

Alternative prey impedes the efficacy of a natural enemy of mosquitoes

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1 *Original Article*

2 **Alternative prey impedes the efficacy of a natural enemy of mosquitoes**

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21

22 **Abstract**

23 Adaptive foraging behaviour in the presence of multiple prey types may mediate stability to
24 predator-prey relationships. For biological control agents, the presence of alternative prey
25 may thus reduce ecological impacts towards target organisms, presenting a key challenge to
26 the derivation of agent efficacies. Quantifications of non-target effects are especially
27 important for generalist biocontrol agents in their regulation of pests, vectors and invasive
28 species. We examined the predatory impact of the notonectid *Anisops debilis* towards larvae
29 of the vector mosquito complex *Culex pipiens* in the presence of varying densities of
30 alternative daphniid prey. Experimentally, we quantified functional responses of *A. debilis*
31 towards target mosquito prey under different background daphniid compositions, and also
32 tested for prey switching propensities by the notonectid predator. Increasing background
33 densities of daphniids significantly reduced the predatory impact of notonectids on
34 mosquitoes, characterised by reductions in attack rates, lengthening of handling times and
35 lessening of maximum feeding rates. Furthermore, notonectids displayed a significant
36 selective preference in favour of daphniid prey over mosquitoes, irrespective of prey
37 proportions in aquatic environments. Accordingly, notonectids did not display a prey
38 switching pattern. We thus demonstrate that the presence of alternative prey can dampen
39 predatory impacts of notonectids towards mosquitoes, as compared to more simplistic
40 pairwise systems with singular prey choice. Accordingly, the effects of stabilising
41 mechanisms, such as adaptive foraging, should be further integrated in biocontrol agent
42 assessments.

43 **Key words**

44 functional response; prey switching; prey preference; trophic interaction strength; *Anisops*;
45 *Culex*

46 **Introduction**

47 Predatory interactions can profoundly influence population- and community-level stabilities
48 (Paine, 1980; Sih et al., 1985; Dick et al., 2017). Within ecosystems, predators can drive
49 cascading effects across trophic levels through both density- and trait-mediated interactions
50 with their prey (Connell, 1972; Paine, 1980; Werner and Peacor, 2003). However,
51 experimental and theoretical inferences of community dynamics are frequently grounded in
52 interaction strengths between simplified consumer-resource pairings, which ignore additional
53 environmental complexities (Bolker et al., 2003; Werner and Peacor, 2003; Schmitz, 2007).
54 Rather, a community module approach, comprising three or more interacting species,
55 provides a powerful tool to examine the effect of predation on community composition (Holt,
56 1997; Paterson et al., 2015). In particular, predators in the wild are often presented with
57 multiple prey types, which may act as a stabilising mechanism within food webs (Polis et al.,
58 1989). Indeed, adaptive feeding behaviours have been identified as key stabilising
59 components which reduce prey risk, alongside factors such as habitat complexity,
60 antipredator behaviour, omnivory and cannibalism (Kratina et al., 2012).

61 Predator-prey interaction strengths have been harnessed and exploited for the biological
62 control of target species, such as mosquitoes (e.g. Kay and Nam, 2005; Cuthbert et al.,
63 2018a). However, many natural enemies are generalists which consume a wide variety of
64 prey species (Simberloff and Stiling, 1996). Accordingly, the proliferation of generalist
65 natural enemies following release is likely to directly impact on non-target organisms through
66 inadvertent predatory interactions or competition, thus potentially reducing levels of
67 ecological impact on target prey. Moreover, biological control agents which adversely affect
68 non-target communities through these processes may, paradoxically, become economically-
69 and environmentally-damaging in themselves (Louda et al., 1997). Quantifications of

70 predatory interaction strengths which consider both target and non-target biota are, therefore,
71 integral to robust biological control agent assessments at the community-level.

