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1 *Short Communication*

2 **Water volume differentially modifies copepod predatory strengths on two prey types**

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21

22 **Abstract**

23 Predatory interaction strengths are highly context-dependent, and in temporary aquatic
24 ecosystems, may be affected by water volume changes. We examine the influence of water
25 volume on *Lovenula raynerae* (Copepoda) functional responses towards two temporary pond
26 prey types. *Daphnia* prey risk was not affected by increasing water volume, whereas for
27 *Culex* prey risk was reduced. Accordingly, water volume changes through the hydroperiod
28 may have species-specific effects on prey, with implications for population persistence under
29 environmental change.

30

31 **Keywords**

32 Search area; functional response; interaction strength; copepod; daphnid; culicid

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43 Determining factors which influence the strength of interactions between species is essential
44 for understanding community-level stabilities and dynamics within ecosystems (McCann et
45 al., 1998; Vázquez et al., 2015). Context-dependencies can modify prey risk from predators
46 in heterogeneous environments and can be measured experimentally to help predict
47 population persistence (Dick et al., 2014). Search area may be a particularly important
48 context-dependency that influences the strength of trophic interactions through, for example,
49 alterations to prey encounter and clearance rates (Uiterwaal and DeLong, 2018). In temporary
50 pond ecosystems, water volume is highly changeable spatiotemporally owing to naturally
51 periodic wet and dry states, potentially altering the nature of trophic dynamics therein. Such
52 undulations in water volumes through the hydroperiod may be an important contributor to
53 species extirpations and reported ‘boom-bust’ dynamics (Wasserman et al., 2018). The effect
54 of water volume on trophic interactions among temporary pond specialist biota is, however,
55 poorly understood. This limits understandings of the influence of predicted future droughts
56 and land use changes for ecological functioning of these biodiverse systems (Dalu et al.,
57 2017).

58

59 Prey risk is known to differ between species where they coexist within aquatic communities
60 (Cuthbert et al., 2018). Differences in behavioural traits between prey species may modify the
61 influence of context-dependencies on predation risk (Lavery et al., 2015). For pelagic
62 predators and prey which occupy three-dimensional space throughout the water column,
63 interaction strengths may be relatively unaffected by increasing search area than towards prey
64 species which remain at the surface or benthos. Likewise, predators which forage in two-
65 dimensional space may be affected to a lesser extent by water volume change towards benthic
66 or surficial prey compared to pelagic prey items. Accordingly, the influence of water volume

67 change could differ between predator-prey participants and may alleviate or exacerbate
68 predation risk depending on fundamental behavioural traits and spatial occupancies.

69

70 The present study uses a functional response approach to comparatively quantify the
71 influence of water volume change for interaction strengths towards two temporary pond prey
72 types. We consider functional responses comparatively as our results are not bolstered by
73 empirical validation of parameters which could facilitate mechanistic interpretation (see Dick
74 et al., 2014). Functional responses quantify resource use as a function of resource density and
75 their shape and magnitude can be a useful indicator of prey population stability outcomes
76 (Holling, 1959; Dick et al., 2014). Focusing on the pelagic temporary pond specialist
77 copepod *Lovenula raynerae* as a predator, functional responses are quantified under five
78 different water volumes towards two common prey types, *Daphnia longispina* (i.e. water
79 flea) and *Culex pipiens* (i.e. mosquito larva). This predator is often numerically dominant in
80 temporary ponds within the study area (Wasserman et al., 2018). In our predator-prey system,
81 given that *D. longispina* is a pelagic species whilst *C. pipiens* is a surface-dweller, we expect
82 interactions with the latter species to be more profoundly affected by the experimental water
83 volume gradient.

84

85 Adult male *L. raynerae* (4.5 – 5.0 mm total length) were collected from a temporary pond
86 close to Makhanda (Grahamstown) in the Eastern Cape Province of South Africa during
87 April 2019 (33°15'02.6"S 26°26'13.1"E). Copepods were transported in source pond water to
88 a controlled environment (CE) room at the Department of Zoology and Entomology, Rhodes
89 University that was maintained at 25 °C (\pm 1 °C) and under a 14:10 light and dark
90 photoperiod regime, corresponding with natural local conditions. Copepods were starved in

91 filtered source water from the collection site for 24 hours prior to experimentation, to allow
92 for gut clearance and standardisation of hunger levels.

