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Sex-skewed trophic impacts in ephemeral wetlands

Biotic interactions in temporary ponds

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21 **Keywords**

22 predator-prey; functional response; zooplankton; population impact; *Lovenula raynerae*

23 **Abstract**

24 1. Predation can have marked impacts on ecosystem structure, function and stability. However,
25 quantifications of biotic interactions frequently overlook demographic variabilities within
26 populations which can modulate interaction strengths, such as sex and reproductive status.
27 Compositional population ratios between males and females, alongside reproductive status, are
28 highly variable temporally in ephemeral aquatic systems, and may profoundly mediate levels of
29 ecological impact and thus stability of trophic groups.

30 2. In the present study, we apply functional responses (resource intake as a function of resource
31 density) to quantify predatory impacts of adult males, non-gravid females and gravid females of
32 the calanoid copepod *Lovenula raynerae* (Diaptomidae), an abundant ephemeral pond specialist,
33 on larvae of the *Culex pipiens* (Culicidae) mosquito complex. We then develop a novel metric to
34 forecast population-level impacts across different population sex ratio scenarios.

35 3. *Lovenula raynerae* demonstrated prey population destabilising Type II functional responses
36 irrespective of sex and reproductive status, yet variable functional response magnitudes were
37 found. While male and non-gravid female copepods exhibited similar functional response
38 maximum feeding rates, gravid female feeding rates were substantially higher, implying higher
39 resource demands for progeny development. Ecological impacts of *L. raynerae* on lower trophic
40 groups increased markedly where their abundances increased but, crucially, also as population
41 sex ratios became more biased towards gravid female copepods.

42 4. We demonstrate that population-level impacts do not only correlate tightly with abundance,
43 but may be further modulated by reproductive status variations. Thus, the development of sex-
44 skewed ratios in favour of gravid females during the hydroperiod likely heightens ecological
45 impacts on lower trophic groups. The implications of these results for prey population stability
46 are discussed in the context of freshwater ecosystems.

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61 **1. Introduction**

62 Predation profoundly affects prey population stability and the overall structuring and functioning
63 of communities at the ecosystem level (Brooks & Dodson, 1965; Carpenter et al., 1975;
64 Wasserman et al., 2013). In particular, invertebrate population dynamics in aquatic systems are
65 heavily influenced by predation (Brooks & Dodson, 1965; Sih et al., 1985; Brendonck et al.,
66 2002; Wasserman et al., 2013), with population demographics in freshwaters highly changeable
67 due to a plethora of biotic and abiotic variables (e.g. Wasserman et al., 2018). Temporal
68 differences in population demographics of resident predators can, in turn, affect interaction
69 strengths towards basal prey (e.g. Alexander et al., 2013), and the nature of these interactions can
70 influence population persistence of many trophic groups (Murdoch, 1969; Dick et al., 2014,
71 2017). Classical models concerning predator-prey interactions have, however, often assumed
72 equivalence between individual predators irrespective of intraspecific life history variabilities
73 (Volterra, 1928; Lotka, 1956; Rosenzweig & MacArthur, 1963). Consequently, effects related to
74 sex ratios or ontogeny have largely been overlooked, undermining our capacity to reliably
75 predict the total impacts of predators on prey groups within ecosystems.

76 Ephemeral wetlands are idealised model systems for testing ecological theories that are broadly
77 applicable to ecology, evolutionary biology and conservation biology, particularly given their
78 small size, relatively simple trophic structuring and clear physical boundaries (De Meester et al.,
79 2005; Dalu et al., 2017b). Further, in contrast to permanent freshwaters, their characteristically
80 short wet phases enable observations of ecological processes over the entire duration of the
81 hydroperiod (Dalu et al. 2017b; Wasserman et al., 2018). As they are internally drained, wet
82 phases in ephemeral systems rely entirely on periodic rainfall. Crustacean groups such as
83 copepods are often numerically abundant in the early-middle stages of hydroperiod as they hatch

84 from dormant eggs *in situ*, and have been reported to occupy the top trophic level in these simple
85 ecosystems for parts of the hydroperiod (Dalu et al., 2017b, c). Indeed, mass-hatching of
86 predatory zooplankton can occur as a once-off event, and may elicit enormous predation pressure
87 on lower trophic groups over short timescales (Brendonck & De Meester, 2003).