72 The functional response has been applied extensively in quantifications of biological control
73 agent *per capita* impacts (Holling, 1959; Lester et al., 1999; Cuthbert et al., 2018a). Whilst
74 experimental functional response systems often comprise simplistic paired predator-prey
75 model species (see Lester and Harmsen, 2002), the presence of alternative prey may decrease
76 the functional response magnitude due to predator switching or satiation (see later), or drive
77 categorical changes to functional response form (Murdoch, 1969; Murdoch and Oaten, 1975).

78 In particular, propensities of predators to switch between prey may drive transitions to type
79 III functional responses empirically. Such changes are thought to impart more stability to
80 populations by remediating destabilising type II responses, which are characterised by a lack
81 of low-density prey refuge (Hassell, 1978; Cuthbert et al., 2019a).

82 Patterns of prey switching (i.e. frequency-dependent predation) and preferences by predators
83 may facilitate coexistence among taxa, in turn potentially stabilising diverse communities
84 (Murdoch, 1969). Switching propensities are considered to be driven by differential
85 profitability and abundance among prey types (McCann et al., 2005). Characteristically,
86 through avoidance of rare prey and disproportionate utilisation of abundant prey, patterns of
87 density-dependent refuge may emerge that mitigate population extirpations within
88 communities (Cuthbert et al., 2018b). This, in turn, may allow for population recovery of rare
89 prey types. Biological control agents which exhibit a propensity to switch between prey types
90 may, therefore, facilitate low density refugia for target prey, thus inadvertently enabling their
91 persistence within communities. Conversely, agents which do not switch from target prey
92 (i.e. demonstrate frequency-independent predation) are desirable, owing to efficient
93 consumption of target prey even when they are rare in environments. Accordingly, studies
94 which explicitly quantify the influence of alternative prey types on ecological impacts

95 towards target organisms are urgently required in biological control and other ecological
96 contexts.

97 Mosquitoes are important vectors of pathogens and parasites which cause disease in humans
98 and wildlife, with infectious disease risks being increasingly exacerbated by ongoing climate
99 change (Lafferty, 2009; Ryan et al., 2019). According to the World Health Organisation
100 (WHO), malaria alone accounted for 435,000 human deaths in 2018. Biological and
101 environmental control measures can assist or augment control strategies targeting vector
102 mosquitoes, without imposing environmental risks associated with the use of chemical
103 insecticides (Cameron and Lorenz, 2013). Many predatory arthropods have been identified as
104 effective natural enemies of mosquitoes (e.g. Shaalan and Canyon, 2009), and have been
105 shown capable of eliminating disease risks at community-scales through reductions of
106 mosquito populations (Kay and Nam, 2005). However, there is currently a lack of
107 understanding of how mosquito prey risk is altered within food webs where they coexist and
108 compete with other organisms (but see Chesson, 1989; Fischer et al., 2013; Kumar et al.,
109 2008; Cuthbert et al., 2019a).

110 Notonectids are important generalist predators in freshwater aquatic ecosystems colonised by
111 mosquitoes (Blaustein, 1998; Dalu et al., 2016; Wasserman et al., 2018). Daphniids have also
112 been identified as an important notonectid prey species, in both natural and artificial
113 ephemeral systems, and are often pioneering crustaceans given their presence within resting
114 egg banks (Brendonck and De Meester, 2003; Wasserman et al., 2016a). Given the capacity
115 of daphniid and mosquito prey to rapidly colonise temporary aquatic habitats, there is high
116 potential for these species to overlap and compete for resources (Stav et al. 2005). Further,
117 both are nektonic prey types which are preferred by notonectid predators (Klecka and Boukal,
118 2012). However, although predatory impacts of notonectids have been shown to be high
119 towards mosquitoes in pairwise laboratory experiments (e.g. Cuthbert et al. 2019b), the

120 presence of daphniids as alternative prey could impede such impacts. In the present study, we
121 thus use a comparative functional response and prey switching approach to quantify the
122 ecological impacts of the pelagic notonectid *Anisops debilis* Gersaeker 1873 (Hemiptera:
123 Notonectidae) towards larvae of the vector mosquito complex *Culex pipiens* (Diptera:
124 Culicidae), in the presence of alternative *Daphnia pulex* (Cladocera: Daphniidae) group prey
125 at varying densities.

