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1 *Short Communication*

2 **Lack of prey switching and strong preference for mosquito prey by a temporary pond**
3 **specialist predator**

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22 **Abstract**

23 1. The strengths of trophic interactions within ecosystems can be mediated by complex
24 mechanisms that require elucidation if we are to understand and predict population- and
25 community-level stabilities. Where multiple prey types co-occur, prey switching (i.e.
26 frequency-dependent predation) by predators may facilitate low prey density refuge effects
27 which promote coexistence. On the other hand, lack of switching and strong preferences by
28 predators can strongly suppress prey populations, which is especially important considering
29 vector species such as mosquitoes.

30 2. In the present study, we quantify prey switching and preference patterns of the temporary
31 pond specialist copepod *Lovenula raynerae* towards larvae of the medically important *Culex*
32 *pipiens* mosquito complex in the presence of different proportions of alternative *Daphnia*
33 *pulex* prey. Further, we examine whether prey switching and preferences are contingent on
34 the sex of the predator.

35 3. *Lovenula raynerae* exhibited a lack of prey switching and strong preference of larval
36 mosquito prey overall, irrespective of predator sex. Also, when larval mosquitoes were
37 available in higher proportions over daphniids, the strength of this positive selectivity
38 increased. There was very little low-density refuge for mosquitoes where they were rare.

39 4. Lack of prey switching and strong preferences towards mosquitoes by predatory
40 paradiaptomid copepods may enhance population-level regulation of disease vector
41 mosquitoes that exploit temporary pond-style habitats. Accordingly, the conservation and
42 promotion of these predators may enable better management of medically important species
43 across landscapes.

44

45

46 **Key words**

47 Prey switching; preference; trophic interaction strength; ephemeral wetland; *Culex pipiens*;
48 *Lovenula raynerae*

49

50 **Introduction**

51 Predation significantly influences the structure of populations and communities within
52 ecosystems (Paine 1980; Sih et al. 1985). Whilst pairwise predator-prey interaction strengths
53 are frequently used in inferences of community dynamics (Tang et al., 2014; Vázquez et al.,
54 2015; Cuthbert et al., 2018c), patterns of prey selectivity are often ignored, despite their
55 capacity to alter predation pressure towards single species (Murdoch, 1969; Cuthbert et al.
56 2018d). In particular, prey switching (i.e. frequency-dependent predation) can have
57 significant implications for the stability of prey populations (Murdoch, 1969). That is,
58 through avoidance of rare prey and disproportionate consumption of abundant prey (Fig. 1),
59 switching behaviour may facilitate stability in population and community co-existence
60 patterns, empirically aligned with type III sigmoidal functional response curves (Croy and
61 Hughes, 1993). Accordingly, high prey switching propensities may reduce the strength of
62 biotic resistance towards particular species (Cuthbert et al. 2018d), while lack of prey
63 switching may suppress favoured prey species, with implications for regulation of important
64 groups, such as medically important mosquitoes (Cuthbert et al. 2018a).

65 Ephemeral aquatic ecosystems are characterised by atypical trophic structuring, with
66 community dynamics contingent on patterns of internal recruitment (i.e. resting egg hatching)
67 and external recruitment via colonisation from other environments during wet phases
68 (Brendonck and De Meester, 2003; Wasserman et al. 2016, 2018). In these habitats, top-down
69 pressure is often driven by predaceous crustaceans which hatch from egg banks at the start of

70 the wet phase (Wasserman et al. 2016). Higher-order insect predators (e.g. notonectids) are
71 typically externally recruited much later (Wasserman et al. 2018), and thus predation pressure
72 in these systems is transient, with implications for invertebrate community dynamics.
73 Mosquitoes successfully colonise different forms of temporary aquatic habitats via aerial
74 dispersal and, by certain genera, oviposition of desiccation-resistant eggs (Tsurim et al. 2013;
75 Townroe and Callaghan 2014). Whilst predatory temporary pond specialists have been
76 recently identified as potentially important natural predators of vector mosquitoes that exploit
77 ephemeral aquatic habitats (Cuthbert et al. 2018b), it is unknown how alternative prey types,
78 which are also recruited into these ecosystems, alter interaction strengths towards
79 mosquitoes. In particular, daphniid prey are often numerically dominant pioneering
80 crustaceans in temporary ponds (Wasserman et al. 2016), and their presence may therefore
81 regulate predation pressure towards mosquitoes where they coexist.