93

94 Two prey types were collected and used in the experiment, *D. longispina* and *C. pipiens*.
95 Daphnids (total length (excluding spine): 1.8 – 2.1 mm) were collected from a reservoir
96 adjacent to the copepod collection site (33°15'04.2"S 26°26'17.1"E). Culicids (total length:
97 2.0 – 3.0 mm) were collected from container-style aquatic habitats on the university campus.
98 Both prey types were housed in the same CE room as the copepod predators until
99 experimentation.

100

101 Two separate feeding experiments were conducted according to prey type, given different
102 feeding durations were required to reach asymptotic consumption rates towards each prey
103 type. Five water volume treatments were applied to glass jars of 5.6 cm diameter (20, 40, 60,
104 80 and 100 mL) using filtered source water from the copepod collection site (as before). Five
105 supplies of each prey type were distributed among each water volume level (2, 4, 8, 16 and
106 32 individuals arena⁻¹; densities as per Table 1). The range of prey densities used in the
107 present study reflects the abundances and high natural variability of biota within temporary
108 wetland ecosystems (Wasserman et al., 2018), and a large range of prey densities is required
109 to facilitate asymptotic declines in feeding rates in functional response experiments (see Dick
110 et al., 2014). Each prey type was allowed to settle for one hour prior to the addition of
111 individual copepod predators. After introduction, predators were allowed to feed on daphnids
112 or culicids for 18 and 4 hours, respectively. Each treatment group was replicated four times
113 for each prey type, and a further replicate of predator-free controls was run for each prey

114 type, water volume and prey density (i.e., 2 prey × 5 volumes × 5 supplies × 4 replicates +
115 controls = 250 experimental units overall).

116

117 Given differences in feeding times towards each prey type (see before), statistical analyses
118 were conducted separately for daphnids and culicids. Poisson generalised linear models with
119 log links were used to examine overall prey consumption as a function of water volume and
120 prey supply, and their interaction. A dispersion test was used to confirm that residuals were
121 not over/underdispersed in models (Kleiber and Zeileis, 2008). Second-order derivations of
122 Akaike's information criterion were used to select models for each prey type which
123 minimised information loss (Barton, 2018), with $\Delta\text{AICc} \leq 2.00$ considered interchangeable
124 (Burnham and Anderson, 2002).

125

126 Functional response types were first characterised used binomial generalised linear models
127 and logit links separately for each prey type and water volume (Juliano, 2001; Pritchard et al.,
128 2017). A significantly negative linear coefficient is indicative of a Type II functional
129 response. Second, we fit Rogers' random predator equation to each treatment to account for
130 the non-replacement of prey during the experimental trials (Rogers, 1972):

$$131 \quad N_e = N_0(1 - \exp(a(N_e h - T)))$$

132 (1)

133 where N_e is the number of prey eaten (i.e., number killed), N_0 is the initial density of prey, a is
134 the attack rate, h is the handling time and T is the total experimental period (hours). The
135 Lambert W function was used to solve the random predator equation (Bolker, 2008). Third,
136 functional response parameters (a , h) were non-parametrically bootstrapped 2000 times to

137 generate 95 % confidence intervals across curves for each prey type and water volume.
138 Statistical analyses were performed in R v 3.4.2 (R Development Core Team, 2018).

139

140 Approximately 97 % of control prey survived overall, and therefore we did not deem it
141 necessary to adjust experimental feeding rates for background prey mortality. The top model
142 examining feeding rates towards daphnids included water volume, prey supply and their
143 interaction ($\Delta\text{AICc} \leq 1.46$). Feeding rates related significantly positively with prey supply
144 (GLM: $z = 8.10, p < 0.001$), but not water volume (GLM: $z = 0.20, p = 0.84$) or their interaction
145 (GLM: $z = 0.96, p = 0.34$). The top model considering feeding rates upon culicids also included
146 water volume and prey supply, but excluded the interaction term ($\Delta\text{AICc} = 2.11$). Here, feeding
147 rates again related significantly positively to prey supply (GLM: $z = 10.53, p < 0.001$), yet also
148 related significantly negatively to water volume (GLM: $z = 4.55, p < 0.001$). Therefore, the
149 effect of water volume differed between prey types, with a greater negative effect on feeding
150 rates towards surface-dwelling culicids as compared to pelagic daphnids (Figure 1).