126

127 **Materials and methods**

128 *Animal collection and husbandry*

129 Adult *A. debilis* (7.45 ± 0.17 mm), were collected using a 1000 μm mesh scoop net from the
130 water column of an impounded stream in Makhanda, Eastern Cape, South Africa
131 ($33^{\circ}19'00.4''\text{S}$ $26^{\circ}31'21.0''\text{E}$). Notonectids were transported in source water to a controlled
132 environment (CE) room in the Department of Zoology and Entomology, Rhodes University,
133 Makhanda, maintained at 25 (± 1 $^{\circ}\text{C}$) and under a 14:10 light and dark photoperiod regime. In
134 the CE room, notonectids were concurrently acclimated and starved for 48 hours prior to
135 experimentation in filtered (100 μm mesh size) source water. Larval *C. pipiens* complex prey
136 from egg rafts collected from aquatic container-style habitats on the university campus were
137 reared to the desired size class in the CE room on a diet of crushed guinea pig food pellets
138 (Agricol, Port Elizabeth). The alternative prey, *D. pulex* were collected by hauling a 64 μm
139 mesh zooplankton net through the water column of small reservoir in Makhanda
140 ($33^{\circ}18'33.9''\text{S}$ $26^{\circ}30'03.2''\text{E}$), transported in source water and housed in the CE room until
141 experimental use.

142 *Experimental protocols*

143 We conducted two experiments to quantify the effects of alternative daphniid prey on
144 notonectid predatory impacts towards larval mosquitoes. First, we quantified functional
145 responses of *A. debilis* towards larval mosquito prey in the presence of varying background
146 densities of daphniids. In the CE room, five densities (2, 4, 8, 16 or 32) of third instar larval
147 *C. pipiens* (4.12 ± 0.19 mm) were introduced separately into 100 mL glass jars (5.6 cm dia.)
148 containing filtered source water. Within each larval mosquito density level, four densities (0,
149 10, 20 or 40) of *D. pulex* (1.75 ± 0.05 mm) were introduced. All experimental groups were
150 fully crossed and replicated five times. Following one hour of prey settling, individual *A.*
151 *debilis* were introduced into experimental arenas containing both prey types and allowed to
152 feed for two hours, after which predators were removed and remaining live prey of both types
153 counted. Controls consisted of a replicate of mosquito/daphniid prey in the absence of
154 predators under all crossed density treatment groups.

155 Second, we examined frequency-dependent predation (prey switching) by notonectids
156 towards both prey types. As before, predators were acclimated and starved, with second-third
157 instar larval *C. pipiens* (3.30 ± 0.10 mm) and *D. pulex* (1.84 ± 0.06 mm) introduced
158 simultaneously into 100 mL experimental arenas. Thirty prey were introduced into each
159 arena, under five different ratios (*C. pipiens:D. pulex*: 5:25, 10:20, 15:15, 20:10, 25:5), with 3
160 replicates per experimental group. After settling, *A. debilis* were introduced individually and
161 allowed to feed for thirty minutes, after which predators were removed and remaining live
162 prey counted. Controls consisted of a replicate of each prey ratio in the absence of predators.

163 Pilot studies were used to inform appropriate feeding times for the two experiments, which
164 are analysed separately.

165 *Statistical analyses*

166 All statistical analyses were performed in R v3.5.1 (R Core Development Team, 2018). In the
167 functional response experiment, generalised linear models were used to examine counts of
168 overall mosquito mortality with respect to the alternative prey treatment density (4 levels)
169 and mosquito density (5 levels), and their interaction. A negative binomial family with log
170 link was implemented owing to residual overdispersion (residual deviance > degrees of
171 freedom). An information theoretic approach was used to select models which minimised
172 information loss *via* second-order Akaike's information criterion (AICc) and model
173 averaging, with the relative variable importance (RVI) of terms additionally discerned
174 (Burnham and Anderson, 2002; Barton, 2015). Models with $\Delta\text{AICc} < 2$ were considered
175 interchangeable (Burnham and Anderson, 2002). In the top model, the significance of factors
176 was inferred using analysis of deviance. Type III sums of squares were implemented in the
177 presence of an interaction term and type II sums of squares were applied where an interaction
178 was not present in the top model (see Langsrud, 2003). Where applicable, least square means
179 estimates were used for pairwise comparisons of significant terms, with Tukey adjustments of
180 p values. A critical α of 0.05 was used in all analyses.