88 Sex ratios within ephemeral aquatic systems can be highly varied through the hydroperiod, and
89 sex-skewed ratios in favour of female copepods may manifest over time due to selective
90 processes such as predation (see male predation hypothesis: Kiørboe, 2006; Gusmão et al., 2013;
91 Wasserman et al., 2018). However, ephemeral aquatic systems remain poorly understood as a
92 result of their spatial and temporal heterogeneity, with interaction strengths between trophic
93 groups very poorly quantified (though see Wasserman et al., 2016a, 2018; Cuthbert et al. 2018a).
94 Indeed, in many arid locations, ephemeral wetlands are not even mapped, let alone studied (see
95 Dalu et al. 2017a). This is despite the fact that these systems often act as hotspots for threatened
96 and endemic species that are unable to persist in more permanent waters due to greater predation
97 pressures (De Meester et al., 2005). Ephemeral ecosystems also often lack intensive higher-order
98 vertebrate predation (Kerfoot & Lynch, 1987; Brendonck et al., 2002) and, moreover, exhibit
99 rapid ecological succession through the restricted wet phases. As environmental change
100 implications for biotic interactions are the most challenging to predict with certainty, quantifying
101 interaction strengths between species is crucial to understanding ecosystem stability (Daufresne
102 et al., 2009; Gilbert et al., 2014), and this is particularly important in ephemeral wetlands where
103 there is a high degree of specialist adaptation and endemism (De Meester et al., 2005; Dalu et al.
104 2017a).

105 Functional responses have been a staple method in elucidating consumer-resource interactions,
106 and have been frequently used to examine biotic context-dependencies of interaction strengths

107 within ecosystems (e.g. Alexander et al., 2013; Barrios-O'Neill et al., 2014; Wasserman et al.,
108 2016b). In a predation context, functional responses depict the predation rate as a function of
109 prey density. Three common functional response forms have been described (Holling, 1959): (1)
110 Type I, specific to filter-feeders (Jeschke et al., 2004), wherein the consumption rate increases
111 linearly with the quantity of resources supplied up to a sharply defined maximum (Holling, 1959;
112 Hassell, 1978); (2) Type II, where the consumption rate falls asymptotically with prey density;
113 (3) Type III, characterised by a sigmoidal form wherein the predation rate increases at low prey
114 densities, before once again falling asymptotically (Holling, 1959; Hassell, 1978). Both the form
115 and magnitude of the functional response can be used to quantify *per capita* ecological impacts
116 of consumers in ecosystems (Dick et al., 2014), and, in turn, predict ecosystem-level stability
117 outcomes arising from predator-prey interactions (e.g. Rosenzweig & MacArthur, 1963). In this
118 respect, Type II forms have been frequently characterised as destabilising due to high levels of
119 resource consumption at low resource (e.g. prey) densities, whereas Type III forms may facilitate
120 stability within communities due to refuge provisioning at low prey densities (e.g. Murdoch,
121 1969; Dick et al., 2014).