151

152 Feeding rates towards both prey types always related significantly negatively to prey supplies
153 across water volumes, and thus functional responses were categorised as Type II (Table 1).
154 Attack rates and handling times were significant for the majority of treatment groups (Table
155 1). Confidence intervals consistently overlapped across prey densities towards daphnids,
156 indicating a lack of significant differences in functional responses among water volume
157 treatments (Figure 2a). By contrast, functional responses towards culicids were influenced to a
158 greater extent by water volume, with significant differences between 20 mL volumes and all
159 other groups at low-intermediate prey supplies (Figure 2b). This, in turn, reflects greater attack
160 rates and lower handling times under the lowest water volume here (Table 1).

161

162 Prey risk differed considerably between prey types across the water volume gradient in the
163 present study, with risk for pelagic daphnid prey less affected by the water volume gradient
164 than the surficial culicid prey. Despite search volumes increasing by several multitudes, and
165 thus prey densities decreasing, daphnid consumption was relatively unaffected and thus higher
166 than expected under higher water volumes. For active pelagic predator-prey pairs, encounter
167 rates are likely less affected by differences in water volume compared to pelagic predators
168 feeding on inactive surface-dwelling prey. In the latter case, prey risk is more variable because
169 the likelihood of being in proximity to surface-dwelling prey increases in shallow waters,
170 whilst prey ‘crowding’ across densities is more prevalent for daphnid prey. Accordingly, for
171 larval mosquito prey, predatory impact is intensified as water volumes decrease given greater
172 encounter rates at the surface, yet predation is less efficient at greater depths. These findings
173 corroborate Dalal et al. (2019), where the strength of notonectid functional responses towards
174 larval mosquitoes differed according to aquatic search areas. However, despite differences in
175 feeding rates, functional response types were unchanged in the present study, with *L. raynerae*
176 consistently displaying saturating Type II curves towards both prey types irrespective of water
177 volume. Given Type II functional responses are characterised by high feeding rates at low prey
178 densities (see Dick et al., 2014), *L. raynerae* is consistently able to capture daphnids and
179 culicids across different water volumes. Nonetheless, attack rates towards mosquitoes were
180 reduced at the highest compared to lowest volume, indicating reduced interaction strengths at
181 low prey densities. Handling times also generally lengthened with increasing water volume for
182 both prey types, causing reduced maximum feeding rates. Previous research has demonstrated
183 large and consistent effects of arena size (i.e. search area) for the determination of foraging
184 rates in laboratory experiments (Uiterwaal et al., 2018), and particularly at low prey densities.

185 Here, we further show that search area can alter foraging efficiencies and functional response
186 parameterisation, but that these effects are prey type-dependent.

187

188 The present study thus demonstrates the importance of search area for trophic interactions in
189 highly dynamic temporary aquatic ecosystems. Whilst empirical inferences arising from
190 laboratory studies should be treated with necessary caution, applications of comparative
191 functional responses can provide useful insights into environmental context-dependencies in a
192 controlled manner. Alterations to hydrological regimes in future associated with climatic and
193 land use changes may influence interaction strengths differentially among prey species, in turn
194 potentially altering population stabilities and community composition. In particular, deepening
195 of temporary ponds for water storage could reduce the efficacy of specialist predators in
196 controlling vector mosquito populations. Indeed, larval mosquitoes have been observed to be
197 more abundant in deep as compared to shallow ponds in the study area (Dalu pers. comm.).
198 This study further highlights the potential for temporary pond specialist predatory zooplankton
199 to regulate mosquito populations which vector pathogens and parasites, and thus to provide an
200 ecosystem service in terms of public health. If these ecosystems are compromised, such as
201 through being deepened by land owners for water storage purposes, the potential for vector
202 mosquito proliferation may increase. Whilst recent work has also demonstrated strong prey
203 selectivity patterns by predators in temporary ponds (Cuthbert et al., 2019), future studies
204 should also examine the influence of water volume on prey preferences in these systems to
205 further elucidate the implications of search area for trophic interactions concerning vector
206 mosquito populations. Field-based surveys to examine how culicid and daphnid prey
207 abundances shift spatiotemporally according to pond characteristics are also warranted.