181 Logistic regression considering the proportion of mosquito prey killed as a function of initial
182 density (continuous predictor) was used to discern functional response types. Here, a
183 significantly negative first order term is indicative of a type II functional response and a
184 significantly positive first order term followed by a significantly negative second order term
185 indicates a type III functional response (Juliano, 2001). As prey were not replaced during the
186 experiment, we fit Rogers' random predator equation (Rogers, 1972; Trexler et al., 1988;
187 Juliano, 2001):

$$188 \quad N_e = N_0(1 - \exp(\alpha(N_e h - T)))$$

$$189 \quad (1)$$

190 where N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack rate, h is
191 the handling time and T is the total experimental period. The *Lambert W* function was
192 implemented due to the recursive nature of the Random predator equation (Bolker, 2008).
193 Non-parametric bootstrapping ($n = 1999$) was used, based on starting parameter estimates, to
194 generate 95 % confidence intervals of the attack rate and handling time parameters.
195 Functional response curves, and these parameters, were then compared on the basis of
196 confidence interval overlaps across prey densities.

197 For the prey switching experiment, generalised linear mixed effects models, assuming a
198 Poisson error distribution with log link, were used to analyse counts of prey mortality with
199 respect to prey type (2 levels) and prey proportion (5 levels), and their interaction. A random
200 effects structure was applied to account for repeated measures of both prey types within each
201 experimental replicate. A model averaging approach was followed to select the model which
202 minimised information loss (see before). Analysis of deviance was used to infer significance,
203 as before. Manly's selectivity indices, modified by Chesson (1983) and assuming non-
204 replacement of prey, were used to quantify preferences towards mosquito prey (Manly, 1974;
205 Chesson, 1983):

$$206 \quad \alpha_i = (\ln((n_{i0} - r_i)/n_{i0})) / \sum_{j=1}^m (\ln((n_{j0} - r_j)/n_{j0})) \quad (2)$$

207 where α_i is Manly's selectivity index for prey type i , n_{i0} is the number of prey type i available
208 at the start of the experiment, r_i is the number of prey type i consumed, m the number of prey
209 types, n_{j0} the number of prey type j available at the start of the experiment and r_j is the
210 number of prey type j consumed. In a two-prey system, α_i ranges from 0 to 1, with 1
211 indicating complete preference, 0 indicating complete avoidance and 0.5 indicating neutral
212 selectivity. If all of a given prey type were consumed, Eqn. 2 was modified by adding one

214 individual to the corresponding prey supply (see Klecka and Boukal, 2012). This assumes
215 that one individual survived, and therefore the index estimate is slightly conservative. To
216 remove extremes prior to analysis, we transformed indices:

217
$$a_t = (\alpha_i(n - 1) + 0.5)/n$$

218 (3)

219 where α_t is the transformed output and n is the sample size. Beta regression was used to
220 analyse the strength of preference indices towards larval mosquito prey across proportional
221 availability (5 levels) (Cribari-Neto and Zeileis, 2010). A nested likelihood ratio test against
222 the null model (0 predictors) was used to infer significance (Zeileis and Hothorn, 2002), with
223 least square means estimates used *post-hoc* (see before).

