized functional response (e.g. [Kalinkat et al., 2013](#); [Barrios-O'Neill et al., 2016](#)).  
61 Using this elegant generalized functional response model revealed that increasing the  
62 attack exponent,  $q$ , just slightly introduces stability of simple consumer-resource pop-  
63 ulation models up to whole food webs, and thereby increases biodiversity ([Williams &](#)  
64 [Martinez, 2004](#); [Rall, Guill & Brose, 2008](#); [Uszko et al., 2015](#)). Inspired by these theoret-  
65 ical findings, researchers aimed to investigate which traits (e.g. body mass [Vucic-Pestic](#)  
66 [et al., 2010](#); [Kalinkat et al., 2013](#); [Barrios-O'Neill et al., 2016](#)) or environmental drivers  
67 (e.g. temperature ([Uszko et al., 2017](#)) or habitat structure ([Barrios-O'Neill et al., 2016](#);  
68 [Li et al., 2017](#))) change the attack exponent,  $q$ , from being zero (a destabilizing type II  
69 functional response) to higher values (a stabilizing generalized functional response).

## 70 The problem of prey depletion - and its possible solutions

71 The above mentioned functional response models (eqns. 1, 2, 3) describe how feeding  
72 rates depend on the number of prey in the environment (Fig. 1a-c). This means that the  
73 independent variable (displayed on the x-axis) must be a constant prey density. In exper-  
74 iments, however, it is hardly possible to keep the prey density constant over time. Most  
75 feeding trials with the aim of estimating a functional response are principally designed  
76 as follows: (1) a selected number of resource items is introduced into an experimental  
77 arena; (2) one or more consumers are added; (3) the experiment is run over a defined  
78 time range; (4) the remaining prey items are counted; (5) the number of prey remaining  
79 is subtracted from the initial number of prey, yielding the number of prey consumed  
80 over time. This has two implications: (1) the measured variable is not a rate, but the  
81 cumulative number of eaten prey items; and (2) the independent variable - the prey  
82 density - decreases over time. This phenomenon is commonly known as prey depletion  
83 (Rogers, 1972).

84 Describing the change of the population density over time is classically done by using  
85 ordinary differential equations (ODE); this approach is applied to model a wide range  
86 of ecological systems, from single populations up to whole multi-trophic communities  
87 (e.g. Verhulst, 1838; Rosenzweig & Mac Arthur, 1963; Rall, Guill & Brose, 2008; Delmas  
88 *et al.*, 2016). To correctly describe the prey depletion during the course of a functional  
89 response experiment, we can set up such an equation using the generalized Holling  
90 functional response (eqn. 3):

$$91 \quad \frac{dN}{dt} = -\frac{bN^{1+q}}{1 + bhN^{1+q}}P. \quad (4)$$

92 This equation describes the change of the prey density,  $dN$ , over time  $dt$ , which is pro-  
93 portional to the feeding rate, i.e. the generalized functional response (eqn. 3), multiplied  
94 the predator density,  $P$ . ODE models must be integrated over time and density to

95 yield the density at a desired point in time - here, the prey density at the end of the  
96 experiment,  $N_{end}$  (Fig. 1d-f, black solid lines). This integration process can be done  
97 analytically (i.e. using mathematical rules to derive a new function having time as an  
98 independent variable and density as a dependent variable); or, if the ODE is too complex  
99 to be solved analytically, it can be solved numerically using computer algorithms that  
100 approximate the real solution, with an accuracy that it is not distinguishable from that  
101 of an analytical solution (i.e. computer simulations). After integration the number of  
102 prey eaten over time,  $N_e$ , is calculated by simply subtracting the remaining prey density  
103 at the end of the simulation (as for experimental data),  $N_{end}$ , from the starting density,  
104  $N_0$  ( $N_e = N_0 - N_{end}$ ). As mentioned above, this generalized equation (4) becomes a  
105 type II functional response if the attack exponent is zero ( $q = 0$ , Fig. 1d), and a type  
106 III functional response if the attack exponent becomes unity ( $q = 1$ , Fig. 1e). In the  
107 following, we present established methods, which use the functional response to predict  
108 the number of eaten prey  $N_e$ .

109 The most simple approximation that could be made to describe the depletion of prey  
110 over the course of the experiment is to multiply the feeding rate,  $F$ , by the number of  
111 predators (more generally: consumers) and the time of the experiment,  $T$ , yielding the  
112 number of prey eaten at the end of the experiment,  $N_e$ :

$$113 \quad N_e = F(N_0)PT. \quad (5)$$

114 Here, the calculation of the feeding rate,  $F$ , can be replaced by any of the above mentioned  
115 functional response models (eqns. 1-3) under the constraint that the density,  $N$ , is  
116 replaced by the starting number of prey items,  $N_0$ . This method is a linearization of the  
117 non-linear process that is precisely described by the ODE (eqn. 4) and yields a linear  
118 decrease of alive prey in the experiment over time (Fig. 1, d-f, dotted lines).

119 Instead of linearizing the ODE (eqn. 4), Royama (1971) and Rogers (1972) presented

120 an analytical solution of the ODE incorporating a type II functional response ( $q =$   
121  $0$ ), commonly known as Rogers Random Predator Equation (RRPE, for the analytical  
122 derivation see supplement, Sec. 2):

$$123 \quad N_e = N_0 (1 - \exp(a(hN_e - TP))). \quad (6)$$

124 The number of prey consumed at the end of the experiment,  $N_e$ , depend here on the  
125 regular functional response parameters attack rate,  $a$ , and handling time,  $h$ , as well as  
126 the total time of the experiment,  $T$ , and the number of predators,  $P$ . This equation is  
127 commonly used to estimate the parameter values for a type II functional response when  
128 prey depletion occurs, and we will refer to it as Rogers Random Predator Equation II  
129 (RRPE-II).

130 With the unknown number eaten,  $N_e$ , appearing on both sides of this implicit equa-  
131 tion (RRPE-II), the problem arises that a simple non-linear fitting algorithm is not  
132 applicable. The most frequently used solution to this problem is to use an iterative  
133 Newton's method (Juliano & Williams, 1987; Juliano, 2001). However, the state-of-the-  
134 art solution is to use the LambertW function instead, which allows an explicit solution  
135 of the implicit RRPE-II (Bolker, 2008):

$$136 \quad N_e = N_0 - \frac{W(ahN_0 \exp(a(hN_0 - TP)))}{ah}, \quad (7)$$

137 see also Fig. 1d, dashed line. This approach has already been incorporated into a  
138 R-package for easy application (Pritchard, 2016; Pritchard *et al.*, 2017).

139 Juliano (2001) suggested that for fitting type III functional responses with prey  
140 depletion, it is possible to simply include the resource density dependency of the attack  
141 rate and replace the time-dependent prey number,  $N$ , by the constant value of the prey



142 number at the start of the experiment,  $N_0$  ( $a = bN \approx bN_0$ ), into the RRPE-II yielding:

$$143 \quad N_e = N_0 (1 - \exp(bN_0 (hN_e - TP))), \quad (8)$$

144 where the parameters are as described above: the number eaten,  $N_e$ , the attack constant,  
145  $b$ , the handling time,  $h$ , the total time,  $T$ , and the number of predators  $P$ . We will  
146 subsequently refer to this approach as Rogers Random Predator Equation III (RRPE-  
147 III).