208

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219

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273 **Table 1.** Functional response linear coefficients, attack rates and handling times for each prey
274 type (daphnid, *Daphnia longispina*; culicid, larval *Culex pipiens*) and water volume treatment

275 group by *Lovenula raynere*, as well as associated p -values. Functional response parameters are
 276 standardised hourly towards each prey group.

Prey	Volume (mL)	Density range (prey mL ⁻¹)	Linear coefficient, p - value	Attack rate, p -value	Handling time, p -value
Daphnid	20	0.1 – 1.6	-0.06, < 0.001	0.15, < 0.001	0.69, < 0.001
Daphnid	40	0.05 – 0.80	-0.08, < 0.001	0.24, < 0.001	1.11, < 0.001
Daphnid	60	0.03 – 0.53	-0.05, < 0.001	0.12, < 0.001	0.77, < 0.001
Daphnid	80	0.03 – 0.40	-0.07, < 0.001	0.16, < 0.001	1.14, < 0.001
Daphnid	100	0.02 – 0.32	-0.08, < 0.001	0.21, < 0.001	1.26, < 0.001
Culicid	20	0.1 – 1.6	-0.09, < 0.001	0.77, < 0.001	0.31, < 0.001
Culicid	40	0.05 – 0.80	-0.05, < 0.001	0.40, 0.001	0.40, < 0.001
Culicid	60	0.03 – 0.53	-0.05, < 0.001	0.29, < 0.001	0.38, < 0.001
Culicid	80	0.03 – 0.40	-0.05, < 0.001	0.67, 0.07	0.72, < 0.001
Culicid	100	0.02 – 0.32	-0.05, < 0.001	0.21, 0.002	0.48, < 0.001

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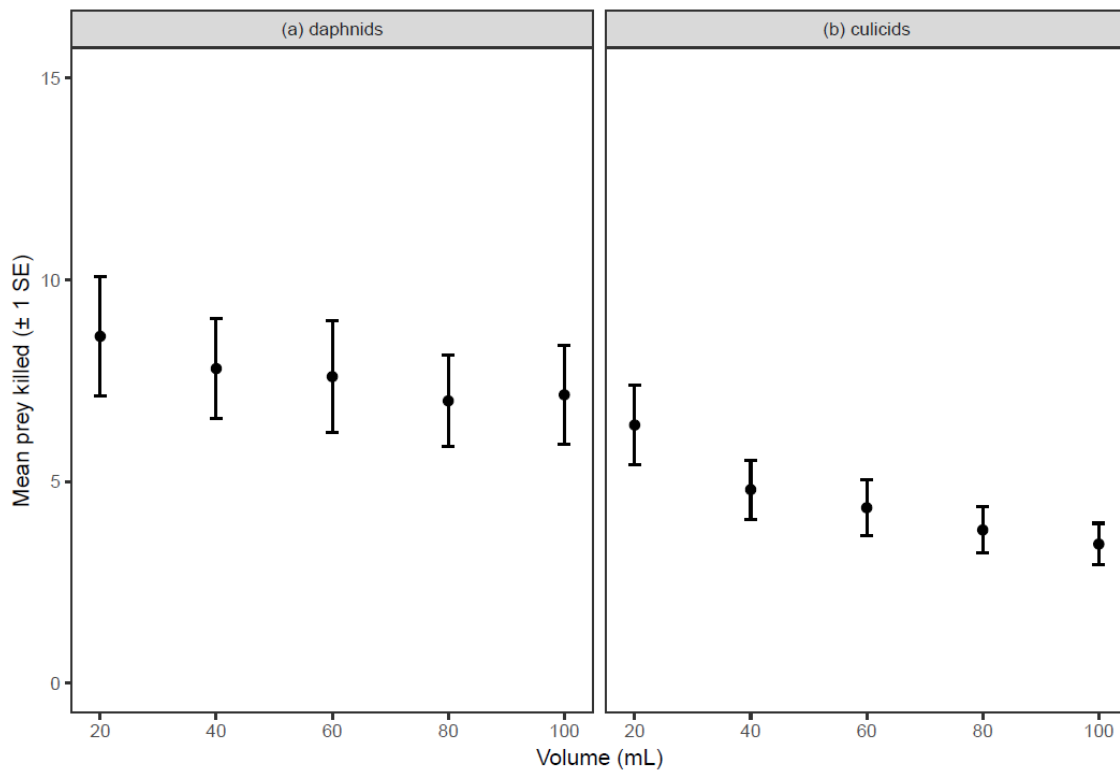
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284 **Figure 1.** Mean (± 1 SE) feeding rates of *Lovenula raynerae* towards daphnid (*Daphnia*
 285 *longispina*, a) and larval culicid (*Culex pipiens*, b) prey across water volume treatments,
 286 irrespective of prey density and feeding duration.