224

225 **Results**

226 Control survival of both prey types exceeded 98 % in each experiment, and thus experimental
227 mortality was not adjusted for background mortality. In the functional response experiment,
228 the top model included alternative prey density (RVI = 1.00) and mosquito density (RVI =
229 1.00) as predictors of mosquito mortality. The ‘alternative prey density \times mosquito density’
230 interaction term was not included ($\Delta\text{AICc} = 22.17$; $\text{RVI} < 0.01$), and thus differences in
231 predation driven by alternative prey were consistent across mosquito densities. Alternative
232 prey had a significant effect on mosquito mortality overall ($\chi^2 = 38.99$, $\text{df} = 3$, $p < 0.001$)
233 (Fig. 1), with significantly fewer mosquitoes consumed under alternative prey densities of 20
234 and 40 compared to where alternative prey were absent (both $p \leq 0.001$). Differences in
235 mosquito mortality rates with 10 daphniids compared to in the absence of alternative prey
236 were not statistically clear ($p = 0.07$), yet tended to be reduced with daphniids. Mosquito
237 mortality was also significantly reduced with 40 alternative daphniid prey as compared to 10

238 ($p = 0.002$), but not 20 ($p = 0.09$) daphniids; mortality rates between 10 and 20 alternative
239 prey were more similar ($p = 0.57$). Significantly more mosquito prey were consumed under
240 higher density availabilities ($\chi^2 = 76.52$, $df = 4$, $p < 0.001$).

241 Type II functional responses were evidenced across all alternative prey treatments, owing to
242 significantly negative first order terms (Table 1; Fig. 2). The maximum alternative prey
243 treatment (40) was an exception to this (Table 1); however, the type II model was shown to
244 minimise information loss as compared to either type III or flexible models *via* AICc (type II:
245 66.27; type III: 68.87; flexible: 67.68) (see Pritchard et al. 2017). Attack rates towards
246 mosquitoes tended to decrease under increasing quantities of alternative prey, whilst handling
247 times generally lengthened (Table 1). Accordingly, mosquito maximum feeding rates were
248 substantially reduced in all instances in the presence of alternative daphniid prey. Functional
249 responses towards mosquitoes by notonectids in the absence of alternative prey were of
250 significantly higher magnitude than all alternative prey treatments under high mosquito
251 densities. Conversely, magnitudes among different densities of alternative prey were more
252 similar (Fig. 2).

253 In the switching experiment, prey type alone was retained in the top model ($RVi = 1.00$);
254 prey proportion ($RVi = 0.16$; $\Delta AICc = 3.28$) and the ‘prey type \times prey proportion’ interaction
255 ($RVi < 0.01$; $\Delta AICc = 13.14$) were relatively unimportant. Accordingly, significantly higher
256 numbers of daphniid prey were consumed than mosquitoes when presented simultaneously,
257 irrespective of proportional availability ($\chi^2 = 28.18$, $df = 1$, $p < 0.001$) (Fig. 3). Notonectids
258 did not display a prey switching propensity between prey types (Fig. 3), instead consuming
259 significantly higher numbers of daphniid prey than expected overall. Nevertheless, preference
260 indices towards mosquito prey were significantly affected by proportional mosquito
261 availabilities ($\chi^2 = 22.73$, $df = 4$, $p < 0.001$), reflecting complete avoidance of mosquito prey
262 at certain low-intermediate proportions (Fig. 3).

263

264 **Discussion**

265 Predatory impacts of the notonectid *A. debilis* towards vector mosquito prey were
266 significantly reduced by the presence of alternative daphniid prey during the present study.
267 As daphniid background densities increased, the functional response curve magnitude of *A.*
268 *debilis* fell concurrently, with attack rates decreasing and handling times lengthening.
269 Furthermore, *A. debilis* did not display a prey switching propensity away from daphniid prey
270 types. That is, irrespective of their proportional availability within the environment, positive
271 selection in favour of daphniids over mosquitoes was displayed. Indeed, complete avoidance
272 (i.e. zero mortality) of mosquito prey was evidenced under certain proportions (i.e. 0.17, 0.5).
273 Accordingly, the efficacy of notonectids as natural enemies towards mosquito prey may be
274 impeded by alternative prey, particularly where cladocerans are available in elevated
275 abundances.