82 In the present study, we examine the prey switching and preferences of the specialist
83 predatory calanoid copepod *Lovenula raynerae* (Calanoida: Diaptomidae) between larvae of
84 the *Culex pipiens* (Diptera: Culicidae) mosquito complex and alternative daphniid prey.
85 *Lovenula raynerae* is endemic to South Africa and is often numerically dominant in its native
86 range, with larval mosquitoes and daphniids comprising important components of their diet
87 (Wasserman et al. 2016; Cuthbert et al. 2019). We compare predatory behaviour of male and
88 female copepods as sex ratios in temporary ponds are known to become sex-skewed over
89 time (Wasserman et al. 2018). Interaction strengths and resource specialisation are also
90 known to vary according to sex and reproductive status in these systems (Dalu et al. 2017;
91 Cuthbert et al. 2019). Therefore, prey selectivity patterns may differ between sexes, resulting
92 in changes to predator-prey dynamics over the hydroperiod.

93

94 **Materials and Methods**

95 The predator *L. raynerae* was collected from an ephemeral pond in the Eastern Cape
96 Province of South Africa (33°15'04.0"S 26°26'16.4"E) by hauling a 64 µm mesh zooplankton
97 net through the water column. These copepods were transported in source water to a
98 controlled environment (CE) room in the Department of Zoology and Entomology, Rhodes
99 University, Makhanda (Grahamstown), maintained at 25 ± 2 °C and under a 14:10 light:dark
100 regime. In the CE room, adult male and female copepods were separately starved in 5 L
101 aquaria containing 100 µm filtered water from the source pond for 24 hours prior to the
102 experiment. *Daphnia pulex* (Cladocera: Daphniidae) group were collected from a permanent
103 waterbody using a zooplankton net, as before (33°18'33.9"S 26°30'03.1"E). Larval *C. pipiens*
104 complex mosquitoes were cultured from egg rafts collected from artificial containers on the
105 university campus in the CE room, and fed *ad libitum* with ground guinea pig food pellets
106 (Agricol, Port Elizabeth).

107 The two prey types (*C. pipiens*, 3 – 5 mm; *D. pulex* 1 – 2 mm) were introduced
108 simultaneously into glass experimental arenas of 5.6 cm diameter containing 50 mL filtered
109 source water. Prey were introduced under five different ratios (*C. pipiens*:*D. pulex*: 2:18,
110 5:15, 10:10, 15:5, 18:2). After prey had settled for 3 hours in experimental arenas, either a
111 single male or female *L. raynerae* was introduced and allowed to feed for 18 hours (i.e. 8:10
112 light:dark). Four replicates were undertaken for each prey ratio and predator sex, and controls
113 consisted of three replicates at each prey ratio in the absence of predators to quantify
114 background mortality resulting from factors other than predation. After the experimental
115 period, predators were removed and remaining live prey counted to quantify mortality.

116 Statistical analyses were performed using R v3.5.1 (R Development Core Team, 2018).

117 Generalised linear mixed effects models assuming a Poisson error distribution and log link

118 were used to examine the number of individuals consumed with respect to prey species,
 119 predator sex and prey proportion and their two- and three-way interactions. Each independent
 120 variable was included as a categorical predictor in the model. A random effects structure was
 121 integrated, with each experimental arena treated as a random intercept to account for multiple
 122 measurements within individual arenas. An information theoretic approach was used to select
 123 the model with parameters which minimised information loss via AICc (Burnham and
 124 Anderson, 2002). Models with $\Delta\text{AICc} < 2$ were considered interchangeable. Analysis of
 125 deviance with type III sums of squares was used to infer significance levels. Manly's
 126 selectivity index, assuming non-replacement of prey, was applied to model prey preferences
 127 towards larval mosquitoes according to their environmental availability (Manly, 1972;
 128 Chesson, 1983):

$$129 \quad (1) \quad \alpha_i = (\ln((n_{i0} - r_i)/n_{i0})) / \sum_{j=1}^m (\ln((n_{j0} - r_j)/n_{j0}))$$

130

131 where α_i is Manly's selectivity index for prey type i , n_{i0} is the number of prey type i available
 132 at the start of the experiment, r_i is the number of prey type i consumed, m the number of prey
 133 types, n_{j0} the number of prey type j available at the start of the experiment and r_j is the
 134 number of prey type j consumed. In a two-prey system, α_i ranges from 0 to 1, with 1
 135 indicating complete preference, 0 indicating complete avoidance and 0.5 indicating neutral
 136 selectivity. To remove extremes prior to analysis, we transformed indices:

$$137 \quad (2) \quad a_t = (\alpha_i(n - 1) + 0.5)/n$$

138 where α_i is the transformed output and n is the sample size. Beta regression was used to
 139 analyse preferences towards mosquitoes according to predator sex and prey proportion, with
 140 AICc used in model selection (as before). Nested likelihood ratio tests were used to infer
 141 significance levels.