122 The present study thus aimed to quantify interaction strengths within ephemeral wetlands across
123 variable population sex ratios. Although functional responses have shown to be robust in
124 quantifications of *per capita* biotic interaction strengths between consumers and resources,
125 assimilations of population-level effects are often lacking, reducing our capacity to project
126 interaction strengths holistically between trophic groups (though see Dick et al., 2017; Cuthbert
127 et al., 2018b, c). Furthermore, methodological advances which address consumer impact
128 implications resulting from changing population demographics temporally have yet to be
129 developed fully. Here, we examine the effects of emergent and field-validated sex-skewed

130 populations on predatory impacts within ephemeral aquatic systems at the *per capita* and then
131 population-level. First, we use comparative functional responses to quantify the ecological
132 impacts of adult males, non-gravid females and gravid females of the calanoid copepod *Lovenula*
133 *raynerae*, a top predator in ephemeral wetlands, towards larval prey of the vectorially-important
134 *Culex pipiens* mosquito complex. Such large copepod species have been previously
135 demonstrated to be voracious consumers of mosquito larvae which colonise ephemeral
136 ecosystems (e.g. Cuthbert et al., 2018a). We then quantify and illustrate population-level trophic
137 impacts of *L. raynerae* using scenarios of sex ratio dynamics within ephemeral aquatic
138 ecosystems. Therein, we develop novel metrics to elucidate how changing population
139 demographics and abundances may drive trophic impacts in such ecosystems.

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141 **2. Methods**

142 *2.1. Animal collection and maintenance*

143 During the 2017–2018 austral summer, adult *L. raynerae* (Suárez-Morales et al., 2015) were
144 collected from an ephemeral pond in the Eastern Cape province of South Africa (33° 16' 47.8" S,
145 26° 35' 39.8" E) by towing a zooplankton net through the upper water column, and were then
146 transported in source water to a controlled environment (CE) room at Rhodes University,
147 Grahamstown, Eastern Cape. Adult males, non-gravid females and gravid females (males, 4.71
148 mm ± 0.11 mm; females, 4.77 mm ± 0.14 mm; gravid females, 4.88 mm ± 0.08 mm) were
149 maintained in the CE room at 25 ± 1 °C in 25 L aquaria and fed *ad libitum* with larval mosquito
150 prey. The focal prey, *C. pipiens* larvae (3.14 mm ± 0.19 mm) were cultured using egg rafts
151 collected from artificial containers on the Rhodes University campus, and reared to the desired

152 size class in the laboratory using a diet of crushed rabbit pellets (Agricol, Port Elizabeth),
153 supplied *ad libitum*. Mosquitoes were identified in accordance with Jupp (1996).
154 Experimentation and acclimation were undertaken under a 12:12 light:dark laboratory
155 photoperiod.

156 2.2. *Functional responses*

157 To derive the effects of sex and reproductive status variations on the *per capita* predatory impact
158 of focal copepods, we employed a 3×6 experimental design with respect to copepod group (3
159 levels) and prey density (6 levels). Adult males, non-gravid females and gravid females of *L.*
160 *raynerae* were provided larvae of *C. pipiens* at six prey densities (2, 4, 8, 16, 32, 64; $n = 4$ per
161 experimental group) in 80 mL arenas of 5.6 cm diameter containing dechlorinated tapwater from
162 a continuously aerated source. Prey were allowed to settle for 2 h prior to the addition of
163 predators, which subsequently fed undisturbed for 5 h. Following the experimental period,
164 predators were removed and remaining live prey counted. Predators were starved for 48 h before
165 use to standardise levels of hunger. Controls consisted of three replicates at each prey density
166 without the addition of predators.

167 2.3. *Statistical analyses and impact projections*

168 All statistical analyses were undertaken in R v3.4.4 (R Core Team, 2018). Generalised linear
169 models (GLMs) assuming a Poisson error distribution were used to analyse overall prey
170 consumption with respect to the ‘copepod group’ and ‘prey density’ factors, and their interaction.
171 Residual deviance did not exceed degrees of freedom and so thus counts were not deemed to be
172 overdispersed here. Non-significant terms were removed stepwise from the model to obtain the

173 most parsimonious fit, with χ^2 used for model simplification *via* analysis of deviance parameter
 174 selection (Crawley, 2007).