276 Functional response magnitudes towards mosquito prey reduced incrementally with
277 alternative daphniid prey density increases. This is further reflected by consistent reductions
278 in raw prey consumption of mosquitoes as the alternative prey became more abundant. Attack
279 rates correspond to the scaling coefficient of functional responses, and describe the initial
280 slope of functional response curves (Hassell and May, 1973; Jeschke et al., 2002). Therefore,
281 the reductions in attack rates as alternative prey increased align with reduced predatory
282 impact under low mosquito prey densities, thus potentially increasing low-density refuge
283 effects for mosquito prey. However, although the presence of alternative prey has been
284 proposed to stabilise communities and facilitate transition from type II to type III functional
285 responses (Steele, 1972; Murdoch and Oaten, 1975), the present study did not find evidence
286 for this, with *A. debilis* displaying a type II functional response irrespective of alternative

287 prey density. Thus, predatory impacts at low mosquito prey densities may be sustained.
288 Nevertheless, under the highest alternative prey density, the functional response type became
289 somewhat equivocal.

290 Handling times increased concurrently with greater alternative prey densities in the present
291 study. Inversely, the handling time corresponds to the maximum feeding rate of the
292 functional response. Accordingly, the functional response maximum feeding rate towards
293 mosquito prey reduced significantly as background densities of daphniids increased.
294 Conversely, Chesson (1989) found alternative daphniid prey to have a less marked effect on
295 mosquito prey consumption in *Notonecta hoffmani*, with only a slight change to attack rates
296 and handling times. This may relate to general behavioural differences between notonectid
297 subfamilies. Although Anisopinae (e.g. *Anisops* spp.), unlike all other diving insects, are able
298 to attain near-neutral buoyancy, Notonectinae (e.g. *Notonecta* spp.) are positively buoyant
299 and rely on clinging to habitat structures to maintain depth (Matthews and Seymour, 2008).
300 Therefore, their greater co-occurrence in the water column may have driven more profound
301 reductions in predatory impacts by *A. debilis*, as compared to *Notonecta* spp. reported in
302 previous studies in simple habitats.

303 Prey switching has been proposed as a central, stabilising mechanism within ecological
304 communities (Murdoch and Oaten, 1975). Experimental applications of prey switching
305 enable quantifications of ecological impacts towards specific prey under different
306 environmental availabilities. In the biocontrol and invasion sciences, species which do not
307 exhibit a prey switching propensity are likely to exert greater ecological impacts on target
308 species, with lower impacts on alternative prey (Cuthbert et al. 2018b). In the present study,
309 *A. debilis* did not display a prey switching propensity between mosquito and daphniid prey.
310 Daphniid prey were positively selected over mosquitoes under all environmental availabilities
311 and, therefore, predatory selection by notonectids was relatively frequency-independent. The

312 continuous movement of cladocerans in the water column compared to the relatively static
313 surface position exhibited by *Culex* mosquitoes likely explains this preference (Scott and
314 Murdoch, 1983). Such inherent differences in prey movement and behaviour likely drive
315 higher detectability of daphniid prey, with notonectids reliant on both visual and tactile
316 mechanisms to capture prey (Peckarsky, 1984; Diéguez and Gilbert, 2003; Gergs et al.,
317 2010). Moreover, previous studies have shown consistently high *per capita* ecological
318 impacts of notonectids towards daphniid prey, with an ability to capture these prey across
319 different aquatic environmental contexts (Wasserman et al., 2016b).