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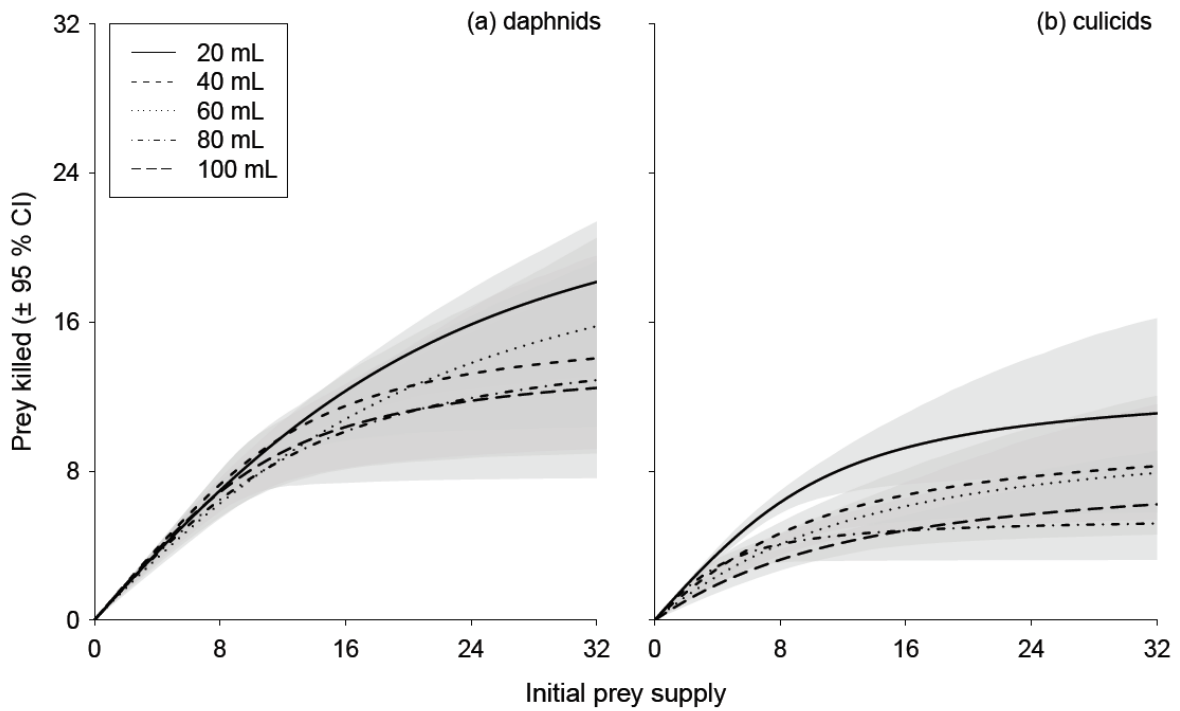
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297 **Figure 2.** Type II functional response curves of *Lovenula raynerae* towards daphnid
 298 (*Daphnia longispina*, a) and larval culicid (*Culex pipiens*, b) prey under different water
 299 volume treatments, irrespective of experimental duration. Shaded areas are bootstrapped 95
 300 % confidence intervals.

301