148 Just as the RRPE-II, this implicit equation can be solved iteratively by Newton's  
149 method for  $N_e$  or by using the LambertW function:

$$150 \quad N_e = N_0 - \frac{W(bhN_0^2 \exp(bN_0 (hN_0 - TP)))}{bN_0h}. \quad (9)$$

151 Regardless of whether this equation is solved implicitly or explicitly, due to the approx-  
152 imation  $a = bN \approx bN_0$  the predicted number of eaten prey  $N_e$  is an approximation to  
153 the type III ODE and not an analytically correct solution (Fig. 1e, dashed line).

154 As an alternative to the type III functional response, [Hassell, Lawton & Beddington](#)  
155 (1977) presented a sigmoid-shaped feeding curve, taking prey depletion into account.  
156 Since the classical type III response is a special case of their wider class of curves (see  
157 supplement, Sec. 3), we derived a simplified version of their original equation describing  
158 how prey will be depleted over time following a type III functional response:

$$159 \quad N_e = \frac{bhN_0^2 + bPTN_0 + 1}{2bhN_0} - \sqrt{\left(\frac{bhN_0^2 + bPTN_0 + 1}{2bhN_0}\right)^2 - \frac{PTN_0}{h}}. \quad (10)$$

160 This equation represents an analytically correct solution of an ODE with a type III  
161 functional response (for the derivation see supplement, Sec. 3). This function is more  
162 complex as the RRPE-III, but it contains exactly the same parameters: the number  
163 eaten,  $N_e$ , the attack constant,  $b$ , the handling time,  $h$ , the total time,  $T$ , and the

164 number of predators  $P$ . But it has the advantage that the dependent variable,  $N_e$ , is  
165 only on the left side of the equation, allowing standard fitting algorithms to be used.

166 While the above models can be used to fit either type II or type III functional  
167 responses, the RRPE can also be used to fit the generalized functional response (eqn. 3)  
168 to data with prey depletion. The power law dependency of the attack rate,  $a = bN^q \approx$   
169  $bN_0^q$ , was incorporated into the RRPE-II (e.g. [Vucic-Pestic et al., 2010](#); [Kalinkat et al.,](#)  
170 [2013](#); [Barrios-O'Neill et al., 2016](#)), yielding:

$$171 \quad N_e = N_0 (1 - \exp(bN_0^q (hN_e - TP))), \quad (11)$$

172 where the parameters are as above: the number eaten,  $N_e$ , the attack constant,  $b$ , the  
173 attack exponent,  $q$ , the handling time,  $h$ , the total time,  $T$ , and the number of predators  
174  $P$ . We will subsequently refer to this approach as generalized Roger's Random Predator  
175 Equation (RRPE-gen).

176 Again, this implicit problem can be solved iteratively by Newton's method or explic-  
177 itly by using the LambertW function

$$178 \quad N_e = N_0 - \frac{W\left(bhN_0^{1+q} \exp(bN_0^q (hN_0 - TP))\right)}{bN_0^q h}. \quad (12)$$

179 Analogous to the RRPE-III, these solutions of the RRPE-gen are an approximation to  
180 the ODE with a generalized FR (Fig. 1f, dashed line).

181 As an alternative, [Uszko et al. \(2015, 2017\)](#) generalized a method developed by [Frost](#)  
182 [\(1972\)](#) in which (1) an approximation of an average resource density,  $\bar{N}$ , is calculated  
183 ( $N_0 \geq \bar{N} \geq N_{end}$ ) - taking prey depletion into account - and (2) the functional response  
184 parameters are estimated using (for further information see supplement, Sec. 4):

$$185 \quad N_e = \frac{b\bar{N}^{1+q}}{1 + bh\bar{N}^{1+q}} PT. \quad (13)$$

## 186 Possible drawbacks of the different methods

187 Using the most simple approach where the feeding rate is simply multiplied by preda-  
188 tor density and time of the experiment (eqn. 5), prey depletion during the time of the  
189 experiment is completely neglected. Because this feeding rate is higher than the actual  
190 feeding rate that is based on a reduced number of prey later in the experiment ( $N_0 > N$   
191 causes  $F(N_0) > F(N)$ , cf. Fig. 1d-f, compare the dotted lines to the solid line created  
192 by the ODE representing the natural depletion of prey), attack rates,  $a$ , will be underes-  
193 timated, regardless whether a type II, a type III or a generalized functional response is  
194 used. As the feeding rate as well as the realized feeding over the course of an experiment  
195 (i.e. the total amount of consumed prey) approaches a satiation level, the estimate of the  
196 maximum feeding rate  $F_{\max}$  (or the handling time  $h = \frac{1}{F_{\max}}$ ) should only be marginally  
197 affected.

198 The RRPE-II is the exact analytical solution of an ODE that describes the depletion  
199 of prey over time with a type II functional response. The resulting depletion of prey over  
200 time is consequently identical if using the RRPE-II or the numerical simulation of an  
201 ODE (Fig. 1d, dashed vs. solid line). This method therefore delivers reliable parameter  
202 estimates if the data can be described by a type II functional response.

203 As the RRPE-II is the exact solution for an ODE with a type II functional response,  
204 there can be negative consequences when it is used to fit non-type II functional responses,  
205 such as the type III and the generalized functional response. The attack rate,  $a = bN^q$ ,  
206 in this case is itself prey number-dependent. Approximating  $N$  by the larger  $N_0$  creates  
207 a larger attack rate and therefore a stronger decrease of prey than given in a simulated  
208 ODE (Fig. 1e-f, dashed vs. solid line). A stronger decrease of prey should lead to an  
209 underestimation of the attack rates (i.e. attack coefficient  $b$ ), whereas the handling time  
210 should be estimated correctly as both methods produce a similar linear decrease of prey  
211 density at high prey densities. An increasing attack exponent,  $q$ , decreases the number  
212 of prey consumed at low prey numbers, as prey depletion is predicted to be too high by

213 using the Rogers Random Predator equation with a type III or generalized functional  
214 response. We assume that the attack exponent,  $q$ , would be overestimated to counteract  
215 this effect.

216 We were not able to create strong expectations for the method by Frost (1972) and  
217 Uszko *et al.* (2015) since this 2-step process can not be visualized as descriptively as the  
218 previous methods. But as the original method is based on a type I functional response,  
219 we assume also deviations from the correct solution in all cases.

220 Using our new analytical solution for a type III functional response (eqn. 10) will  
221 result in a correct estimation of functional response parameters. But more importantly,  
222 our method to fit numerical simulations of ODEs allows to include different functional  
223 response models and will always return correct parameter estimations.

## 224 **The problem of non-consumer mediated prey growth and mortality**

225 Another problem that often arises in experiments is that background mortality or growth  
226 of the prey could occur. For example, the assumption of constant prey numbers of the  
227 experiment could be violated not only because of prey removal by predators, but also  
228 because of prey mortality, or population growth, what is often the case if using microbial  
229 or algal prey (e.g. Fussmann *et al.*, 2017; Uszko *et al.*, 2017). Standard ways to deal  
230 with this are to exclude any data that is biased with mortality or growth, leading to a  
231 substantial loss of data, or to ignore the problem if it is not too pronounced, accepting  
232 that the resulting bias in parameters is likely to be small (e.g. Vucic-Pestic *et al.*, 2010;  
233 Uszko *et al.*, 2017). However, it is also possible to minimize bias without excluding  
234 data, by fitting the parameters using simulations of ODEs (see e.g. Rall & Latz, 2016).  
235 Additional mortality can be accounted for by adding a mortality rate,  $m$ , to the ODE  
236 (eqn. 4). This a standard way to model mortality in population and food web modeling  
237 (e.g. Fussmann *et al.*, 2014; Kalinkat *et al.*, 2013; Williams & Martinez, 2004; Rosenzweig

238 & Mac Arthur, 1963; Rall, Guill & Brose, 2008)

$$239 \quad \frac{dN}{dt} = -F(N)P - mN \quad (14)$$

240 for arbitrary functional response models  $F(N)$ .