175 Several approaches have been developed for the analysis of functional responses, with model
 176 selection dependent on whether a particular study design is phenomenological or mechanistic in
 177 its aims (Jeschke et al., 2002). As mechanistic applications of attack rate and handling time
 178 parameters are reliant on empirical validations of parameter estimates, however, here we employ
 179 a phenomenological approach to examine comparatively the functional response types and
 180 parameter estimates in a factorial design (see also Alexander et al. 2012; Dick et al. 2014).
 181 Functional response analyses were thus undertaken using the ‘frair’ package in R (Pritchard et
 182 al., 2017). Logistic regression of the proportion of prey consumed as a function of prey density
 183 was used to infer functional response types. A Type II functional response is characterised by a
 184 significantly negative first order term, whilst a Type III functional response is characterised by a
 185 significantly positive first order term followed by a significantly negative second order term
 186 (Solomon, 1949; Holling, 1959). As prey were not replaced as they were consumed, we fit
 187 Rogers’ random predator equation which accounts for depleting prey densities over the
 188 experimental period (Trexler et al., 1998; Juliano, 2001):

$$189 \quad N_e = N_0(1 - \exp(a(N_e h - T)))$$

190 Eqn. 1.

191 where N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack constant, h
 192 is the handling time and T is the total experimental period. The *Lambert W* function was used to
 193 make the random predator equation solvable (Bolker, 2008). Initial functional response fits were
 194 non-parametrically bootstrapped 2000 times to generate bias-corrected and accelerated 95%

195 confidence intervals, enabling the functional responses to be considered in population terms
 196 across prey densities (e.g. Barrios-O'Neill et al., 2014).

197 We then used handling time (h) estimates from Eqn. 1 to quantify maximum feeding rates over
 198 the experimental period ($1/h$) for each copepod group, before calculating ecological impacts of *L.*
 199 *raynerae* across varied intraspecific sex ratios, where impact with gravid females g is derived as:

$$200 \quad g = ((1/h_m) \times p_m) + ((1/h_f) \times p_f)$$

201 Eqn. 2.

202 where $1/h$ is the maximum feeding rate of males (m) or gravid females (f), and p is the proportion
 203 of males or gravid females within a given population. As handling times and, inversely,
 204 maximum feeding rates of males and non-gravid females were highly similar, we used the mean
 205 initial estimate of maximum feeding rate ($1/h$) between these groups to derive a baseline null
 206 impact level using Eqn. 2, unchanged across sex ratio variabilities. We thus created an impact
 207 index aligned with gravid female copepods by dividing their proportioned impact score against
 208 this null baseline, where impact index I is:

$$209 \quad I = (g/b)$$

210 Eqn. 3.

211 resulting from the division of the proportioned impact with gravid females g by the baseline
 212 impact between non-gravid and male copepods b . Then, using proportional abundance
 213 estimations as a multiplier, Eqn. 3 can be modified to project population-level impacts, where PI
 214 is:

$$215 \quad PI = I \times p_{ab}$$

216 Eqn. 4.

217 where p_{ab} is the proportion of maximum population abundance at a given time. We then used
218 biplots to display PI graphically for different sex ratio scenarios, given varied copepod
219 population compositions.

220 3. Results

221 No prey mortality was observed in control treatments and thus all experimental deaths were
222 attributed to predation. This was further evidenced visually and by partially consumed remains of
223 culicid prey. Type II functional responses were observed for each predator treatment as evident
224 from significantly negative first order terms (Table 1; Figure 1). Overall consumption was
225 significantly affected by the sex and reproductive status of copepods ($\chi^2 = 7.55$, $df = 2$, $p = 0.02$),
226 driven by greater predation levels by gravid females compared to males and non-gravid females.
227 Overall consumption also increased significantly as prey densities increased ($\chi^2 = 136.55$, $df = 5$,
228 $p < 0.001$), and this effect was consistent across different copepod groups as there was no
229 significant ‘sex \times prey density’ interaction effect ($\chi^2 = 2.12$, $df = 10$, $p = 0.99$). Gravid females
230 displayed a substantially higher functional response magnitude, with considerably lower
231 handling times corroborating with greater maximum feeding rates than males or non-gravid
232 females (Table 1; Figure 1). Conversely, functional response magnitudes of male and non-gravid
233 female *L. raynerae* were highly similar (Figure 1).