320 Notonectids have been demonstrated to be key predator species which often occupy top
321 trophic positions in temporary aquatic habitats (Dalu et al., 2016), and have the capacity to
322 shape the structuring of communities and eliminate pelagic species (Blaustein, 1998). Aerial
323 dispersal during their adult life history stages enables efficient colonisation of transient
324 aquatic habitat patches, where vector mosquitoes may proliferate. Our results demonstrate
325 that, in communities fostering multiple alternative prey types, risk reductions may be
326 imparted to target mosquito prey in biocontrol programs that utilise such predators.
327 Increasing densities of alternative prey resulted in consistent decreases in predatory impact,
328 and clear preferential selection for alternative prey was exhibited across proportional
329 availabilities. Our results corroborate with Chesson (1989) and Fischer et al. (2013), where
330 different notonectid species were found to selectively prefer cladocerans over larval
331 mosquitoes. Given the coexisting prey types in aquatic food webs, increasing diversity of
332 lower trophic groups likely reduces the efficiency of notonectids in regulating vector mosquito
333 populations. Contrastingly, cladoceran populations may be more severely impacted.
334 However, studies incorporating a greater range of prey types would elucidate these findings
335 further. The potential for notonectids to drive temporal localised extirpation of planktonic
336 crustaceans within temporary wetland systems has recently been highlighted (Wasserman et

337 al. 2018). The production of dormant eggs by crustaceans under adverse conditions may
338 facilitate population resurgence following dry periods (Stross and Hill, 1965; Wasserman et
339 al., 2016a).

340 Whilst caution should be excercised when relating laboratory experiment results to complex
341 real-world systems, classical ecological concepts such as functional responses, prey
342 preferences and prey switching offer great utility in comparative derivations of ecological
343 impacts relevant for the assessment of biocontrol agents under context-dependencies. Future
344 research should thus continue to experimentally integrate mechanisms which may stabilise
345 pairwise predator-prey relationships, such as prey switching, omnivory, cannibalism and
346 habitat complexity, in order to better quantify the influence of external factors on biocontrol
347 agent impacts towards target organisms.

348

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358

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514 Table 1. First order terms and functional response parameter estimates from *Anisops debilis*
515 feeding on larval *Culex pipiens* prey in the presence of different daphniid alternative prey
516 densities.

Alternative prey	First order term, p	Attack rate (a), p	Handling time (h), p	Maximum feeding rate (1/h)
0	-0.03, 0.005	0.73, < 0.001	0.06, 0.004	17.99
10	-0.06, < 0.001	0.72, 0.001	0.18, < 0.001	5.70
20	-0.03, 0.05	0.36, 0.01	0.17, 0.03	6.05
40	-0.03, 0.013	0.21, 0.11	0.38, 0.10	2.64

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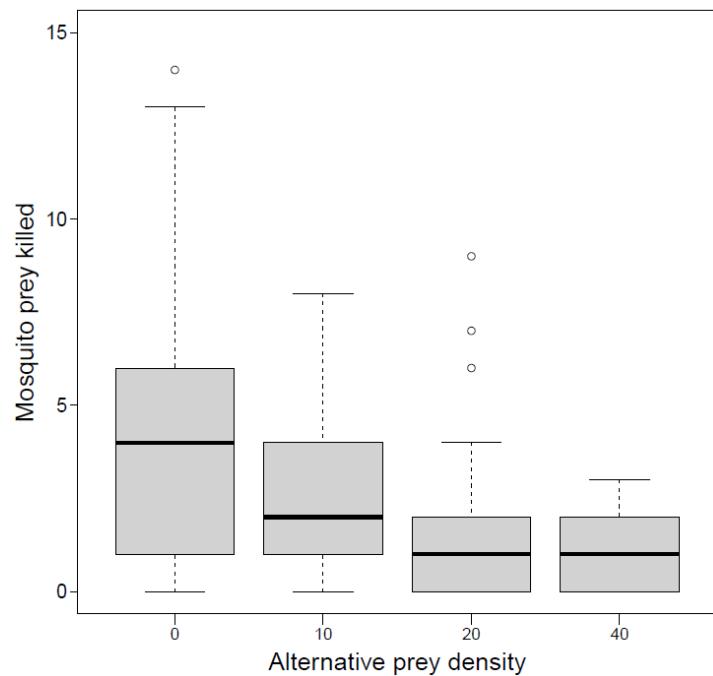
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530 Fig. 1. Boxplot showing larval *Culex pipiens* consumption by *Anisops debilis* across all
 531 mosquito prey densities in the presence of different densities of alternative daphniid prey.
 532 The horizontal bar displays the median, the box gives the interquartile ranges and the
 533 whiskers show the largest and smallest values up to $1.5 \times$ interquartile range.