241 The growth of prey is often described by simple phenomenological growth models  
242 such as the logistic growth (Verhulst, 1838) or by Gompertz growth model (Gompertz,  
243 1825; Paine *et al.*, 2012). The logistic growth can be added to the ODE model by simply  
244 adding the growth term as the mortality above. In the case of the logistic growth the  
245 ODE becomes:

$$246 \quad \frac{dN}{dt} = -F(N)P + rN \left(1 - \frac{N}{K}\right), \quad (15)$$

247 where  $K$  is the carrying capacity, the number of prey a system can sustain, and  $r$ ,  
248 the intrinsic growth rate that controls the prey growth at low prey densities but also  
249 determines the mortality of prey if the prey density is above the carrying capacity. The  
250 rest of the parameters are as above in the case of a simple functional response ODE.

251 In the cases of both prey mortality and combined prey growth and mortality, we  
252 expect biased functional response parameters if the estimation is not corrected for these  
253 additional effects. Assuming experiments where prey mortality occurs (eqn. 14, e.g.  
254 using insects, spiders or crustaceans) this could lead to an overestimation of the attack  
255 rate or the attack coefficient, an underestimation of the attack exponent (the lower  
256 the exponent, the higher the feeding at low prey numbers), and an underestimation of  
257 the handling time (the lower the handling time, the higher the maximum consumed  
258 number of prey) to counteract the additional effect of mortality. In the case where the  
259 prey is growing and dying according to the above mentioned growth model (eqn. 15),  
260 there would likely be an underestimation of attack rate (which describes feeding at  
261 low prey numbers) or attack coefficient and potentially an overestimation of the attack  
262 exponent to counteract the additional growth of prey at low numbers. At high prey

263 numbers exceeding the carrying capacity, background prey mortality occurs and there  
264 would likely be an underestimation of handling times (which describes feeding at high  
265 prey numbers) to counteract this effect. Using the extended ODE models and fitting  
266 them numerically to the data should overcome the problem. We further expect that  
267 using additional control data (no predators present) will improve the accuracy of the  
268 parameter estimation, because effects of natural growth (or death) and predation can  
269 be disentangled.

270 Here, we present a new framework of how to fit functional response models to data.  
271 We combine numerical simulations of ODE models with an iterative maximum likelihood  
272 estimator using R (Rall & Latz (2016), but see DeLong, Hanley & Vasseur (2014) for  
273 alternatives) This allows us to fit any functional response model to data more flexible  
274 and precisely than traditional methods. Our approach produces similar results if using  
275 the special case of a strict type II functional response as Juliano's and Bolker's method  
276 that use Rogers Random Predator Equation. Also, we expect that in the special case  
277 of a "strict" type III functional response, the parameter estimation by the analytical  
278 solution and numerical simulation methods should deliver similar results. In the case  
279 of the generalized functional response, which is widely used in current ecological stud-  
280 ies (Vucic-Pestic *et al.*, 2010; Barrios-O'Neill *et al.*, 2016; Kalinkat *et al.*, 2013; Uszko  
281 *et al.*, 2015; Pawar, Dell & Savage, 2012; Li *et al.*, 2017) we expect that our method  
282 outperforms traditional methods dramatically. Moreover, fitting numerical simulations  
283 of ODE models also allows to cope with side effects like prey growth and mortality that  
284 otherwise may bias or even prevent the estimation of the functional response parameters.

## 285 **Materials and Methods**

286 We simulated 1000 datasets based on ODE models (eqn. 4) for the type II, the type  
287 III and the generalized functional response each. For numerical simulation, we used

288 the deSolve package (Soetaert, Petzoldt & Setzer, 2010). We drew attack coefficients,  
289 handling times and, in the generalized case, attack coefficients from random distributions  
290 (see supplement, Sec. 5). Each dataset contained in total 960 observations of eaten prey  
291  $N_e$  from initial prey numbers  $N_0$  ranging from 1 to 48 individuals. We further simulated  
292 1000 datasets for the generalized functional response including prey mortality (eqn. 14)  
293 and also 1000 datasets for the generalized functional response including prey growth  
294 (and natural prey death, if the prey number exceeds the carrying capacity, eqn. 15).  
295 Again, see the supplement (Sec. 5) for details on data simulation.

296 We used an iterative maximum likelihood method (bbmle package, function `mle2()`,  
297 Bolker (2008); Bolker & R Development Core Team (2016)) to fit the models to sim-  
298 ulated data and also experimental datasets (see below). Unless stated otherwise, we  
299 assumed binomially distributed numbers of eaten prey. This means that for each ob-  
300 servation  $(N_0^{(i)}, N_e^{(i)})$  ( $i = 1, \dots, n$ ), a prediction for the number of eaten prey  $\hat{N}_e^{(i)}$  was  
301 calculated based on the respective model and its parameters. The observation  $N_e^{(i)}$  was  
302 then modeled as being binomially distributed with  $N_0^{(i)}$  trials and a success probability  
303 of  $\frac{\hat{N}_e^{(i)}}{N_0^{(i)}}$  to compute the likelihood. See the manual (Sec. 6) for more information on the  
304 construction of likelihood functions and the fitting routines.

305 The growth model requires a different statistical approach. Through growth, the  
306 number of prey present at the end of the experiment  $N_{end}$  can exceed the number of  
307 initial prey  $N_0$ . Negative numbers of eaten or dead prey  $N_e = N_0 - N_{end}$  occur and  
308 make the binomial distribution unsuitable for this model. Instead, we use  $N_{end}$ , which  
309 is always non-negative. For each observation  $(N_0^{(i)}, N_{end}^{(i)})$  ( $i = 1, \dots, n$ ), the prediction  
310 of the number of prey present  $\hat{N}_{end}^{(i)}$  at the end of the experiment was calculated by  
311 numerical simulation of the ODE. The observation  $N_{end}^{(i)}$  was modeled as being lognor-  
312 mally distributed with location parameter  $\log(\hat{N}_{end}^{(i)})$  and scale parameter  $\sigma$ . This scale  
313 parameter is automatically estimated in the iterative maximum likelihood routine, too  
314 (Crawley, 2012, Chap. 7.3.3). The lognormal distribution takes into account that residu-

315 als generally have a larger variance for large prey abundances. See the manual (Sec. 6.6)  
316 for a detailed description of this likelihood function.

317 For the data without prey growth or mortality, we fitted all corresponding feeding  
318 models and compared the original simulation parameters to the estimates. For simulated  
319 data including background prey mortality, we tested the performance of fitting the ODE  
320 model neglecting mortality (eqn. 4) and the ODE model including mortality (eqn. 14).  
321 We also used the mortality model to fit simulated data which used half of the 960  
322 observations as control data, i.e. no predators are present and prey death occurs by  
323 natural mortality only. For data including prey growth and mortality, we also tested the  
324 performance of fitting the ODE model neglecting growth (eqn. 4) and the ODE model  
325 including growth (eqn. 15). We also used the growth model to fit simulated data which  
326 used half of the 960 observations as control data, i.e. no death by predation occurs. We  
327 evaluated the performance all models by comparing the  $\log_{10}$ -ratios of estimated and  
328 true parameters (Berlow *et al.*, 1999; Rall & Latz, 2016).