234 Impact index values increased substantially where intraspecific proportions became sex-skewed
235 in favour of gravid females, driven by the marked maximum feeding rates of gravid female *L.*
236 *raynerae* relative to males and non-gravid females (Table 2). Generally, population-level impacts
237 increased as copepods approached maximal abundances and with skewed populations in favour

238 of gravid females (Figure 2). Where sex ratios were relatively stable, population impacts
239 increased concurrently only with abundance (Figure 2a). However, where populations became
240 increasingly sex-skewed towards gravid females under higher abundances, population-level
241 impacts at maximal abundances were greater than under the stable sex ratio scenario (Figure 2b),
242 and, inversely, where proportions of gravid females decreased with increasing overall abundance
243 (Figure 2c).

244 **4. Discussion**

245 Demographics within species populations can be highly variable across spatiotemporal gradients,
246 and such variations can have significant implications for biotic interactions within ecosystems,
247 such as predation (Alexander et al. 2013; Wasserman et al., 2018). Given the important role of
248 predation in the structuring and functioning of aquatic ecosystems (Brooks & Dodson, 1965;
249 Carpenter et al., 1975; Wasserman et al., 2013), understanding the implications of demographics,
250 such as sex ratio variabilities, is critical for robust interaction strength quantifications between
251 trophic groups. Further, the development of measures to predict ecological impacts is crucial.
252 The present study demonstrates biotic context-dependencies in interaction strengths between the
253 freshwater calanoid copepod *L. raynerae* and basal culicid prey, wherein maximum feeding rates
254 were similar between male and non-gravid female copepods, but were elevated in gravid female
255 copepods. Thus, the effects of sex demographics on ecological impacts are in turn dependent on
256 reproductive status. Further, given their highly dynamic communities (Wasserman et al., 2018),
257 we demonstrate that trophic impacts may exhibit marked variations over the course of the
258 hydroperiod in ephemeral freshwater ecosystems, with these impacts in turn dependent on the
259 structuring of sex ratios relative to abundances within populations. Our results demonstrate how
260 quantifications of demographic variations in consumptive traits can be used to help predict

261 ecological impacts, with our approach equally applicable to consumer-resource interactions in
262 other ecosystems.

263 Functional responses have been widely applied to quantify the impacts of predators on prey
264 populations (see for example Dick et al., 2014; Cuthbert et al., 2018b). However, studies often
265 standardise predator characteristics, such as sex or size (e.g. Lavery et al., 2015; Wasserman et
266 al. 2016a; South et al., 2017). Whilst this is important with respect to trophically-analogous
267 species comparisons, this approach may reduce our capacity to derive holistic accounts of
268 ecological impact for species with complicated population demographics. In our model system,
269 we show that *L. raynerae* exhibits a Type II functional response irrespective of sex or
270 reproductive status. This functional response form is associated with destabilising pressures
271 towards prey populations (see Dick et al., 2014) and thus may drive localised extinctions of prey.
272 Indeed, *L. raynerae* adult males have previously been shown to exert a similar functional
273 response towards daphniid prey (Wasserman et al., 2016a). This contrasts with other calanoid
274 species which demonstrate a sigmoidal functional response, conducive to greater potential for
275 prey population stability due to low density prey refugia (Wasserman et al., 2016a). Moreover, *L.*
276 *raynerae* has been shown to be a top predator and a particularly strong competitor with other
277 copepods in ephemeral ponds, with greater prey capture efficiencies and shorter handling times
278 (Wasserman et al., 2016a; Dalu et al., 2017c). Thus, the predatory impact of *L. raynerae* may be
279 particularly high towards low density basal prey populations irrespective of sex demographics.
280 The feeding niche of *L. raynerae* has also been shown to be relatively small, and fluctuates with
281 relative resource availabilities, with zooplankton forming a large dietary component (Dalu et al.,
282 2016). For this species, consumptive traits have additionally been shown to be similar between
283 sexes (Dalu et al., 2017c), particularly during the early pond stage when mosquitoes are most