142

143 **Results and Discussion**

144 Irrespective of sex, adult *L. raynerae* preferentially selected *C. pipiens* prey over *D. pulex*
145 across the majority of proportional availabilities (Fig. 1). The prey species, predator sex and
146 prey proportion terms were included in the top model. The ‘prey species × predator sex’ and
147 ‘prey species × prey proportion’ interactions were also included. *Culex pipiens* were
148 consumed significantly more than *D. pulex* overall ($\chi^2 = 5.71$, $df = 1$, $p = 0.02$), and prey
149 consumption increased significantly as a given prey type was available in higher proportions
150 ($\chi^2 = 85.16$, $df = 4$, $p < 0.001$). There was no significant difference in consumption between
151 predator sexes ($\chi^2 = 2.87$, $df = 1$, $p = 0.09$), and significantly higher consumption towards
152 larval mosquitoes was consistent between sexes and proportions owing to non-significant
153 ‘prey species × predator sex’ ($\chi^2 = 3.12$, $df = 1$, $p = 0.08$) and ‘prey species × prey
154 proportion’ ($\chi^2 = 8.86$, $df = 4$, $p = 0.06$) interaction terms. However, female preferences
155 tended to be less marked than males, and preference differences between prey were generally
156 highest under greater availabilities. Selectivity indices towards mosquito prey surpassed 0.5
157 at proportional availabilities exceeding 0.5 for both predator sexes, indicating selective
158 preference towards mosquito prey at these densities (Fig. 2). The prey proportion term alone
159 was retained in the top model, with preference indices increasing significantly where
160 mosquitoes were available in higher proportions ($\chi^2 = 21.66$, $df = 4$, $p < 0.001$).

161 The temporary pond specialist copepod *L. raynerae* exhibited a lack of prey switching from,
162 and strong preference for, *C. pipiens* mosquito prey when alternative *D. pulex* prey were
163 available. Also, as larval mosquito prey proportions increased, positive selectivity for this
164 prey type intensified, while there was very little low density refuge for the mosquito.
165 Importantly, these prey selectivity patterns were largely consistent across predator sexes, with

166 sex ratios previously shown to differ temporally and alter interaction strengths in temporary
167 ponds (Wasserman et al. 2018; Cuthbert et al. 2019). Given the documented development of
168 sex-skewed demographics in favour of female copepods in these systems (Wasserman et al.
169 2018), similarities in prey preferences may facilitate sustained top-down pressure on larval
170 mosquitoes irrespective of sex demographics over the hydroperiod. Indeed, predatory
171 paradiaptomid copepods have been recently identified as important natural enemies for
172 mosquitoes which vector pathogens and parasites (Cuthbert et al. 2018b). Whilst their
173 interaction strengths have been examined under various context-dependencies (e.g. Cuthbert
174 et al. 2019), there has hitherto been a lack of examination of prey switching and preferences
175 in temporary pond biota. Patterns of prey selectivity in favour of larval mosquitoes may
176 enhance the regulation of disease vector species which exploit these ephemeral ecosystems,
177 whilst potentially alleviating predation pressure on specialist zooplankters, such as daphniids.

178 Although larval mosquito and daphniid prey represent important dietary components of *L.*
179 *raynerae* (Wasserman et al. 2016; Cuthbert et al. 2019), the presence of other prey types in
180 these systems may further alter prey selection propensities. However, pairwise prey
181 preference examinations between common prey offers novel comparative insights into
182 predator-prey dynamics in these atypical ecosystems, where trophic structuring is relatively
183 simplified during the early stages of the hydroperiod. Nevertheless, owing to the importance
184 of prey switching for population-level stability (Murdoch 1969), even small low-density
185 refuge effects for larval mosquito prey may allow for development to the adult stage in
186 instances where larvae are rare. Such density-dependent variation in selectivity could be
187 driven by changes in search image or feeding behaviour as a given prey type becomes more
188 abundant (Begon et al. 2006), or through physical or behavioural differences among prey.

189 Whilst this study presents the first quantification of prey switching patterns and prey
190 preferences in arid temporary pond specialists, further investigation is required to elucidate

191 the potential context-dependencies of switching behaviours, and lack thereof, within these
192 highly dynamic temporary pond ecosystems.

193

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202 The authors declare that they have no conflicts of interest.

203

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277 Fig. 1. Proportion of mosquito and daphniid prey in diet of adult (a) male and (b) female
278 *Lovenula raynerae* across different proportional prey availabilities. Means are ± 1 SE. The
279 solid line indicates the expected values under neutral selectivity. The dashed line represents a
280 hypothetical switching pattern. Note that the x -axis corresponds to proportional availability of
281 both prey types for comparative purposes.

282

283 Fig. 2. Manly's selectivity indices towards larval mosquito prey by male and female
284 *Lovenula raynerae* across different proportional availabilities. Means are $+ 1$ SE. The dashed
285 line indicated expected values under neutral selectivity.