329 We fitted our new ODE-based models (eqn. 4) to six experimental datasets from  
330 the literature and compared the results to the studies' original methods, which are as  
331 follows. Sentis, Morisson & Boukal (2015) used the RRPE-III to fit dataset D1, while the  
332 RRPE-gen was fitted to dataset D2 in Vucic-Pestic *et al.* (2010). Uszko *et al.* (2015) used  
333 Frost's method with a generalized FR for dataset D3. Note that this dataset consists of  
334 prey densities instead of prey individuals, which requires a lognormal distribution (for  
335 details see the manual, Sec. 6.5). Barrios-O'Neill *et al.* (2015) fitted the RRPE-gen to  
336 experimental data featuring a low (D4), medium (D5) or high (D6) spatial refuge for  
337 prey, which result in lower, medium and higher attack exponents.

338 The additional dataset D7 (L. Archer, 2017, personal communication) includes nat-  
339 ural prey mortality and it also contains control data without any predators present. As  
340 with simulated data (see above), we compared the performance of the generalized ODE  
341 neglecting mortality (eqn. 4) to the models including mortality (eqn. 14) without and



342 with using control data.

343 In a last example, we use dataset D8 (Fussmann, 2017) which features natural prey  
344 growth and death. The example also includes control data without predators present.  
345 Similar to the simulated data, we fit the generalized ODE neglecting growth (eqn. 4)  
346 and the model including a growth term (eqn. 15) with and without using control data.

## 347 Results

### 348 Feeding models

349 The results of fitting type II, type III and generalized functional response feeding mod-  
350 els to simulated data are depicted in Fig. 2. For the data simulated with a **type II**  
351 response, our new ODE model (eqn. 4), and also the old models by Bolker (eqn. 7) and  
352 Juliano (eqn. 6) represent analytically correct feeding models. They provide an unbiased  
353 estimation of attack rates and handling times, i.e. the mean error over 1000 fits equals  
354 zero. Fitting the functional response term directly to the data (eqn. 5) leads to a heavily  
355 biased estimation, because the method does not correct for depleted prey. As expected,  
356 attack rates are systematically underestimated. Handling times are underestimated, too.  
357 When using Frost's method for correction (eqn. 13), these errors are reduced, but the  
358 estimates are still biased.

359 In the case of a **type III** response, our new ODE model (eqn. 4) and also the model  
360 based on Hassell's method (eqn. 10) provide analytically correct solutions for the number  
361 of eaten prey. Both return unbiased estimates for attack rates and handling times. For  
362 the method of Bolker (eqn. 9) and Juliano (eqn. 8), the approximation of  $a = bN$  by  $bN_0$   
363 causes a severe underestimation of attack coefficients. Also, the handling time estimates  
364 are biased. Again, a direct fit of the functional response to the data (eqn. 5) leads to  
365 a heavy underestimation of attack coefficients as well as biased handling times. While  
366 Frost's correction for depleted prey (eqn. 13) features an overall unbiased estimation of

367 attack coefficients, the spread of errors is comparably large and handling times estimates  
368 are still biased.

369 For a **generalized** model with flexible attack exponent, our new ODE model (eqn. 4)  
370 is the only correct feeding model for our simulated data. Therefore, it is the only  
371 method which provides a jointly unbiased estimation of attack coefficients, handling  
372 times and attack exponents. As above, the methods of Bolker (eqn. 12) and Juliano  
373 (eqn. 11) underestimate attack coefficients due to the approximation of  $a = bN^q$  by  $bN_0^q$ .  
374 The deviation from all three true parameters is even stronger when directly fitting the  
375 functional response (eqn. 5) and Frost's correction for prey depletion (eqn. 13) produces  
376 overall biased estimates.

### 377 **Prey mortality and prey growth**

378 We compared three new ODE approaches of dealing with natural prey mortality (Fig. 3).  
379 When fitting a mortality-free model (eqn. 4) to data which includes natural mortality,  
380 attack coefficients and maximum feeding  $F_{\max} = \frac{1}{h}$  are systematically overestimated  
381 as compensation for the missing mortality term. The estimates of attack exponents  
382 are also biased as expected. Using a model including mortality (eqn. 14) leads to an  
383 unbiased prediction of all parameters. However, the error ranges for handling time  $h$  and  
384 mortality coefficient  $m$  are still relatively large, because effects of predation and natural  
385 mortality are correlated. But, if control data is used, the accuracy of predicted  $h$  and  $m$   
386 is considerably improved, because predation and mortality effects can be disentangled.

387 Similarly, we compared three new ODE approaches of fitting data including natural  
388 prey growth and death (Fig. 4). Neglecting growth in the model (eqn. 4), handling  
389 times  $h$  are, unexpectedly, unbiased, but feature a comparatively large error range.  
390 Attack exponents  $q$  are, also unexpectedly, slightly underestimated. In combination with  
391 the severely underestimated attack coefficients  $b$  we assume that attack rates  $a = bN^q$   
392 are generally underestimated as expected because they have to correct for the missing

393 growth term in the model. When including this term (eqn. 15), all functional response  
394 parameters and also the growth term's parameters, growth rate  $r$  and carrying capacity  
395  $K$ , are unbiased. By fitting this growth model to data, which uses half of the number  
396 of observations as control data, the accuracy of the unbiased estimates is drastically  
397 improved.

## 398 **Experimental data**

399 When fitting our new ODE model (eqn. 4) to experimental datasets, the predicted  
400 curves of eaten prey were almost identical to the studies' original methods (Fig. 5).  
401 Both methods performed similarly in fitting the observed data. However, our focus lies  
402 on the parameters which produce these curves and on their discrepancies. Therefore, we  
403 do not provide model comparisons (e.g. AIC scores), but report these differences in the  
404 estimates (Table 1) and contrast them to our results found in simulated data.

405 The handling times  $h$  estimates are generally similar when comparing by the original  
406 and our new ODE method for all datasets. When dealing with a type III (dataset D1)  
407 or a generalized response (datasets D2, D3) with similarly fitted attack exponents  $q$ ,  
408 the attack coefficients  $b$  are underestimated by the RRPE and also by Frost's method,  
409 compared to the new ODE approach. This confirms our findings of the comparisons  
410 using simulated data and our assumptions about biased attack rates of the RRPE: By  
411 ignoring prey depletion and approximating  $a = bN$  by  $bN_0$  (or  $a = bN^q$  by  $bN_0^q$  in  
412 the generalized case),  $N_0 > N$  causes an underestimation of attack coefficients  $b$ . In  
413 datasets D4–D6, we observed both under- and overestimation of attack coefficients  $b$  by  
414 the RRPE-gen. Also, the attack exponents are underestimated. We emphasize that for  
415 generalized functional responses, attack coefficients and attack exponents in  $a = bN^q$   
416 can only be interpreted jointly.

417 For the dataset D7 featuring natural prey mortality, we compared our generalized  
418 ODE model neglecting mortality (eqn. 4) to the ODE model including a mortality rate

419 (eqn. 14) with and without using control data (Fig. 6, Table 2, see also the manual,  
420 Sec. 3). Again, the different models produce similar curves when fitting data with  
421 predators present, while the parameter estimates are quite different. As expected, the  
422 maximum feeding rate  $F_{\max} = \frac{1}{h}$  compensates for natural prey death and is therefore  
423 highly overestimated when fitting a model without mortality term, i.e. the handling time  
424  $h$  is underestimated. When fitting the mortality model without using control data, a neg-  
425 ative mortality rate  $m$  is predicted, which actually means natural prey growth instead of  
426 prey mortality. But the estimate is not significant and features a high standard deviation,  
427 because effects of feeding and natural prey mortality (or growth) cannot be disentangled.  
428 Using the same mortality model including additional control data, a positive mortality  
429 rate  $m$  is correctly estimated and we observe a reduced uncertainty (smaller standard  
430 error) in the estimates for  $m$ . Control data enables the precise separation of feeding and  
431 natural death.