284 abundant. It is therefore likely that such predatory traits drive substantial impacts upon lower
285 trophic groups in these systems, especially given the recurrent destabilising Type II functional
286 responses of *L. raynerae* (Wasserman et al., 2016a; Cuthbert et al., 2018a). However,
287 quantifications of variations in biotic interaction strengths driven by processes such as prey
288 preferences and switching across predator demographic variabilities could further enhance
289 predictive efforts surrounding interaction strengths and cascade effects to prey through
290 ecosystems (e.g. Murdoch, 1969; Cuthbert et al., 2018d).

291 Although the functional response form of *L. raynerae* was similar through their sex and
292 reproductive demography, there were substantial variations in functional response magnitude.
293 Handling times were lowest for gravid female copepods, resulting in the highest maximum
294 feeding rates across copepod groups. In turn, there were no significant differences between males
295 and non-gravid females, indicating that a greater nutritional uptake is driven in line with
296 reproductive status in copepods. The elevated feeding rates of gravid females shown here likely
297 translates into greater *per capita* pressures on basal prey when this group is abundant. Globally,
298 copepods are a highly diverse and widespread group, forming substantial components of aquatic
299 ecosystems (Dussart & Defaye, 2001). Given sexual dimorphism is prevalent in many copepod
300 species, with females often more voracious due to heightened energy demands associated with
301 size and reproduction, it is likely our results would be paralleled in other ecosystems (e.g.
302 Laybourn-Parry et al., 1988; Marten and Reid, 2007). The application of functional responses
303 holds great potential in the quantification of demographic implications for consumer-resource
304 interactions across ecosystems. Standardised laboratory experiments may yield high explanatory
305 power in comparing interactions, both between and within species, and have been shown to

306 correlate tightly with known ecological impacts in the field and with independent impact
307 measures (Dick et al., 2014; 2017).

308 Sex ratios can be particularly dynamic through time due to selective processes such as predation,
309 and have been shown to change markedly over the hydroperiod in ephemeral aquatic ecosystems
310 (e.g. Wasserman et al., 2018). In turn, interaction strengths between trophic groups also vary
311 substantially over the course of the hydroperiod (Schneider & Frost, 1996; O' Neill & Thorp,
312 2014), with predation pressures characteristically dominated by invertebrates in these systems.
313 Although recent advances have sought to integrate population-level impacts with *per capita*
314 effects in order to derive comprehensive ecological impact predictions in the context of invasive
315 species (Dick et al., 2017) and biological control (Cuthbert et al., 2018b), there has been little
316 consideration hitherto for population demographic variabilities which may further modulate
317 impact. Such quantifications could provide improved insights into population-level consumer-
318 resource interactions across ecosystems. In our study system, we demonstrate that the integration
319 of sex ratios, and particularly reproductive status, may further enhance predictions for
320 population-level impacts on lower trophic groups in ephemeral ponds and other ecosystems.
321 Thus, here, as female *L. raynerae* have been shown to dominate zooplankton assemblages in the
322 middle and late hydroperiod within ephemeral aquatic ecosystems (Wasserman et al., 2018),
323 ecological impacts during this period are likely elevated if large proportions of copepods are
324 gravid and present in high abundances. We postulate that this may indeed be the case, given the
325 necessity of dormant egg production towards the end of the hydroperiod, coupled with frequent
326 mass-hatching events (Brendonck & De Meester, 2003). Indeed, the high consumption rates
327 demonstrated in the present study may promote high fitness and gravidity within populations
328 while prey are abundant, thus further exacerbating ecological impacts through feedbacks. Given

329 that ephemeral aquatic ecosystems remain poorly studied despite their ecological significance
330 (Dalu et al., 2017a), our displayed derivations of population-level impacts are based on
331 hypothetical sex ratio scenarios across the course of the hydroperiod. However, extreme sex ratio
332 variations have indeed been demonstrated in these systems through field observations (see
333 Wasserman et al., 2018).