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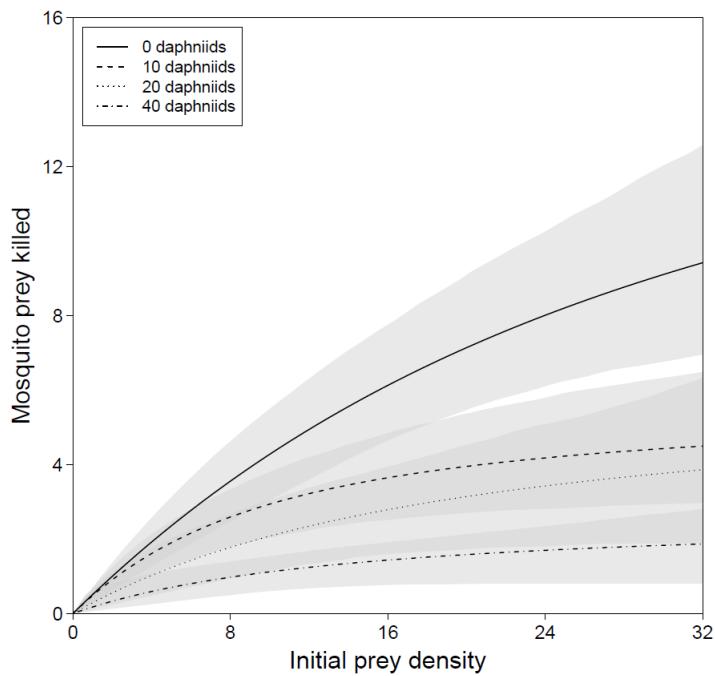
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544 Fig. 2. Functional responses of *Anisops debilis* towards larval *Culex pipiens* prey in the
 545 presence of different background densities of alternative daphniid prey. Shaded areas
 546 represent 95 % confidence intervals.

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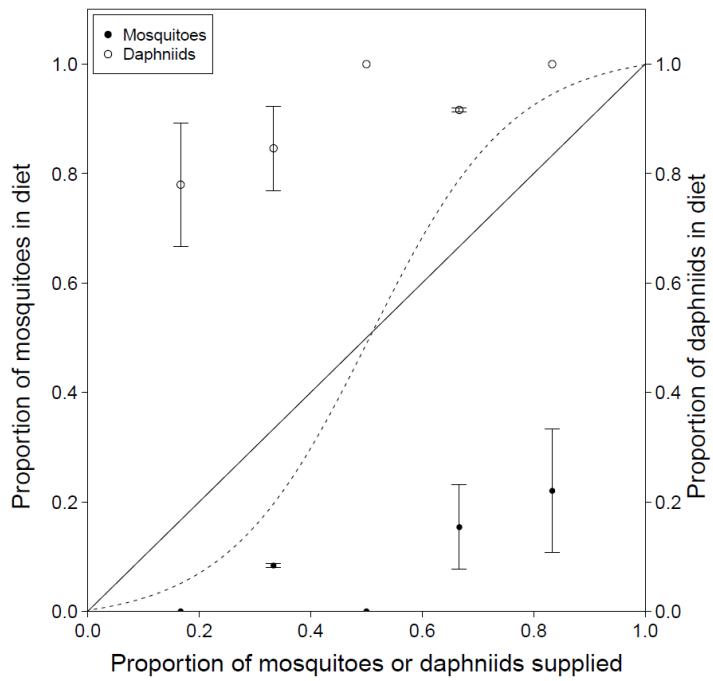
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557 Fig. 3. Proportional predation patterns by *Anisops debilis* between larval *Culex pipiens* and
 558 daphniid prey. The solid line represents expected consumption values under equal selective
 559 preference and the dashed sigmoid line represents a hypothetical prey switching pattern.
 560 Means are \pm SE.