432 Dataset D8 includes natural prey growth and death and we compared our generalized  
433 ODE model ignoring background growth (eqn. 4) to the ODE model including a logistic  
434 growth term (eqn. 15) with and without using control data (Fig. 6, Table 3). Note that  
435 the parameters  $r$ ,  $K$ ,  $b$  and  $h$  are estimated on their log scale. If parameters differ by  
436 several orders of magnitude, this can improve the efficiency of the iterative maximum  
437 likelihood algorithm; see the manual (Secs. 5, 6.6) for details. Surprisingly, the parameter  
438 estimates for fitting the model neglecting growth and the full model including control  
439 data are similar, although their predictions do differ for large initial prey densities.  
440 Fitting the growth model without control data produces heavily-biased estimates. A  
441 large carrying capacity  $K$  and a large growth rate  $r$  lead to a decrease in predicted dead  
442 prey for large initial prey densities. Using control data, the uncertainty in all parameters  
443 is significantly reduced (smaller standard errors), because effects of feeding and natural  
444 growth ( $N < K$ ) (or natural loss,  $N > K$ ) can be separated precisely.

## 445 Discussion

446 We compared different popular methods and our new ODE-based approach for fitting  
447 functional response models to feeding experiments, using both simulated and experimen-  
448 tal datasets. We estimated parameters of type II, type III and the generalized functional  
449 response models via maximum likelihood. Additionally, we investigated models includ-  
450 ing background prey mortality or growth. Based on our results, we give the following  
451 recommendations:

452 While our new ODE-approach generally yields unbiased estimates by correcting for  
453 prey depletion, direct methods (without requiring numerical simulation) perform equally  
454 when using the type II ( $q = 0$ ) or the strict type III model ( $q = 1$ ). Bolker's explicit  
455 solution (Bolker, 2008) of the RRPE-II (eqn. 7) can be used for fitting type II responses.  
456 For type III responses, we propose using our explicit version (eqn. 10) of Hassell's ap-  
457 proach (Hassell, Lawton & Beddington, 1977) as the fit of an analytical solution is way  
458 faster than fitting simulations to data (see supplement, Sec. 6).

459 However, when including the attack exponent  $q$  as a free parameter, only numeri-  
460 cal simulation of ODEs guarantees unbiased estimates. This is of utmost importance  
461 for ecological research as even a small shift of the attack exponent,  $q$ , from 0 (strict  
462 type II functional response) to approximately 0.2 (e.g. Williams & Martinez, 2004) in-  
463 creases stability of trophic ecological networks (i.e. food webs) dramatically and thereby  
464 also increases species coexistence and biodiversity (Rall, Guill & Brose, 2008). Studies  
465 investigating empirically the attack exponent increased in number over the last years  
466 (Vucic-Pestic *et al.*, 2010; Kalinkat *et al.*, 2013; Barrios-O'Neill *et al.*, 2015, 2016; Uszko  
467 *et al.*, 2015, 2017). Such publications will benefit from our new approach as it allows ecol-  
468 ogists to correctly estimate the functional response parameters that are needed to gain  
469 the understanding of stability and diversity patterns in complex ecological communities.

470 Besides these obvious and needed advancements, our ODE-based method is highly

471 flexible. It is not limited to the three functional response models described here - any  
472 type of functional response describing the prey-dependent feeding rate can be integrated.  
473 Using simulations of ODEs that are fitted to data further allows ecological modelers to  
474 include additional terms like prey mortality or growth, as presented in this study. We  
475 showed, however, that control data is required to disentangle effects of natural mortality  
476 or growth and predation.

477 Additionally to this main article, we provided a in-depth description of our method  
478 as a manual, R-source files, and data. This will allow researchers that want to apply  
479 our method to their own functional response data an easy entry into our methodology  
480 and the possibility to practice using the method with worked examples before using  
481 it to analyze their own data. Moreover, the source files attached in the supplement  
482 can be adapted to include other functional response models than those used here (see  
483 [Juliano \(2001\)](#) and [Jeschke, Kopp & Tollrian \(2002\)](#) for a variety of possible models).  
484 In addition, specific mortality and growth models can be incorporated, e.g. using the  
485 Gompertz growth model instead of the logistic growth model - a growth model often  
486 used in microbiology ([Paine \*et al.\*, 2012](#); [Fussmann \*et al.\*, 2017](#)).

487 We also show in the supplement (Sec. 7) how data availability changes the outcome  
488 of the parameter fitting. Generally, we found that even sparse data is sufficient to  
489 estimate the parameters correctly, but especially the estimation of handling time is highly  
490 uncertain if higher densities of prey are not measured in an experiment (Supp. Fig. 2).

491 In conclusion, we found that our new method to estimate functional response param-  
492 eters from a feeding experiment with prey depletion - the decrease of prey number over  
493 time without replacement - is superior to traditional approaches. To our knowledge,  
494 it is the only method that allows for precise parameter estimation of the generalized  
495 functional response, which is currently one of the most frequently-used descriptions of  
496 feeding interactions in ecology. It moreover allows easy adaptation and inclusion of un-  
497 wanted effects like prey growth and mortality, what was impossible with traditional ap-

498 proaches. We believe that our approach to estimate functional response parameters will  
499 enable researchers in the future to estimate precise parameter values, using mortality-  
500 and growth-biased data, and thereby deepen understanding of how interactions drive  
501 stability and biodiversity of complex ecological communities.

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## 513 **Data accessibility**

514 We attached the empirical data used in that study as supplemental information together  
515 with an in-depth description of the fitting methods in the manual, including R-source  
516 files allowing to reproduce our method.

517

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Table 1: Functional response parameters for experimental data (D1–D6).  $n$  = number of observations,  $b$  = attack coefficient,  $h$  = handling time,  $q$  = attack exponent. Standard errors are shown in parentheses.  $P$ -values:  $\cdot P < 0.1$ ,  $* P < 0.05$ ,  $** P < 0.01$ ,  $*** P < 0.001$ .