334 In conclusion, the results of the present study show that sex-skewed population demographics
335 can profoundly influence predation rates, which ultimately may drive fluctuations in population-
336 level ecological impacts temporally. We present a novel approach which could improve the
337 forecasting of ecological impacts in ecosystems through the integration of *per capita*, abundance
338 and compositional effects within populations. Here, although female copepods are more
339 voracious, this effect is dependent on their state of gravidity, with only gravid and ovigerous
340 females exhibiting significantly higher feeding rates than males. Accordingly, we expect impacts
341 on lower trophic groups to be greatest where gravid females disproportionately dominate
342 zooplankton populations across the hydroperiod. To this end, further research should seek to
343 elucidate the effects of multiple con/interspecific predators on predatory impact in these atypical
344 aquatic systems, in order to ascertain the direct effects of multiple predators on consumption
345 rates, alongside variations in ecological impacts across life history stages. Further examinations
346 of temporal demographics across a multitude of ecosystems would be highly informative in
347 identifying large-scale implications of sex ratio variations for interaction strengths.

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356 **Conflicts of interest**

357 The authors declare no conflicts of interest.

358 **Data accessibility**

359 Underlying functional response data are available in the online supplementary information.

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504 Table 1. First order terms and significance levels resulting from logistic regression of the
 505 proportion of prey killed as a function of prey density, and rounded functional response
 506 parameter estimates across differing predator treatments resulting from Rogers' random predator
 507 equation.

Predator	First order term, p	Attack rate (a), p	Handling time (h), p	Maximum feeding rate ($1/h$)
Male	-0.02, < 0.01	0.42, < 0.001	0.10, < 0.001	9.96
Female	-0.02, < 0.001	0.73, < 0.001	0.11, < 0.001	9.44
Gravid female	-0.02, < 0.001	0.60, < 0.001	0.06, < 0.001	16.37

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518 Table 2. Impact index scores for *Lovenula raynerae* across different sex ratios, where
 519 proportioned impacts with gravid females are indexed relative to a null baseline comprised of
 520 non-gravid females and males (see Eqns. 2, 3).

Proportion male and non-gravid female	Proportion gravid female	Non-gravid female (null) baseline impact (<i>b</i>)	Gravid female impact (<i>g</i>)	Impact index (<i>g/b</i>)
0.9	0.1	9.70	10.37	1.07
0.8	0.2	9.70	11.03	1.14
0.7	0.3	9.70	11.70	1.21
0.6	0.4	9.70	12.37	1.28
0.5	0.5	9.70	13.03	1.34
0.4	0.6	9.70	13.70	1.41
0.3	0.7	9.70	14.37	1.48
0.2	0.8	9.70	15.04	1.55
0.1	0.9	9.70	15.70	1.62

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527 Figure 1. Functional responses of adult male, non-gravid female and gravid female *Lovenula*
528 *raynerae* towards common culicid prey. Shaded areas represent bootstrapped ($n = 2000$)
529 confidence intervals and points are raw data ($n = 4$ per experimental group).

530 Figure 2. Scenarios of differential impacts of *Lovenula raynerae* (Eqns. 3, 4), using functional
531 response results, associated with changing hypothetical sex ratios and proportion (prop.) of
532 maximal abundances, where: a) sex ratios remain balanced; b) sex ratios become increasingly
533 skewed towards gravid females; and c) sex ratios become increasingly skewed towards male or
534 non-gravid females. Population-level impacts are read diagonally, from bottom-left to top-right.