

Alternative prey impedes the efficacy of a natural enemy of mosquitoes

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2	Alternative prey impedes the efficacy of a natural enemy of mosquitoes
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21	

22 Abstract

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

Predatory interactions can profoundly influence population- and community-level stabilities 47 (Paine, 1980; Sih et al., 1985; Dick et al., 2017). Within ecosystems, predators can drive 48 cascading effects across trophic levels through both density- and trait-mediated interactions 49 with their prey (Connell, 1972; Paine, 1980; Werner and Peacor, 2003). However, 50 51 experimental and theoretical inferences of community dynamics are frequently grounded in interaction strengths between simplified consumer-resource pairings, which ignore additional 52 environmental complexities (Bolker et al., 2003; Werner and Peacor, 2003; Schmitz, 2007). 53 54 Rather, a community module approach, comprising three or more interacting species, provides a powerful tool to examine the effect of predation on community composition (Holt, 55 1997; Paterson et al., 2015). In particular, predators in the wild are often presented with 56 57 multiple prey types, which may act as a stabilising mechanism within food webs (Polis et al., 1989). Indeed, adaptive feeding behaviours have been identified as key stabilising 58 components which reduce prey risk, alongside factors such as habitat complexity, 59 antipredator behaviour, omnivory and cannibalism (Kratina et al., 2012). 60 Predator-prey interaction strengths have been harnessed and exploited for the biological 61 control of target species, such as mosquitoes (e.g. Kay and Nam, 2005; Cuthbert et al., 62 2018a). However, many natural enemies are generalists which consume a wide variety of 63 prey species (Simberloff and Stiling, 1996). Accordingly, the proliferation of generalist 64 natural enemies following release is likely to directly impact on non-target organisms through 65 inadvertent predatory interactions or competition, thus potentially reducing levels of 66 ecological impact on target prey. Moreover, biological control agents which adversely affect 67 non-target communities through these processes may, paradoxically, become economically-68 and environmentally-damaging in themselves (Louda et al., 1997). Quantifications of 69

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

72 The functional response has been applied extensively in quantifications of biological control agent per capita impacts (Holling, 1959; Lester et al., 1999; Cuthbert et al., 2018a). Whilst 73 experimental functional response systems often comprise simplistic paired predator-prey 74 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 categorical changes to functional response form (Murdoch, 1969; Murdoch and Oaten, 1975). 77 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 populations by remediating destabilising type II responses, which are characterised by a lack 80 81 of low-density prey refuge (Hassell, 1978; Cuthbert et al., 2019a).

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

95 towards target organisms are urgently required in biological control and other ecological96 contexts.

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

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

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

126

127 Materials and methods

128 Animal collection and husbandry

129	Adult A. debilis (7.45 \pm 0.17 mm), were collected using a 1000 μ m mesh scoop net from the
130	water column of an impounded stream in Makhanda, Eastern Cape, South Africa
131	(33°19'00.4"S 26°31'21.0"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 (\pm 1 °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, <i>D. pulex</i> were collected by hauling a 64 μ m
139	mesh zooplankton net through the water column of small reservoir in Makhanda
140	(33°18'33.9"S 26°30'03.2"E), transported in source water and housed in the CE room until
141	experimental use.

142 *Experimental protocols*

We conducted two experiments to quantify the effects of alternative daphniid prey on 143 notonectid predatory impacts towards larval mosquitoes. First, we quantified functional 144 responses of A. debilis towards larval mosquito prey in the presence of varying background 145 146 densities of daphniids. In the CE room, five densities (2, 4, 8, 16 or 32) of third instar larval C. pipiens $(4.12 \pm 0.19 \text{ mm})$ were introduced separately into 100 mL glass jars (5.6 cm dia.) 147 containing filtered source water. Within each larval mosquito density level, four densities (0, 148 10, 20 or 40) of D. pulex (1.75 \pm 0.05 mm) were introduced. All experimental groups were 149 fully crossed and replicated five times. Following one hour of prey settling, individual A. 150 151 debilis were introduced into experimental arenas containing both prey types and allowed to feed for two hours, after which predators were removed and remaining live prey of both types 152 counted. Controls consisted of a replicate of mosquito/daphniid prey in the absence of 153 154 predators under all crossed density treatment groups. Second, we examined frequency-dependent predation (prey switching) by notonectids 155 towards both prey types. As before, predators were acclimated and starved, with second-third 156 instar larval C. pipiens $(3.30 \pm 0.10 \text{ mm})$ and D. pulex $(1.84 \pm 0.06 \text{ mm})$ introduced 157 simultaneously into 100 mL experimental arenas. Thirty prey were introduced into each 158 159 arena, under five different ratios (C. pipiens:D. pulex: 5:25, 10:20, 15:15, 20:10, 25:5), with 3 replicates per experimental group. After settling, A. debilis were introduced individually and 160 161 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

are analysed separately.

165 *Statistical analyses*

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

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

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

189

(1)

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

For the prey switching experiment, generalised linear mixed effects models, assuming a 197 198 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 minimised information loss (see before). Analysis of deviance was used to infer significance, 202 as before. Manly's selectivity indices, modified by Chesson (1983) and assuming non-203 replacement of prey, were used to quantify preferences towards mosquito prey (Manly, 1974; 204 205 Chesson, 1983):

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

207

where
$$a_i$$
 is Manly's selectivity index for prey type *i*, n_{i0} is the number of prey type *i* available
at the start of the experiment, r_i is the number of prey type *i* consumed, *m* the number of prey

(2)

210 types, n_{j0} the number of prey type *j* available at the start of the experiment and r_j is the

- number of prey type *j* consumed. In a two-prey system, α_i ranges from 0 to 1, with 1
- 212 indicating complete preference, 0 indicating complete avoidance and 0.5 indicating neutral
- selectivity. If all of a given prey type were consumed, Eqn. 2 was modified by adding one

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

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

218

(3)

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

224

225 **Results**

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

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).

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

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

264 **Discussion**

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

Functional response magnitudes towards mosquito prey reduced incrementally with 276 alternative daphniid prey density increases. This is further reflected by consistent reductions 277 278 in raw prey consumption of mosquitoes as the alternative prey became more abundant. Attack rates correspond to the scaling coefficient of functional respones, and describe the initial 279 slope of functional response curves (Hassell and May, 1973; Jeschke et al., 2002). Therefore, 280 281 the reductions in attack rates as alternative prey increased align with reduced predatory impact under low mosquito prey densities, thus potentially increasing low-density refuge 282 effects for mosquito prey. However, although the presence of alternative prey has been 283 284 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 for this, with A. debilis displaying a type II functional response irrespective of alternative 286

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

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

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

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

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

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

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

348

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514	Table 1. First order	terms and function	al response parameter	r estimates fron	n Anisops debilis
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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 (<i>a</i>),	Handling time	Maximum
			р	(<i>h</i>), <i>p</i>	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, 013	0.21, 0.11	0.38, 0.10	2.64
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Fig. 1. Boxplot showing larval *Culex pipiens* consumption by *Anisops debilis* across all mosquito prey densities in the presence of different densities of alternative daphniid prey. The horizontal bar displays the median, the box gives the interquartile ranges and the whiskers show the largest and smallest values up to $1.5 \times$ interquartile range.



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



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