dataset	method	$n$	$b$	$h$	$q$
D1 (Sentis, Morisson & Boukal, 2015)	new ODE III	70	0.083 *** ( $\pm 0.009$ )	0.008 *** ( $\pm 0.000$ )	
	old RRPE III	70	0.069 *** ( $\pm 0.007$ )	0.008 *** ( $\pm 0.000$ )	
D2 (Vucic-Pestic <i>et al.</i> , 2010)	new ODE gen	54	0.112 * ( $\pm 0.056$ )	0.040 *** ( $\pm 0.004$ )	0.597 ** ( $\pm 0.197$ )
	old RRPE gen	54	0.108 * ( $\pm 0.052$ )	0.039 *** ( $\pm 0.003$ )	0.565 ** ( $\pm 0.176$ )
D3 (Uszko <i>et al.</i> , 2015)	new ODE gen	30	0.295 ** ( $\pm 0.095$ )	10.807 *** ( $\pm 1.832$ )	0.247 * ( $\pm 0.102$ )
	old Frost gen	30	0.274 *** ( $\pm 0.082$ )	10.426 *** ( $\pm 1.897$ )	0.223 * ( $\pm 0.095$ )
D4 (Barrios-O'Neill <i>et al.</i> , 2015)	new ODE gen	44	2.688 *** ( $\pm 0.350$ )	0.050 ( $\pm 0.032$ )	-0.312 ( $\pm 0.236$ )
	old RRPE gen	44	4.060 $\cdot$ ( $\pm 2.251$ )	0.051 ( $\pm 0.046$ )	-0.410 ( $\pm 0.467$ )
D5 (Barrios-O'Neill <i>et al.</i> , 2015)	new ODE gen	27	0.325 ( $\pm 0.230$ )	0.066 * ( $\pm 0.027$ )	0.425 ( $\pm 0.461$ )
	old RRPE gen	27	0.306 ( $\pm 0.227$ )	0.064 * ( $\pm 0.026$ )	0.392 ( $\pm 0.415$ )
D6 (Barrios-O'Neill <i>et al.</i> , 2015)	new ODE gen	44	0.019 ( $\pm 0.027$ )	0.172 *** ( $\pm 0.021$ )	2.298 * ( $\pm 0.961$ )
	old RRPE gen	44	0.021 ( $\pm 0.024$ )	0.169 *** ( $\pm 0.021$ )	1.937 ** ( $\pm 0.669$ )

Table 2: Functional response parameters for experimental data (D7, L. Archer, 2017, personal communication).  $n$  = number of observations,  $b$  = attack coefficient,  $h$  = handling time,  $q$  = attack exponent,  $m$  = mortality rate. Standard errors are shown in parentheses.  $P$ -values:  $\cdot P < 0.1$ ,  $* P < 0.05$ ,  $** P < 0.01$ ,  $*** P < 0.001$ .

	method	$n$	$b$	$h$	$q$	$m$
D7	ODE	13	2.415 *** ( $\pm 0.699$ )	0.018 ( $\pm 0.014$ )	-0.060 ( $\pm 0.272$ )	
	ODE + mort	13	3.329 * ( $\pm 1.643$ )	0.005 ( $\pm 0.008$ )	-0.062 ( $\pm 0.173$ )	-0.995 ( $\pm 1.648$ )
	ODE + mort + control	31	2.207 ** ( $\pm 0.748$ )	0.031 ( $\pm 0.022$ )	-0.049 ( $\pm 0.354$ )	0.279 *** ( $\pm 0.043$ )

Table 3: Functional response parameters for experimental data (D8, Fussmann, 2017).  $n$  = number of observations,  $b$  = attack coefficient,  $h$  = handling time,  $q$  = attack exponent,  $r$  = growth rate,  $K$  = carrying capacity. Standard errors are shown in parentheses.  $P$ -values:  $\cdot P < 0.1$ ,  $* P < 0.05$ ,  $** P < 0.01$ ,  $*** P < 0.001$ .

	method	$n$	$\log(b)$	$\log(h)$	$q$	$\log(r)$	$\log(K)$
D8	ODE	53	-19.356 *** ( $\pm 2.954$ )	-1.250 *** ( $\pm 0.146$ )	0.751 ** ( $\pm 0.267$ )		
	ODE + growth	53	-16.387 *** ( $\pm 3.217$ )	-1.768 *** ( $\pm 0.535$ )	0.499 $\cdot$ ( $\pm 0.283$ )	-7.238 *** ( $\pm 0.485$ )	16.934 NA
	ODE + growth + control	179	-19.401 *** ( $\pm 2.181$ )	-1.257 *** ( $\pm 0.111$ )	0.763 *** ( $\pm 0.198$ )	-8.580 *** ( $\pm 0.376$ )	13.115 *** ( $\pm 0.346$ )



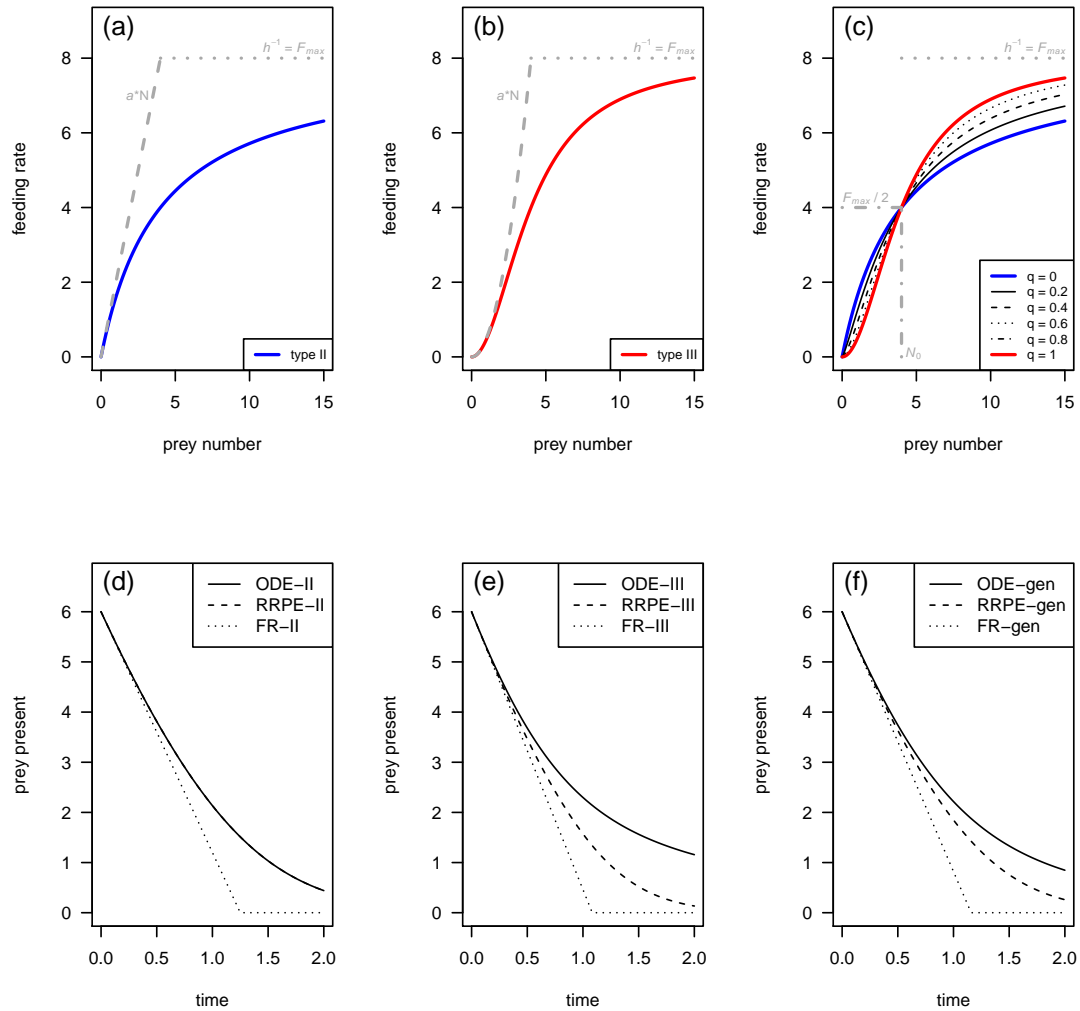


Figure 1: Top: Feeding rate  $F(N)$  for three different functional response models, Holling's type II (a), Holling's type III (b), and the generalized response (c). Bottom: Predicted number of prey present  $N(t) = N_0 - N_e(t)$  over time  $t$  for the type II (d), type III (e) and a generalized ( $q = 0.5$ ) functional response (f), while ignoring prey depletion (dotted), using the RRPE (dashed) and our new numerical solution of the ODE (solid).

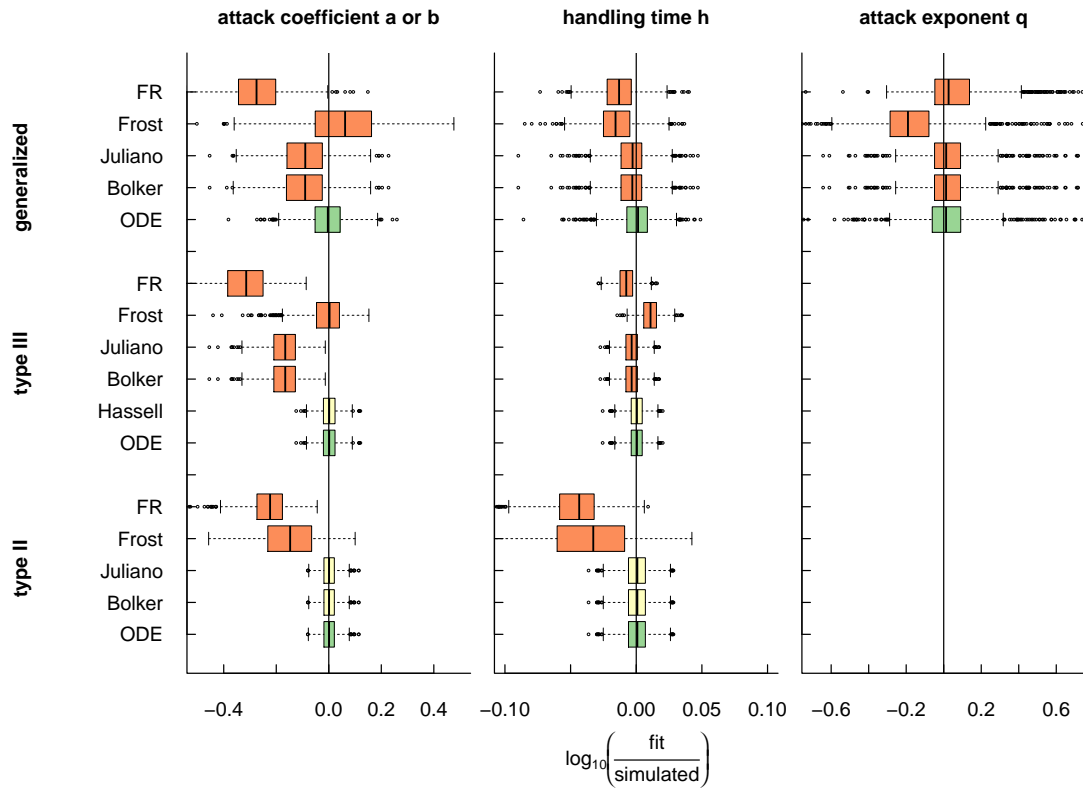


Figure 2: Evaluation of feeding models for the type II, type III and generalized functional response. The boxplots show the error distributions of fitted parameters  $\log_{10}\left(\frac{\text{fit}}{\text{simulated}}\right)$  in 1000 simulated datasets. Green and yellow indicate analytically correct feeding models, orange indicates approximations.

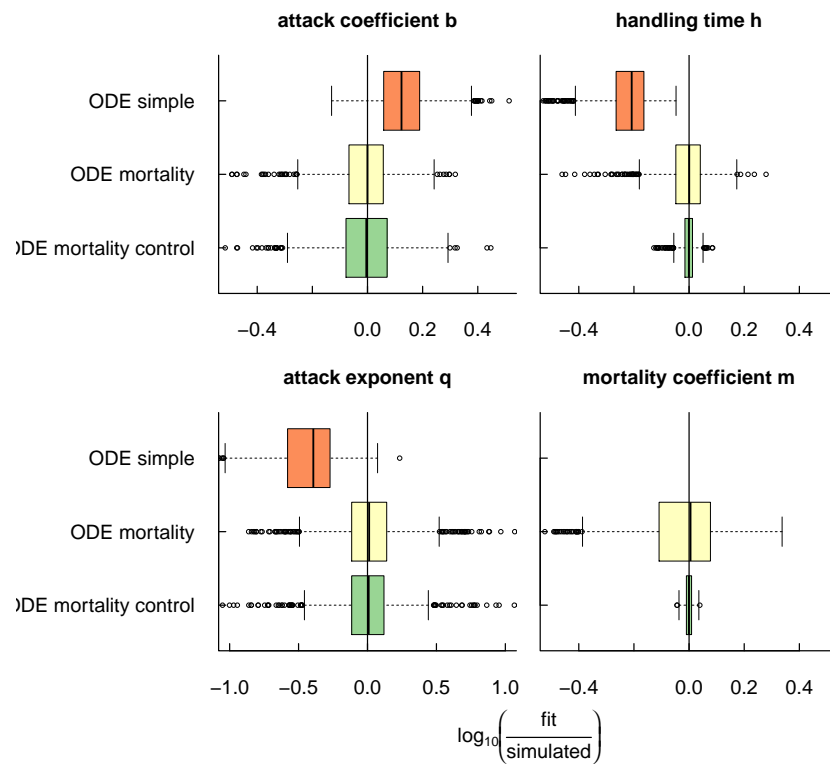


Figure 3: Evaluation of the ODE model with an additional prey mortality term. The boxplots show the error distributions of fitted parameters  $\log_{10}\left(\frac{\text{fit}}{\text{simulated}}\right)$  in 1000 simulated datasets.

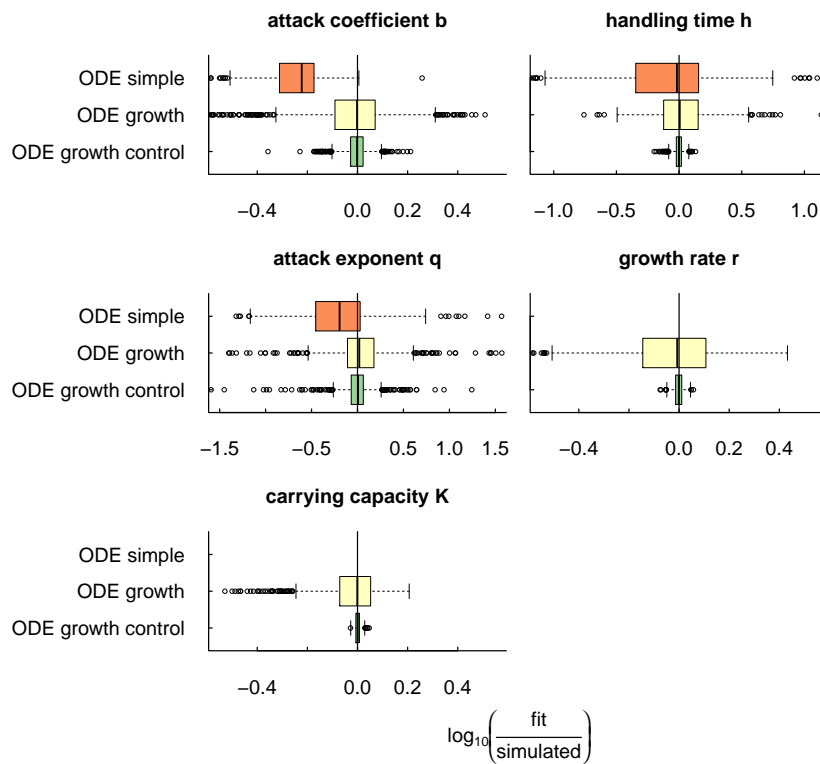


Figure 4: Evaluation of the ODE model with an additional prey growth and mortality term. The boxplots show the error distributions of fitted parameters  $\log_{10}\left(\frac{\text{fit}}{\text{simulated}}\right)$  in 1000 simulated datasets.

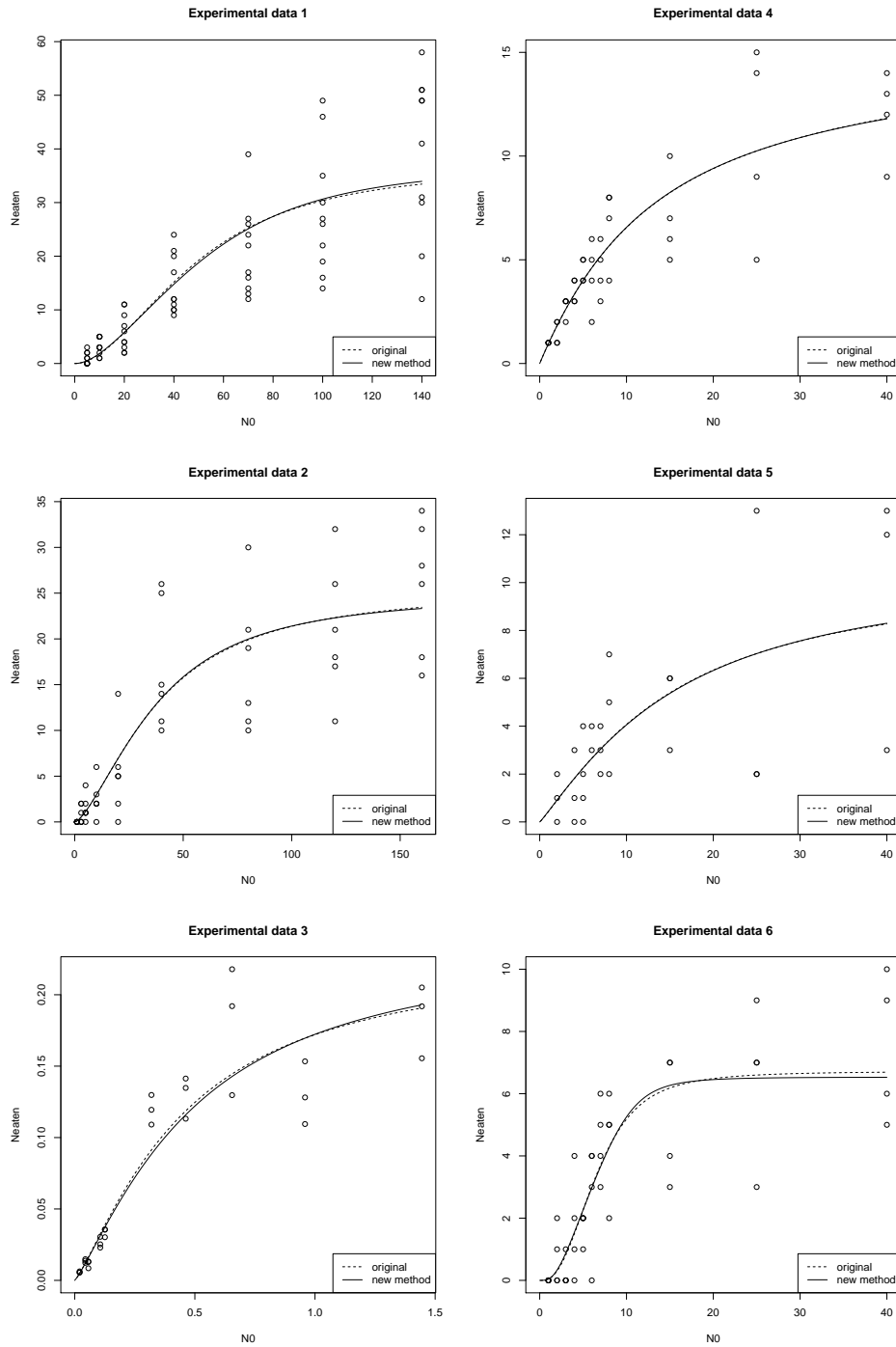


Figure 5: Fits of the original and our new ODE-based parameter estimation method to six experimental datasets D1–D6.

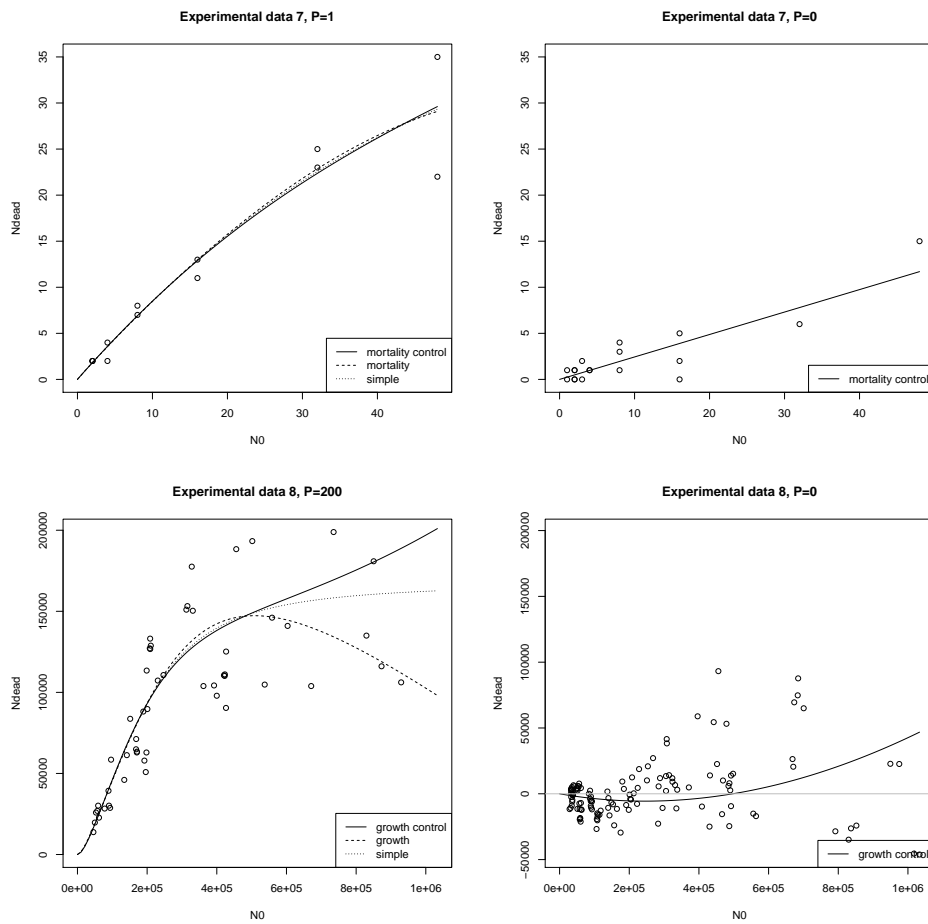


Figure 6: Fits of our new ODE-based models to experimental datasets D7 including background prey mortality (top) and D8 including background prey growth and mortality (bottom); feeding experiments (left) and control experiments (right).